A preliminary synthesis of pollination biology in the Cape flora

A G Rebelo (editor)

SOUTH AFRICAN NATIONAL SCIENTIFIC PROGRAMMES REPORT NO

141

1987

A preliminary synthesis of pollination biology in the Cape flora

A G Rebelo (editor)

A report of the Committee for Terrestrial Ecosystems
National Programme for Ecosystem Research

SOUTH AFRICAN NATIONAL SCIENTIFIC PROGRAMMES REPORT NO

141

1987

Issued by
Foundation for Research Development
Council for Scientific and Industrial Research
P O Box 395
PRETORIA
0001
South Africa

from whom copies of reports in this series are available on request

Printed in 1987 in the Republic of South Africa

ISBN 0 7988 4115 X

Editor's address:

A G Rebelo
Percy FitzPatrick Institute of
 African Ornithology
University of Cape Town
Private Bag
RONDEBOSCH
7700

GAcsir 24H4803*8712

PREFACE

I am pleased to have the opportunity to make a few prefatory comments on this volume. Nearly a decade has passed since John Rourke of the Compton Herbarium, Kirstenbosch, and I initiated our studies of rodent pollination in certain groups of proteas in the Cape flora, or fynbos as it is known locally. It is gratifying to see at this time an entire volume devoted to the problem of pollination in this most fascinating of world ecosystems. Compendia are generally written for one of two reasons. Either they summarize knowledge in a rapidly expanding field, or as in this case, they attempt to identify the more exciting problems in a particular field, review what information is available, and possibly speculate about questions of special interest. This volume attempts all of these things to various degrees.

The fynbos biome is remarkable. Among all of its fascinating aspects, eg the virtual absence of indigenous trees, the paucity of annuals, adaptation to periodic burning, and its relatively narrow geographical restriction to the nutritionally depauperate Table Mountain Sandstone, none is more intriguing than the exceptionally rich species diversity (8 504 species) and high endemism (68%). The species diversity approaches that of tropical rainforests, but the percentage of endemism must be among the highest known. How these characteristics are reflected in pollination systems is a fascinating question in as much as at least some of the insect groups (eg bees), birds and mammals do not exhibit comparably high species diversity, or endemism in the fynbos per se.

Perhaps no field in biology provides the same opportunity as pollination biology for the study of such intimate mutualistic and coevolutionary interrelationships between organisms. Furthermore, the magnitude of these interrelationships are equally astounding when we consider that they involve the flowers of hundreds of thousands of plant species and probably an even greater number of animals, mostly insects. Furthermore, the flower is not fully appreciated for its unique developmental attributes. Much insight is to be gained by viewing the flower as a structure with a continuous ontogenetic life history with three distinct functions. First as an attracting agent, secondly as a nurse organ for developing ovules, and thirdly as a dispersal structure for the seeds.

To understand the role of pollination in the evolution of the fynbos is an enormous undertaking that is clearly still in its infancy, but hopefully this volume will lay the groundwork and stimulate further intensive studies along these lines. Because of the enormity of the task, and because of the general interest in the subject by the educated lay public, I believe it is appropriate to suggest an active involvement by amateur naturalists in pollination biology. South Africa has a public generally much more aware of its natural history heritage than most countries, and this interest should be fostered by the academic biological community in an effort to speed up the work. There are many problems in which observations made by the interested lay public can be of immense value if properly supervised, as for example, the splendid photographic assistance rendered by Pieter and Connie Smits in the study of rodent pollination.

The fascination of the flower-pollinator interaction by the educated public generally is evidenced by the continued appearance of delightful popular publications in this area, particularly by B J D Meeuse and his coworkers (University of Washington, Seattle).

Apart from the strictly scientific aspects, the fynbos biome, as in so many areas of the earth today, faces increasing problems of extinction due to overdevelopment resulting from excessive human population pressure. The introduction of particularly aggressive weedy species is an additional threat of greater magnitude in the fynbos biome than in many other world biomes. These problems are particularly acute in flora where many of the species are so highly localized. Hopefully this volume will stimulate efforts to learn more about the pollinatory characteristics of this outstandingly unique plant assemblage and to promote the establishment of appropriate reserves.

Delbert Wiens
Department of Biology
University of Utah
Salt Lake City, Utah
USA

ABSTRACT

This preliminary synthesis was designed to promote an understanding of pollination as a process in the Cape flora by summarizing the literature, outlining patterns and processes, and identifying gaps in knowledge. Various aspects of pollination biology are covered. Chapters reviewing plant breeding systems, insect, bird, mammal and wind pollination, and gene flow are introduced by a perspective on the role of the fossil record in pollination biology. A speculative chapter on the constraints affecting pollination syndromes is followed by the implications which pollination biology may have on management. A key worded bibliography presents the local literature. Research themes considered by the various authors as critical to our understanding of pollination biology in the Cape flora are also outlined. A short synopsis of research currently underway completes the synthesis.

SAMEVATTING

Hierdie voorlopige sintese is saamgestel om kennis van bestuiwing as 'n proses in die Kaapse flora te bevorder. Dit gee 'n opsomming van die literatuur, beskryf patrone en prosesse en wys op leemtes in kennis. Verskeie aspekte van bestuiwingsbiologie word gedek. Hoofstukke wat 'n oorsig gee oor die voortplantingsmeganismes van plante, insek-, voël-, soogdier- en windbestuiwing, en geenvloei, word ingelei deur 'n perspektief oor die rol van die fossielrekord in bestuiwingsbiologie. 'n Spekulatiewe hoofstuk oor die beperkings wat bestuiwingsindrome beïnvloed, word gevolg deur die implikasies wat bestuiwingsbiologie op bestuur mag hê. 'n Bibliografie met sleutelwoorde verteenwoordig die plaaslike literatuur. Navorsingstemas wat deur die verskeie outeurs as kritiek beskou word vir ons kennis van bestuiwingsbiologie in die Kaapse flora word ook aangegee. Die sintese word afgesluit deur 'n kort opsomming van die navorsing wat tans onderneem word.

ACKNOWLEDGEMENTS

The following are acknowledged and thanked for their roles in producing this synthesis.

D Wiens (Department of Biology, University of Utah), W R Siegfried (Percy FitzPatrick Institute for African Ornithology), T Lowrey (Department of Botany, University of the Witwatersrand) and W J Bond (Saasveld Forestry Research Centre) reviewed the entire manuscript and provided helpful criticism.

L Leach (Karoo Botanic Gardens) and P A Bean (Bolus Herbarium) provided information on the breeding systems of Euphorbia and Agathosma respectively, and in addition D Snijman (Compton Herbarium) and P Goldblatt (Missouri National Botanic Garden) commented helpfully on early drafts of the chapter on plant breeding systems. B G Collins (Western Australian Institute of Technology), J H Giliomee (Department of Entomology, University of Stellenbosch), R P Prys-Jones and W R Siegfried (Percy FitzPatrick Institute for African Ornithology, University of Cape Town), K Steiner (Compton Herbarium) and V B Whitehead (South African Museum) are thanked for their comments on the chapter on bird pollination. B G Collins (Western Australian Institute of Technology) commented usefully on the chapter on pollination by mammals. R H Anderson (Plant Protection Research Institute, Stellenbosch), P M Holmes (Department of Botany, University of Cape Town), I A W Macdonald (Percy FitzPatrick Institute for African Ornithology, University of Cape Town), W J Middelmann (13 Lady Anne Avenue, Newlands) and B W van Wilgen (Jonkershoek Forestry Research Centre) all provided useful comments on the management chapter.

M L Jarman (FRD, CSIR - Cape Town office) facilitated the initiation of the exercise, chaired review sessions and played a major role in the latter stages of review and editing of this report; T Greyling and E Mantle of FRD, CSIR - Cape Town office, respectively provided liaison services and undertook the entire typography of the original manuscript. E A Steer (Fish Hoek) did the key word indexing of the bibliography.

All chapter contributors gave freely of their time and ideas while participating in editorial review workshops during 1986 and 1987.

TABLE OF CONTENTS

Page

PREFACE (iii)

ABSTRACT (v)

SAMEVATTING (v)

ACKNOWLEDGEMENTS (vi)

INTRODUCTION - A G Rebelo 1

CHAPTER 1. Pollination biology and the fossil record - A Scholtz 6

CHAPTER 2. Breeding systems in the Cape flora - K E Steiner 22

CHAPTER 3. Insect pollination in the Cape flora - V B Whitehead, J H Giliomee and A G Rebelo 52

CHAPTER 4. Bird pollination in the Cape flora - A G Rebelo 83

CHAPTER 5. Mammal pollination in the Cape flora - A G Rebelo and G J Breytenbach 109

CHAPTER 6. Wind pollination in the Cape flora - D Koutnik 126

CHAPTER 7. Gene flow in plant populations - A V Hall 134

CHAPTER 8. Pollination and community ecology - A G Rebelo and M L Jarman 155

CHAPTER 9. Management implications - A G Rebelo 193

CHAPTER 10. Bibliography of pollination biology relating to the Cape flora 212

CONCLUSIONS 240

SUBJECT KEYWORD INDEX 241

PLANT TAXONOMICAL KEYWORD INDEX 244

APPENDIX 1: Research themes of critical importance - A G Rebelo 248

APPENDIX 2: Work currently underway in southern Africa 250

LIST OF CONTRIBUTORS 255

RECENT TITLES IN THIS SERIES 256

INTRODUCTION

A G Rebelo

The Cape Floral Kingdom is renowned for its extraordinarily high richness of plant species (8 504 species in ca 90 000 km^2 - Bond and Goldblatt 1984). Yet, very few studies have been undertaken of the breeding systems of plants or pollination processes, which might have contributed significantly to this high species richness.

The species richness of the Cape flora is probably the most commonly quoted subject in opening paragraphs in reports dealing with the fynbos biome. Equal focus could centre on the Cape floral region having:

- the area with the highest ratio of ornithophilous plant species to avian nectarivore species recorded to date (Rebelo this volume).
- the second richest assemblage of mammal pollinated plant species (Breytenbach and Rebelo this volume);
- the richest bee fauna in Africa with as many tribes, subfamilies and families as the rest of Africa (Michener 1979);
- the centre of distribution of a largely endemic, diurnal, anthophilous beetle tribe, the monkey beetles (Scarabaeidae: Rutelinae: Hopliini, ca 37 genera with over 500 species), which visit Asteraceae flowers (Scholtz and Holm 1985);
- the high incidence of geophytic lilioid taxa (15% of the flora - half of which comprise over 40% of extant Iridaceae worldwide), many of which flower in early seral assemblages (Goldblatt 1983; Bond and Goldblatt 1984);
- spring floral displays covering large areas, comprising mainly Asteraceae (Raitt 1985);
- a rich anthophilous fly fauna (Bowden 1978); and
- the low incidence of annuals (six per cent of the flora (Bond and Goldblatt 1984)).

The conservation of this rich flora and its associated fauna, is becoming more urgent, since developing land uses are rapidly reducing the extent of natural communities. Coupled with this reduction in area (only 31% of lowland areas remain natural) is a high infestation rate by invasive woody plant species (which occur in 24% of the remaining natural vegetation) (Jarman 1986). Conservation of the flora requires that essential processes, such as pollination and seed dispersal, continue undisturbed in nature reserves. However, we know little about such ecological processes in the Cape flora.

The Fynbos Biome Project was initiated by the National Programme for Ecosystem Research (NPER) (administered by the Council for Scientific and Industrial Research (CSIR)) in 1979 in an effort to coordinate and stimulate research, and to synthesize available scientific information within the region. In 1985 the Steering Committee of the Fynbos Biome Project commissioned the Pollination Biology Working Group to compile and edit a preliminary synthesis of all available information on pollination biology in the Cape flora.

This report is the preliminary synthesis of what little research has been undertaken on various aspects of pollination biology in the Cape flora. Also included are accounts of breeding systems and pollination biology, interpreted from the local flora in the light of published literature, and some speculation and conjecture, based mainly on unpublished ideas.

The aims of this preliminary synthesis are four-fold:

- to summarize the meagre local information, including all published and unpublished data, speculation and concepts;
- to provide a preliminary exposition of pollination patterns and processes which may operate in the Cape flora, in the light of knowledge reported in the international literature;
- to identify the principal gaps in knowledge, and provide a prescription for research;
- to create an interest and awareness of pollination biology in the Cape flora.

THE AREA CONSIDERED

The Cape Floral Region has in recent years become synonymous with the fynbos biome. Such a treatment hides the relative importance of the other vegetation types in contributing to the high species richness of the flora. The north-western Karoo, especially, resembles fynbos in its high species richness and endemism, while renosterveld has a high number of endemic geophytes. In this synthesis the term Cape flora is used to denote the flora in that area of southern Africa in which 40% or more of the annual rainfall falls in winter (Figure 1). This includes the following vegetation types (Figure 2):

- the Cape Floral Kingdom comprising fynbos, renosterveld and strandveld (sensu Moll et al 1984) which comprise the 'Cape regional centre of endemism' (sensu White 1983);
- and the bushy karoo shrubland, succulent karoo shrubland and montane grassy karoo shrubland of the 'Karoo-Namib Regional centre of endemism' (sensu White 1983).

Some other peripheral vegetation assemblages are also included, namely:

- Kaffrarian Thicket and Afromontane Forest.

Only a small portion of this area is strictly mediterranean in climate, while about half the area receives 60% of its rainfall in winter (Figure 1). However, the only published catalogue of plant species for the area is that of Bond and Goldblatt (1984) for the Cape Floral Region, which includes only a portion of the Cape flora (Figure 1). For all species comparisons in this synthesis, Bond and Goldblatt (1984) was used as the data source.

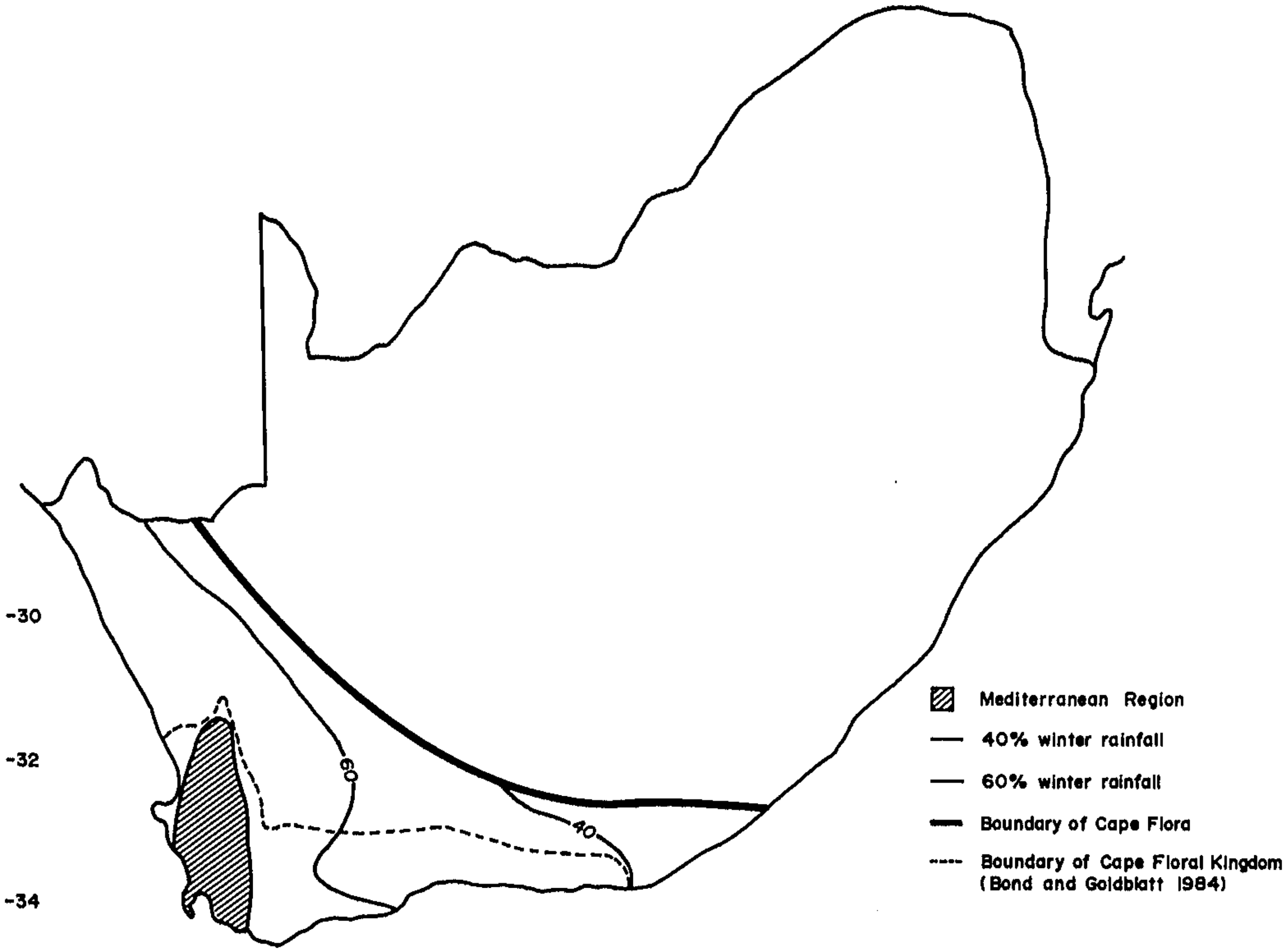


FIGURE 1. The boundary of the Cape limits of the flora, as delimited in this synthesis. A catalogue of plant species is only available for the Cape Floral Region (sensu Bond and Goldblatt 1984). Also shown are the 40% and 60% winter rainfall boundaries.

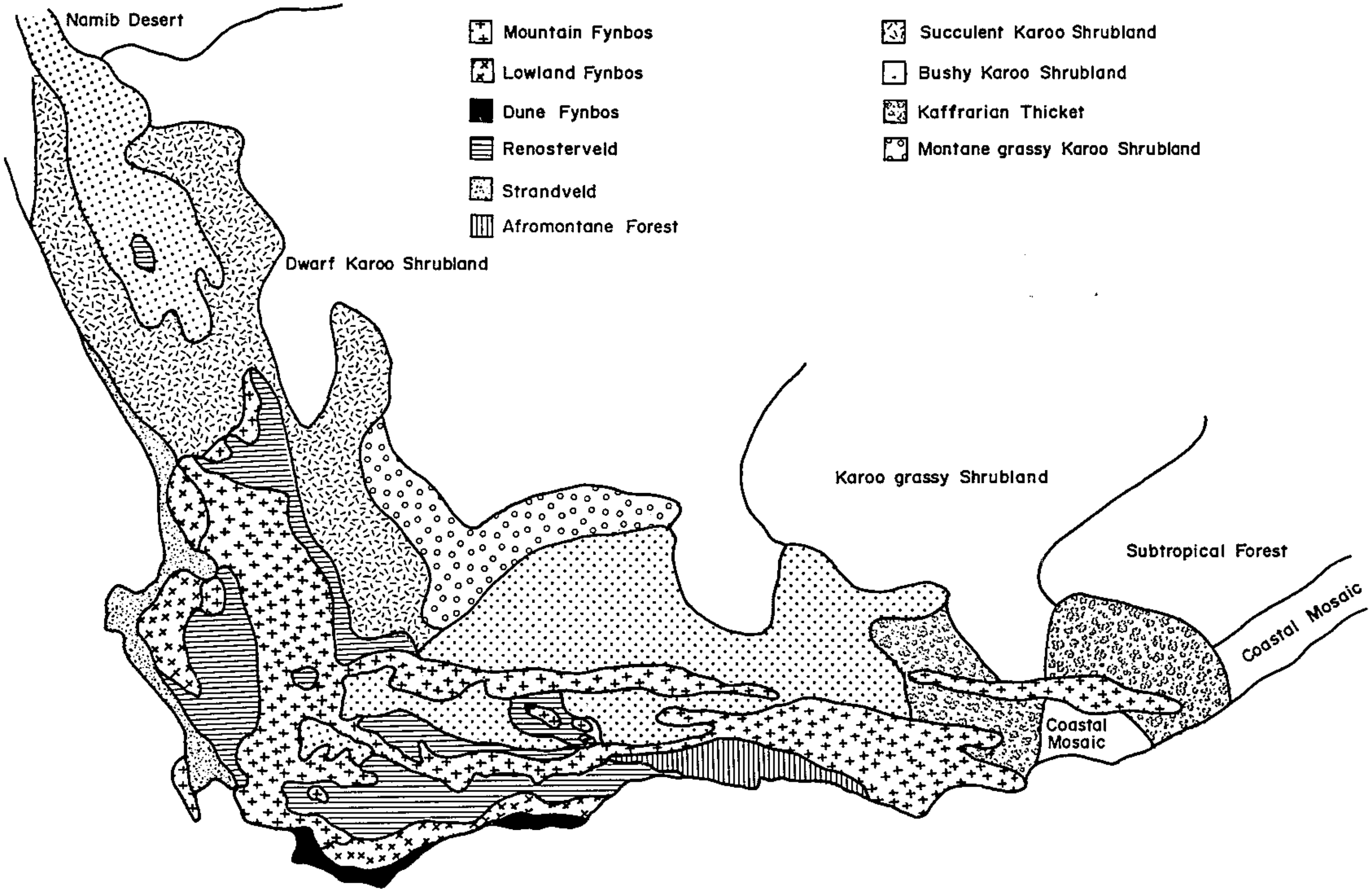


FIGURE 2. The major vegetation units comprising the Cape flora, as defined in this synthesis. The Cape Floral Kingdom (Cape Regional Centre of Endemism) comprises fynbos, renosterveld, strandveld, Afromontane forest and Kaffrarian thicket. Elements of the Karoo Regional Centre of Endemism included in the Cape flora are also shown.

REFERENCES

Bond P and Goldblatt P 1984. Plants of the Cape flora: a descriptive catalogue. Journal of South African Botany, Supplementary Volume 13.

Bowden R N 1978. Diptera. In: Werger M J A (editor) Biogeography and ecology of southern Africa. W Junk, The Hague.

Goldblatt P 1983. Geography of Iridaceae in Africa. Bothalia 14, 559-564.

Jarman M L (editor) 1986. Conservation priorities in lowland regions of the fynbos biome. South African National Scientific Programmes Report 87, CSIR, Pretoria. 55 pp.

Michener C D 1979. Biogeography of the bees. Annals of the Missouri Botanic Gardens 66, 277-347.

Moll E J, Campbell B M, Cowling R M, Bossi L, Jarman M L and Boucher C 1984. A description of the major vegetation categories in and adjacent to the fynbos biome. South African National Scientific Programmes Report No 83. CSIR, Pretoria. 29 pp.

Raitt L M 1985. Why are Namaqualand's flowers so attractive? African Wildlife 39, 139-143.

Scholtz C H and Holm E (editors) 1985. Insects of southern Africa. Butterworths, Durban.

White F 1983. The vegetation of Africa. UNESCO, Switzerland.

CHAPTER 1 POLLINATION BIOLOGY AND THE FOSSIL RECORD

A Scholtz

Very little information of interest to pollination biologists has been extracted from the southern African fossil record to date. This situation is only likely to improve if more interaction occurs between modern comparative morphological- and functional-type analyses on the one hand, and the description of the fossil record on the other.

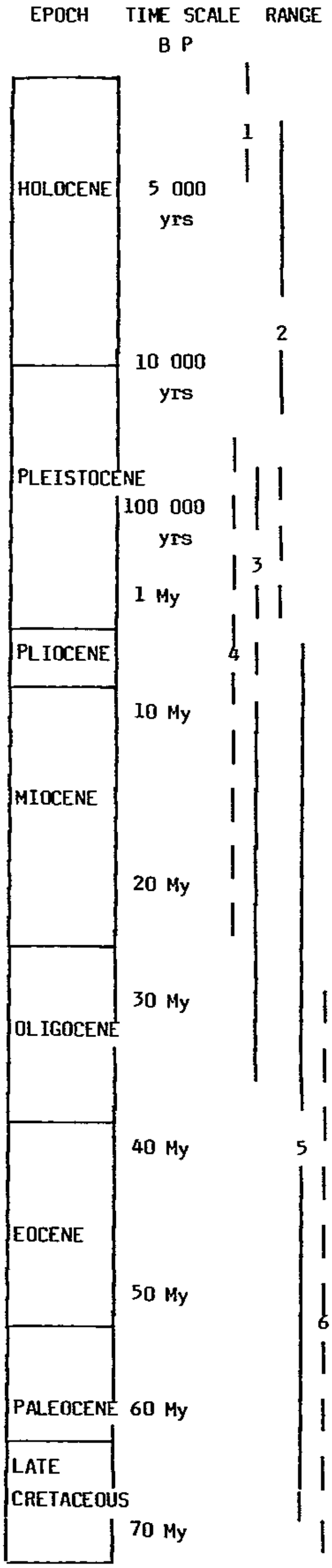
INTRODUCTION

Researchers studying recent biological phenomena often encounter disjunct distributions of plant taxa or pollinators, relict pollination syndromes, swarms of closely related species, refugia, centres of speciation or rapidly expanding populations. Many of these reflect events in the recent past and therefore a detailed palaeobotanical and palaeoclimatic history of this time range is of particular relevance to biologists. Unfortunately, good quality fossiliferous deposits of Holocene and Late Pleistocene age (last 125 000 years) are relatively rare in the Cape Province (Figure 1.1) and the majority of sites containing useful deposits of this age are those studied by archaeologists.

Generally, less information is recoverable from older fossil records. However, palaeontological studies depend on the quality and distribution of available fossiliferous deposits. For instance, locally, more is known about early Pliocene (five to three million years) large faunas than those of more recent mid-Pleistocene (one to 0,5 My). This is because high quality fossiliferous deposits of early Pliocene age in the Langebaanweg/Saldanha area have been extensively studied (Hendey 1983a). During the late Cretaceous and early Tertiary period (90 to 40 My) numerous crater-lake deposits were formed in the vents of kimberlitic volcanoes and these, scattered in a swathe stretching from the northern Cape to Botswana, preserve a remarkable range of plant material (Rennie 1931; Scholtz 1985; Rayner 1986). Therefore, the quality of angiosperm macrofossil collections will probably always be best for the Late Cretaceous and early Tertiary time ranges.

Overall terrestrial deposits containing fossiliferous sediments are rare. This is due to southern Africa having experienced a relatively dry climate during the Cenozoic and tectonic uplift, especially in the more mesic eastern half of the subcontinent, resulting in an erosional rather than depositional landscape.

The fossil record is always severely limited. This constrains the nature and scope of hypotheses that can be investigated in palaeobotany. Within these constraints the exhaustive exploitation of the fossil record for morphology, taxonomy, geographical distribution of organisms, climate and the functional relationship between these are necessary. The modern biological world needs to be understood in similar terms. The present is a key to the past as much as the past is a key to the present.



1. Peats and organic rich sediments associated with small or ephemeral streams, mountain sponges or behind coastal dune barriers. Irregular depositional environments and local edaphic changes decrease the value of these sites, but due to their abundance and distribution they are valuable for reconstructing vegetation and climatic change. In addition, charcoal and other plant remains at archaeological sites may provide relevant data (Wells 1965; Parkington and Poggenpoel 1971; Deacon 1976; Deacon 1979; Scholtz unpublished).

2. Peats and organic rich sediments associated with spring deposits may produce unreliable data because of the irregular depositional environment and possible indirect relationships between spring activity and precipitation. A few coastal lakes, eg Groenvlei or Rietvlei, may provide relatively large and valuable records (Martin 1968; Schalke 1973; Scott 1982a)

3. Sites in the Kalahari basin, such as Etosha Pan, may provide intermittent playa-lake sediments in this time range. Unusual sites formed by geomorphic processes such as warping, eg the uppervalley of the Kafferkuilsrivier near Riversdale, may also provide long sequences. (No current data).

4. Coastal marine deposits, eg Noordhoek, Langebaanweg, provide important evidence, but only contain odd short temporal sequences. Onshore lagoonal deposits, eg Knysna Beds, additionally provide some plant macroscopic remains allowing better differentiation of vegetation in local edaphic zones (Rogers 1908; Phillips 1927; Thiergart et al 1963; Coetzee 1980; Coetzee and Rogers 1982).

5. Sedimentary sequences contained in epicontinental offshore basins are often marred by important time gaps, but otherwise provide a relatively continuous record. By their depositional nature, however, these sediments record only major and generalized changes in vegetation climate and the distribution of specific taxa (Martin 1959; Muller-Stoll and Madel 1962; Scott 1976; Stapleton and Beer 1977; McLachlan and Pieterse 1978; Morgan 1978).

6. Numerous crater-lake sedimentary sequences associated with vents of kimberlite volcanoes provide high quality palynological information. Well preserved plant macrofossils are obtained from these sites which occur in the northern Cape and Botswana (Kirchheimer 1934; Scholtz 1985; Rayner 1986).

FIGURE 1.1 The southern African fossil record; types of deposits, time ranges and quality of information.

This chapter is intended to:

- introduce pollination biologists to the nature of the fossil record and the palaeobotanical/palaeoclimatic evidence gleaned from it;
- outline the types of research which might provide useful historical data for studies in pollination biology; and
- briefly summarize current, relevant knowledge of the local fossil record.

Since both the type of fossil evidence and its relation to the biological present differ markedly between the recent and distant past, the fossil record will be dealt with in two sections.

THE USE OF THE FOSSIL RECORD TO POLLINATION BIOLOGISTS

Due to the limitations of the fossil record in any one region, palaeobotany comprises syntheses of information widely dispersed in time and space. Nevertheless broad outlines of the fossil record and of earth history can be sketched. As working hypotheses such sketches are accepted as a framework for research in virgin territory. In this respect the importance given to evidence obtained from a few unusually well preserved and rich fossil localities (which are usually exploited by researchers at the major institutions active in the field) should be noted. Particularly in America and USSR, suitable fossiliferous deposits are being systematically sampled for inflorescences in association with other plant organs. These observations represent highlights in information recovery, but, because of the chance nature of finding suitable specimens and the painstaking work involved, are likely to remain isolated events. Examples of this type of work, where pollination syndromes have been diagnosed from the fossil record, are the works of Crepet (1979a, 1981), Crepet and Daghlian (1981), Zavada and Crepet (1981) and Friis and Skarby (1981). For recent reviews of the state of palaeobotanical research see Knoll and Rothwell (1981) and Smoot and Taylor (1985). The latter specifically discusses pollination biology in the context of well preserved inflorescences and associated pollen. Plant macrofossils are abundant in some of the southern African crater-lake deposits and there is a good possibility that well preserved inflorescences could be recovered from these sites (eg Banke).

Our knowledge of the evolution and distribution of animal vectors in the past is even more fragmentary (see Crepet 1979b). It is likely that in the long time scale most pollination biologists will continue to make use of the fossil record in an ad hoc fashion (ie scanning the literature in the hope that some useful information will be discovered). This may be justified in terms of the poor state of palaeontological research. However, a more systematic approach integrating pollination biology with palaeobotany is desirable. This will entail adopting a research philosophy perhaps still uncommon in pollination biology, namely, an approach based primarily upon analysing the distribution of pollination syndromes on morphological/functional, phylogenetic, ecological and biogeographical axes. As Muller (1984) noted, "..... a close analysis of the morphology of fossil types in comparison with form and function in recent equivalents will allow us to detect the evolutions of many adaptations in the reproductive sphere."

In decreasing order of precision, the following four types of information of potential relevance to a pollination biologist can be obtained from palynological record (Figure 1.2):

- a description of the morphological types represented in an assemblage (the pollen of anemophilous species being better represented than entomophilous species);
- a list of the taxa represented;
- a crude reconstruction of vegetation type and structure; and
- the inferred climate that prevailed in a region at a specific time.

A pollination biologist-cum-palaeobotanist would have to organize modern data in ways which would relate to these types of information (Figure 1.2). For instance, what significance can be attributed to specific pollen morphological types? Are pollination syndromes associated with certain taxa, pollen morphological types, or climates? Do any general rules govern the relationships between pollen morphological types, climate and vegetation structure?

Several papers have been published on the functional significance of particular features of pollen morphology (eg Hesslop-Harrison 1976; van Campo 1976; Bolick 1978; Muller 1979) in which three categories of functional significance are distinguished:

- features of pollen morphology and exine structure which relate directly to the associated mode of pollination, eg wind pollinated pollen is usually relatively small, spherical and smooth exined;
- features of exine structure which relate directly to principles of harmomegathy (the functional principles relating to how an exoskeleton will alter its shape in response to changes in moisture potential in order to maintain viable living cells). For instance, Bolick (1978) notes that the mechanical efficiency of the pollen of Helianthaceae probably correlates with the adaptation of members of the tribe to relatively dry habitats; and
- features of pollen morphology which can be correlated with biochemical functions. Thus Heslop-Harrison (1976) has proposed that tectate-columellate and cavate exine structure provide sites for the storage of incompatability proteins and enzymes.

Zavada's (1984) work illustrates that valuable information can be obtained when the functional significance of a particular morphology (viz pollen exine morphology) is wedded to its distribution in the fossil record. Modern day comparative data for angiosperm pollen show that reticulate-perforate exine sculpturing is associated with sporophytic self-incompatability (SSI), while imperforate or microperforate sculpturing is associated with gametophytic self-incompatability (GSI) (Table 1.1). Zavada (1984) points out that the earliest unequivocal angiosperm pollen

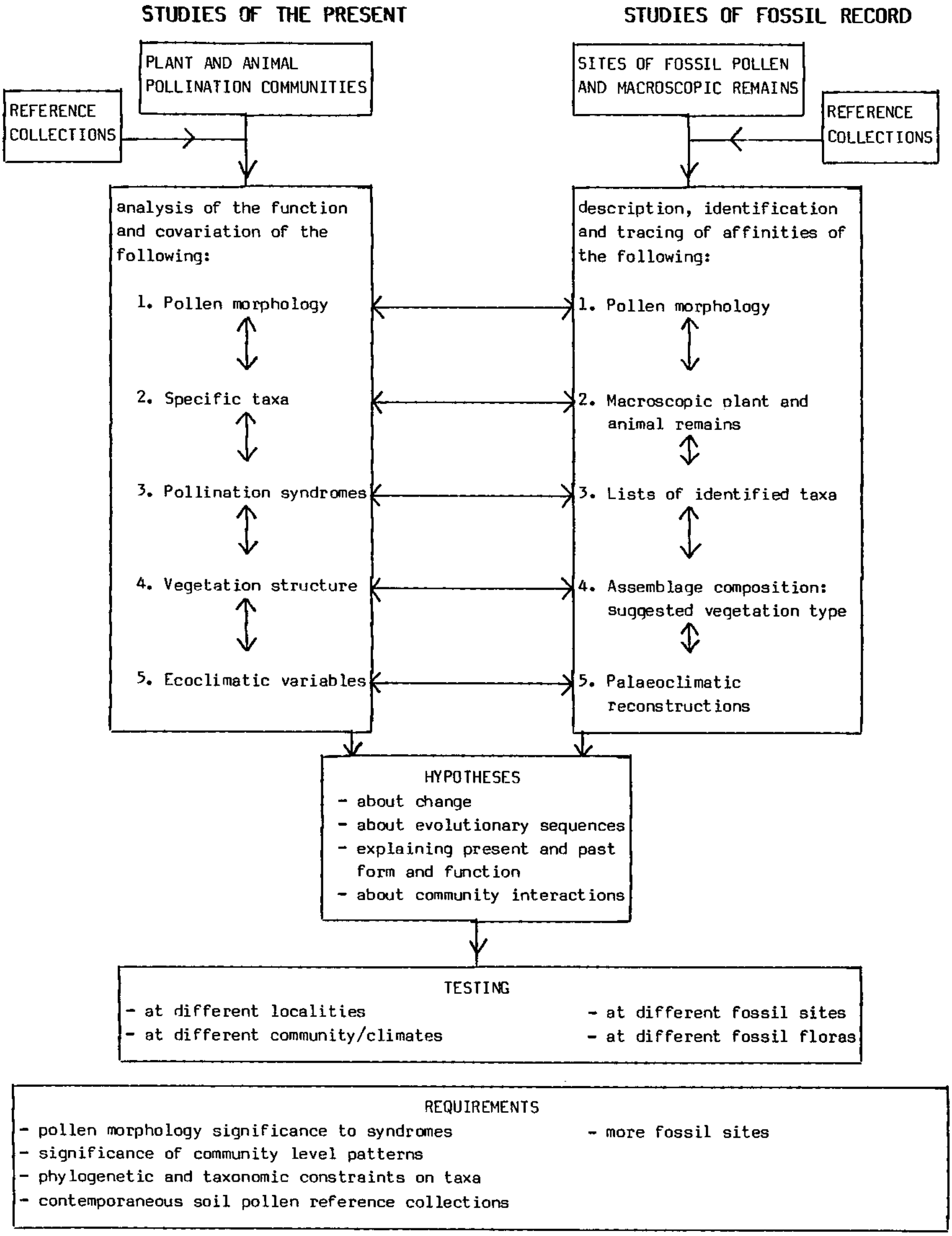


FIGURE 1.2 The interrelationships between information, reference collections, pollination biology and the fossil record.

TABLE 1.1 Self-incompatibility, associated pollen characters and the fossil record (after Zavada 1984, which contains all references)

TAXON		EXINE SCULPTURING	SIZE OF PERFORATION	
Taxa with gametophyic self-incompatability				
Commelinaceae:	Tradescatia	microperforate	0,04	Mean 0,1
Poaceae:	many genera	imperforate	0,0	
Fabaceae:	Trifolium	reticulate	0,0	
	Medicago	microreticulate	0,0	
Liliaceae:	Lilium	reticulate	0,3	
Onagraceae:	Oenothera	imperforate/microperforate	0,0	
Papaveraceae:	Papaver	imperforate	0,0	
Rosaceae:	Prunus	microperforate	0,03	
	Pyrus	microperforate	0,006	
	Malus	imperforate	0,0	
Solanaceae:	Nicotiana	imperforate	0,0	
	Petunia	imperforate	0,0	
	Solanum	imperforate	0,0	
Taxa with sporophytic self-incompatability				
Homomorphic flowers				
Compositae:	Crepis	perforate	0,4	Mean 1,4
	Cosmos	perforate	0,6	
Cruciferae:	Brassiea	reticulate	1,0	
	Iberis	reticulate	0,8	
	Raphanus	reticulate	0,8	
Rubiaceae:	Galium	reticulate	0,2	
Heteromorphic flowers				
Boraginaceae:	Cordia	reticulate	1,7	
Connaraceae:	Cnestis	reticulate	0,5	
Genteniaceae:	many genera	various sculpturing	ca 1,1	
Guttiferae:	Hypericum	reticulate	0,5	
Fabaceae:	Bauhinia	striate/baculate/perforate	1,1	
Linaceae:	Linum	baculate (intectate)	1,7	
Oleaceae:	Forsythia	reticulate	1,4	
Oxalidaceae:	Oxalis	reticulate	0,6	
Plumbaginaceae:	Armeria	reticulate	4,3	
	Acantholimon	reticulate	6,0	
	Cerastostigma	baculate	1,2	
	Goniolimon	reticulate	4,6	
	Limonium	reticulate	4,4	
	Limonastrum	reticulate	1,0	
	Plumbago	baculate	1,2	
Polemoniaceae:	Gilia	reticulate	0,9	
	Phlox	reticulate	4,9	
Polygonaceae:	Fagopyrum	reticulate	0,7	
Primulaceae:	Douglasia	reticulate	0,3	
	Glaux	reticulate	0,2	
	Hottonia	reticulate	0,6	
	Lysimachia	reticulate	0,6	
	Primula	reticulate	0,8	
Rubiaceae:	many genera	reticulate	ca 1,6	
Early recognizable dispersed angiosperm pollen				
Afropollis sp		reticulate	2,0	Mean 1,6
Asteropollis asteroides		reticulate	0,6	
Clavatipollenites hughesii		reticulate	1,0	
Liliacidites sp		reticulate	0,9	
Retimonocolpites jardinus		reticulate	2,2	
R peroreticulatus		reticulate	2,6	
Stellatopollis barghornii		reticulate	2,6	
Winteraceous pollen		reticulate	1,3	

types which occur in lower Cretaceous deposits (eg Afropollis, Clavatipollenites and Retimonocolpites), display the SSI pattern. These occurrences probably record the development of sporophytic self-incompatability rather than any other angiosperm characteristic.

Of importance to pollination biology is a further correlation observed in modern day studies: sporophytic self-incompatability is correlated with physiologically advanced stigmatic areas and large showy flowers or aggregate inflorescences. Zavada (1984) concludes, " .... the early origin of self-compatability may have played an important role in the diversification of angiosperms by providing the selective impetus for the carpellate condition, promoting outbreeding and at the same time permitting the advantages of insect pollination to be fully realised."

In a recent study on the pollen and pollination syndromes of the genus Erythrina (Fabaceae), Hemsley and Ferguson (1985) have shown that the pollen of hummingbird pollinated species is medium-sized, with medium-sized lumina, and lacks (or has sparse) sexinous granules in the lumina. The pollen of passerine bird pollinated species is characterized by small lumina and moderate to dense occurrence of granules within the lumina. These pollen types were also correlated with differences in floral morphology and nectar composition. Hemsley and Ferguson (1985) suggest that the particular morphology of pollen associated with hummingbird pollination is functionally related to the fine microscopic structure of hummingbird feathers. This knowledge of the correlation between pollen morphology and a pollination syndrome means that considerably more knowledge of its evolution may be gained from the fossil record.

The study of the correlations between pollination and vegetation types or climate is not much advanced. The general correlation between wind pollination, climate and vegetation structure is known (Whitehead 1969; Koutnik this volume). Various anecdotal references and suggestions as to how specific syndromes might be related to vegetation structure and climate exist (Faegri and van der Pijl 1979; Rebelo this volume), but few detailed studies are available. Arroyo et al (1982) studied how pollination mechanisms are selected for along an altitudinal gradient.

Evidence of relevance to understanding the past is often produced in analyses of the present which contain a biogeographical component. For example, recent work by Cottrell (1985) has shown that in terms of the distribution, habits and larval food of the butterfly genera endemic to the Cape Province, none of these genera have coevolved with the Cape flora for any substantial period of time. This type of approach may produce relevant information on both the long- and short-time scale.

THE CAPE FLORA: THE LONG TIME SCALE

LATE CRETACEOUS TO
PLEISTOCENE

During the early Cretaceous the flora of the region was similar to that of the rest of Gondwanaland (Herngreen and Chlonova 1981). Podocarpaceous gymnosperms and pteridophytes were ubiquitous in middle and high palaeolatitudes, while araucariaceous, cheirolepidaceous and ephedraceous gymnosperms dominated in the tropics. Characteristic of the palynological record of this time is the wide distribution of many palynomorphs.

A wide range of plant and animal remains in southern Africa, of Late Cretaceous to Paleocene age, including pollens and spores (Kirchheimer 1934; Scholtz and Deacon 1982; Coetzee et al 1983; Scholtz 1985), leaves (Rennie 1931), wood (Adamson 1931), vertebrates (Edwards and Hawkins 1965; Estes 1977; Smith 1986a,b) and invertebrates - including insects (Smith 1986b), are preserved in the fossiliferous crater-lake deposits associated with the vents of the numerous kimberlitic volcanoes. These are seldom exposed by river incision or other natural processes, and fossils are usually recovered from boreholes. Palynomorphs are the most abundant plant fossils: they are well preserved and many can be identified with extant taxa at a generic or higher taxonomic level.

By the late Cretaceous, however, the flora of southern Africa had become distinct from that of the rest of Gondwanaland and, within the region itself, various floras can be recognized. While the dominance of ephedraceous pollen in the tropics had been succeeded during the late Cretaceous by the strong representation of a range of palmaceous forms, the southern African record is more complex. Deposits of this age from the north-western interior sector are characterized by the continued prominence of *Araucariacites* and *Araucariapollenites* pollen and the common occurrence of the form genera *Constantinisporis*, *Cretacaeiporites*, *Fenestriorites*, *Bahiaporites*, *Tricolpites* (Gunnerites), *Clavatipollenites* and *Chlonovaia* (Scholtz and Deacon 1982; Scholtz 1985; Scholtz unpublished). On the east coast and to the south podocarpaceous pollen with affinity to the genera *Podocarpus*, *Dacrydium* and *Microcachrys* are more prominent (McLachlan and Pieterse 1978; Scholtz unpublished).

The Cretaceous-Tertiary boundary is marked worldwide by extinction of elements common in the Cretaceous and by other changes in the composition of floras (Tschudy et al 1984). The nature of these changes is at present better documented in the Northern than in the Southern Hemisphere.

The early tertiary (Palaeocene) flora of the north-western interior sector appears to have been of a relatively dry subtropical type, with gymnosperms (Podocarpaceae and Araucariaceae) still represented but with more modern elements already present. These include, amongst the angiosperms, members of the Proteaceae, Restionaceae and Ericaceae (families presently largely confined to fynbos heathland and Afromontane habitats), Casuarinaceae, Epacridaceae and Gyrostemonaceae (families with strong Southern Hemisphere distribution), Gunneraceae (a family not well represented in the Northern Hemisphere at present) and the Euphorbiaceae, Caesalpinaceae, Palmaceae and Ulmaceae (families with tropical and subtropical association). Forms with affinity to the Thymelaeaceae are also recorded. The association of Proteaceae, Restionaceae and Ericaceae is, however, rare, and it would seem that the distribution of this association was linked to the occurrence of quite specific ecoclimatic conditions. Scholtz (1985) has suggested that members of these families formed part of the understorey of a relatively dry, mixed hardwood and softwood, subtropical, open canopied forest. On the east coast during the same time a *Podocarpus* dominated forest flourished (Scholtz unpublished).

Evidence from the east coast for Eocene times is that Podocarpaceae, Widdringtonia, Cunoniaceae, Casuarinaceae, Proteaceae and Restionaceae were present in the vicinity of lowland wet sites together with a diversity of other angiosperms (Thiergaart et al 1963; A Scholtz personal observation). Ericaceae were, however, absent or rare in the vegetation

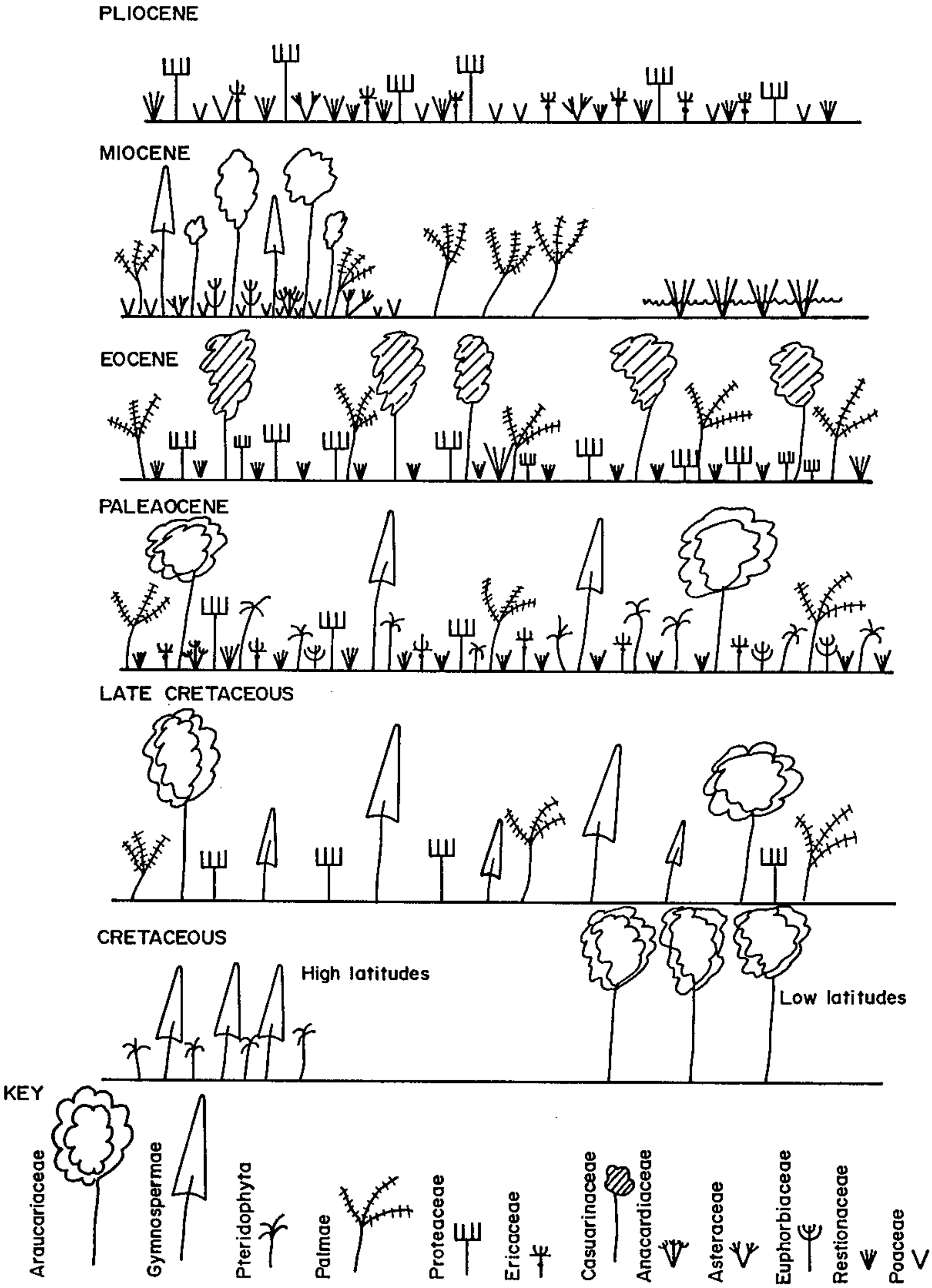


FIGURE 1.3 Diagramatic reconstruction of the vegetation structure since the Late Cretaceous.

types recorded in the Knysna Beds. This was a time of generally warm, humid climates during which the poles were ice free (Deacon 1983a).

There are as yet no polliniferous deposits definitely known to be of Oligocene age reported from southern Africa. This is a time period marked by abrupt cooling worldwide and a regression of sea levels (Deacon 1983a). Pollen assemblages of possibly early Miocene age from the Noordhoek site on the Cape Peninsula have been studied by Coetzee (1980) and Coetzee and Rogers (1982). They record a number of vegetation types ranging from a "mixed forest of gymnosperms with subtropical-tropical angiosperm elements" to associations dominated by palms and to swamp vegetation. Conspicuous amongst these communities are a large number of taxa now extinct in the south-western Cape or in Africa, including members of the Winteraceae, Casuarinaceae and Sparganiceae. Many forms with affinity to taxa now present in fynbos, strandveld and Afromontane forest are recorded during the later Miocene.

Pollen assemblages from the late Miocene deposits from the Noordhoek and Langebaan sites include many forms prominent in fynbos vegetation associations today, including Asteraceae, Thymelaeaceae, Ericaceae, Restionaceae and Rosaceae, with Poaceae also well represented. Coetzee (1980) suggests that the well documented pronounced cooling of global climates at the end of the Tertiary may have resulted in the extinction of subtropical/tropical taxa recorded in the Miocene in the south-western Cape.

During the Plio-Pleistocene, global climates have oscillated between cooler and warmer than at present, with the norm being considerably colder. Cooler climates were often associated with drier conditions, although wet periods have been recorded in various regions during the predominantly cool periods. The transition between climates characterized by glaciations in high latitudes and warmer climates (or interglacials) sometimes occurred rapidly and both the oscillation between climates and the variable rapidity of the repeated transitions have shaped modern taxa and vegetation. The details of this sequence of events in the southern African subcontinent are not well known.

Deacon (1983b) provides a relevant review of the earth history of the last 70 My, and more details are given in Deacon et al (1983).

THE SHORT TIME SCALE

Late Pleistocene and Holocene
ca 25 000 to the present

Figure 1.4 illustrates a few features of the climatic history over the past 25 000 years, based on evidence from four separate studies done on different categories of material, from different locations and over different time scales (these features are supported by other studies (Martin 1968; Butzer and Helgren 1972; Schalke 1973; Deacon et al 1983)):

- planktonic foraminiferae from a short, 700 year old, nearshore marine sequence off Walvis Bay, which documents changes in surface seawater temperatures off the west coast of southern Africa (Herbert 1986);
- palynological analysis of a 4 000 year old peat, which documents the expansion and contraction of forest vegetation in the George area (Scholtz 1986);

- analysis of an 8 000 year old cave sequence from the Barkley East area, north eastern Cape (Tusenius 1986); and
- analysis of charcoal assemblages from a 60 000 year old cave sequence in the Cango Valley (Scholtz 1986).

The latter two studies investigate changes in wood anatomy which can be related to changes in soil moisture availability and plant transpiration.

Nine climatic periods (Figure 1.4) can be delimited for the southern and south-western Cape, as follows:

1. Temperatures low with little rain in summer, favouring karroid scrub vegetation.
2. Temperatures low and dry throughout the year, favouring karroid scrub vegetation.
3. Temperatures remain low, although precipitation increases and becomes aseasonal. This consistently favourable precipitation to evaporation ratio led to expansion of mesic vegetation types.
4. Precipitation lower than in the preceding period and more seasonal in southern Cape. A decline in summer rainfall perhaps indicated.
5. The longest episode of low rainfall experienced during the Holocene. In the southern Cape little rainfall received during summer with some indication that temperatures were lower.
6. Summer rainfall sufficient to allow expansion of mesic vegetation types, especially Afromontane forest, in the southern Cape. Butzer and Helgren (1972) suggest this period be termed the "climatic optimum" for the Holocene.
7. Decrease in rainfall especially during the summer.
8. Climate similar to present.
9. Cold surface water recorded off the west coast coinciding with Northern Hemisphere "little ice-age" (16th, 17th and 18th centuries). May have caused severe reduction of summer rainfall by preventing inland penetration of cold fronts during winter.

Only when more information is available from sites in the western Cape will palaeobotanists be able to attempt to reconstruct past patterns of vegetation for that region.

Werger (1983) related patterns of distribution of drier vegetation types of South Africa to much wetter-cooler or wetter and cooler periods of climate which may have existed in the past in both summer and winter rainfall regions. These patterns include:

- island-like occurrence of Afro-montane vegetation on mesic sites in the Highveld grassland/False Karoo transition area;

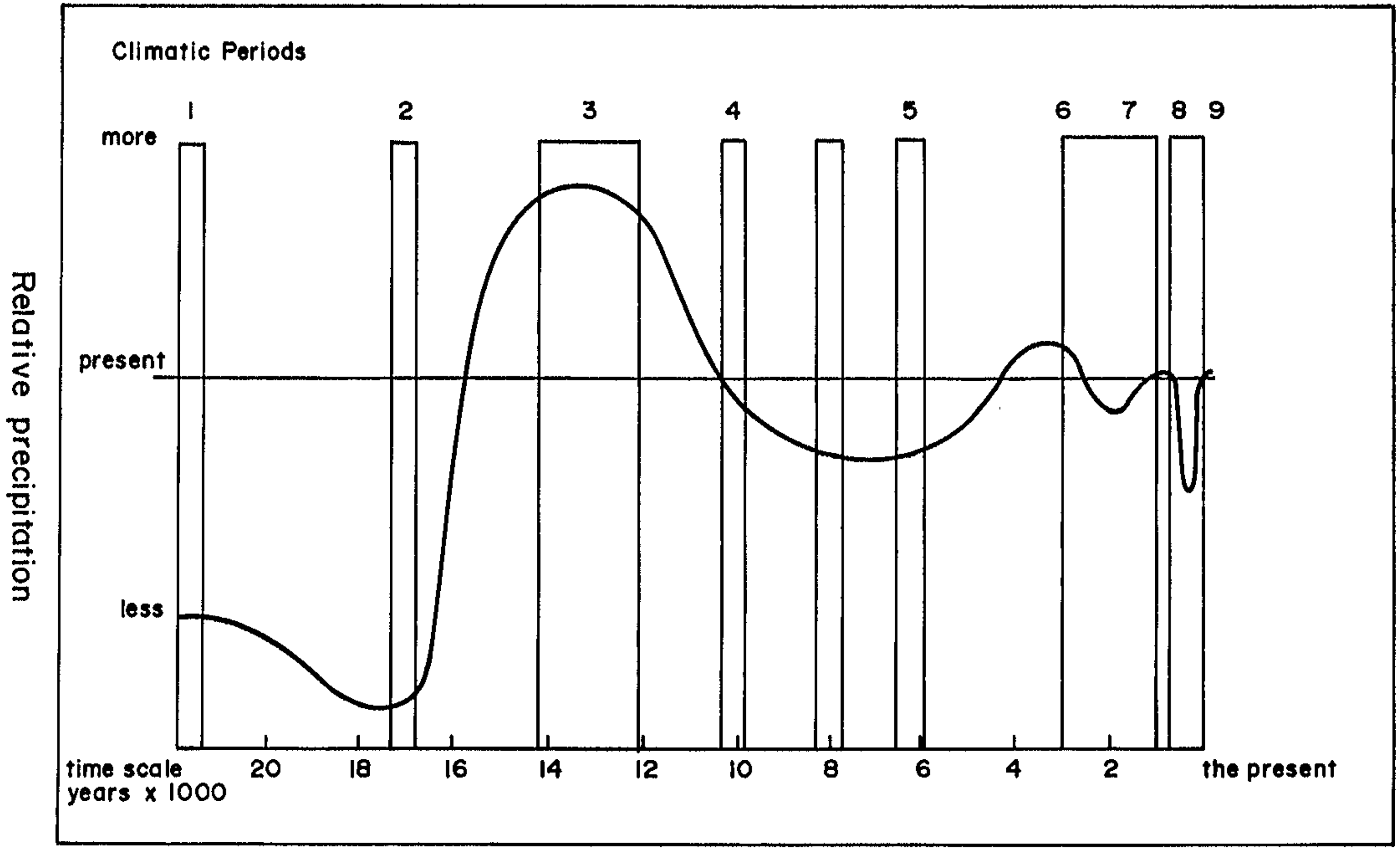


FIGURE 1.4 Relative precipitation curve for the last 22 000 years.

- similar types of occurrence of Sudano-Zambesian scrub patches in the area around the Orange/Vaal confluence, westward of the regions where that vegetation type apparently naturally occurs today;
- island-like occurrence of frost-tolerant, dry, karroid dwarf scrub vegetation of predominantly C3-plants on peaks in the winter rainfall area of Namaqualand; and
- a particular type of patchy distribution of certain species of succulents within the succulent vegetation of the escarpment area of Namaqualand.

Modern vegetation distributions apparently reflect wetter and/or cooler climatic periods in the recent past (ca 15 to 20 000 BP in the southern Cape) better than the harsher climates experienced prior to and after these periods. Present evidence suggests that precipitation during the Holocene, a relatively mesic period within the Pleistocene (Deacon et al 1983), was generally less than it is at present.

Similarly, Acocks (1979) attempted to reconstruct the probable composition, extent, productivity and colour of the "pristine" vegetation of the arid western half of southern Africa before disturbance by people other than hunter-gatherers. By the time the first scientific descriptions of the flora and vegetation were attempted in the early 19th century, much of the vegetation was already altered.

However, Acocks (1979) did not undertake detailed studies of the vegetation of the mountains and coastal forelands of the Cape. Hendey (1983a) has suggested the changes to vegetation caused by human presence during the past few millenia, including the possible effects of eliminating large indigenous herbivores. Janzen (1984) discusses the major changes that may have occurred when large, seed dispersing herbivores were excluded from the vegetation.

During the last 100 000 years, the influence of man via veld management practices involving fire has helped to shape vegetation (Deacon 1983c).

CLOSING REMARKS

Few substantial implications for a better understanding of the history and evolution of pollination syndromes can be drawn from these broad outlines of vegetation and climatic history in the subcontinent. The major changes in flora such as the replacing of pure coniferous forest of the mid-Cretaceous, firstly by forests with an angiosperm component, and later by mixed forests dominated by angiosperms; or the change from closed to open canopied forest to shrubland or grassland, must have been accompanied by major changes in dominant pollination syndromes. However, it would be a mistake to assume that these vegetation changes invariably occurred over wide regions and were irreversible. Rather, these changes may have occurred several times in different regions, whereas yet other regions probably functioned as refugia. Changes in vegetation probably also occurred at very different tempos. All these factors, at present indiscernible in the fossil record, would have greatly affected the distribution and evolution of pollination syndromes in space and time.

Through more systematic interaction between present day studies of pollination biology, where the relationship between relevant variables can be observed, and the fossil record, whose basic data consists only of fossilized plant and animal tissue, more information about the evolution and past patterns of distribution of pollination syndromes can be gained.

REFERENCES

Acocks J P H 1979. The flora that matched the fauna. Bothalia 12(4), 673-709.

Adamson R S 1931. Notes on some petrified wood from Banke, Namaqualand. Transactions of the Royal Society of South Africa 19, 255-258.

Arroyo M T K, Primack R and Armesto J 1982.Community studies in pollination ecology in the high temperate Andes of central Chile. 1. Pollination mechanisms and altitudinal variation. American Journal of Botany 69,82-97.

Bolick M R 1978. Taxonomic, evolutionary and functional considerations of Compositae pollen ultrastructure and sculpture. Plant Systematics and Evolution 130, 209-218.

Butzer K W and Helgren D M 1972. Late Cenozoic evolution of the Cape coast between Knysna and Cape St Francis, South Africa. Quaternary Research 2, 143-169.

Coetzee J A 1980. Tertiary environment changes along the south western African coast. Palaeoecology of Africa 23, 197-203.

Coetzee J A and Rogers J 1982. Palynological and lithological evidence for the Miocene palaeoenvironment in the Saldanha region (South Africa). Palaeogeography, Palaeoclimatology and Palaeoecology 39, 71-85.

Coetzee J A, Scholtz A and Deacon H J 1983. Palynological studies and the vegetation history of the fynbos. In: Deacon H J, Hendey Q B and Lambrechts J J N (editors) Fynbos palaeoecology: a preliminary synthesis. South African National Scientific Programmes Report No 75. CSIR, Pretoria. pp 156-173.

Cottrell C B 1985. The absence of coevolutionary associations with Capensis floral elements plants in the larval/plant relationships of southwestern Cape butterflies. In: Vrba E S (editor) Species and speciation. Transvaal Museum, Pretoria.

Crepet W L 1979a. Insect pollination: a palaeontological perspective. Biological Science 29, 102-107.

Crepet W L 1979b. Some aspects of the pollination biology of Middle Eocene angiosperms. Review of Palaeobotany and Palynology 27, 213-238.

Crepet W L 1981. The status of certain families of the Amentiferae during the Middle Eocene and some hypotheses regarding the evolution of wind pollination in dicotyledonous angiosperms. In: Niklas K(editor) Palaeobotany, Palaeoecology and Evolution.

Crepet W L and Daghlian 1981. Lower Eocene and Paleocene Gentianaceae: Floral and palynological evidence. Science 214, 75-77.

Deacon H J 1976. Where hunters gathered: a study of Holocene Stone Age people in the eastern Cape. Claremont: South African Archaeological Society Monograph Series 1.

Deacon H J 1979. Excavations at Boomplaas Cave: a sequence through the Upper Pleistocene and Holocene in South Africa. World Archaeology 10, 241-257.

Deacon H J 1983a. An introduction to the fynbos region, time scales and palaeoenvironments. In: Deacon H J, Hendey Q B and Lambrechts J J N (editors) Fynbos palaeoecology: A preliminary synthesis. South African National Scientific Programmes Report No 75. CSIR, Pretoria. pp 1-20.

Deacon H J 1983b. The comparative evolutions of mediterranean-type ecosystems: a southern perspective. In: Kruger F J, Mitchell D T and Jarvis J U M (editors) Mediterranean-type ecosystems: the role of nutrients. Berlin, Springer-Verlag. pp 3-40.

Deacon H J 1983c. The peopling of the fynbos region. In: Deacon H J, Hendey Q B and Lambrechts J J N (editors) Fynbos palaeoecology: A preliminary synthesis. South African National Scientific Programmes Report No 75. CSIR, Pretoria. pp 183-204.

Deacon H J, Hendey Q B and Lambrechts J J N (editors) 1983. Fynbos palaeoecology: A preliminary synthesis. South African National Scientific Programmes Report No 75. CSIR, Pretoria. pp 216.

Edwards C B and Hawkins J B 1965. Kimberlites in Tanganyika with special reference to the Mwadui occurence. Economic Geology 61, 537-554.

Estes R 1977. Relationships of the South African fossil frog Eoxenopoides reuningi (Anura, Pipidae). Annals of the South African Museum.

Faegri K and van der Pijl J 1979. The principles of pollination ecology. Pergamon Press, Oxford.

Friis E M and Skarby A 1981. Structually preserved angiosperm flowers from the upper Cretaceous of southern Sweden. Nature 291, 485-486.

Hemsley A J and Ferguson I K 1985. Pollen morphology of the genus Erythrina (Leguminosae: Papilionoideae) in relation to floral structure and pollinators. Annals of the Missouri Botanical Gardens 72, 570-590.

Hendey Q B 1983a. Palaeoenvironmental implications of the Late Tertiary vertebrate fauna of the fynbos region. In: Deacon H J, Hendey Q B and Lambrechts J J N (editors) Fynbos palaeoecology: A preliminary synthesis. South African National Scientific Programmes Report No 75. CSIR, Pretoria. pp 100-115.

Herbert R S 1986. Late Holocene climatic change: the little Ice-Age and El Nino from planktonic foraminifera in sediments off Walvis Bay, South West Africa. Unpublished MSc Thesis. University of Cape Town.

Herngreen G W F and Chlonova A F 1981. Cretaceous microfloral provinces. Pollen et Spores 23, 441-555.

Heslop-Harrison J 1976. The adaptive significance of the exine. In: Ferguson I K and Muller J (editors) The evolutionary significance of the exine. Linnean Society Symposium Series Number 1, Academic Press. pp 27-37.

Janzen D H 1984. Dispersal of small seeds by big herbivores: foliage is the fruit. The American Naturalist 123, 338-353.

Kirchheimer F 1934. On the pollen from the upper Cretaceous dysodil of Banke, Namaqualand (South Africa). Transactions of the Royal Society of South Africa 21, 41-50.

Knoll A H and Rothwell G W 1981. Palaeobotany: perspectives in 1980. Palaeontology 71, 7-35.

Martin A R H 1959. South African palynological studies. 1. Statistical and morphological variations in the South African species of Podocarpus. Grana 2, 40-53.

Martin A R H 1968. Pollen analysis of Groenvlei Lake sediments. Knysna (South Africa). Review of Palaeobotany and Palynology 73, 107-144.

McLachlan I R and Pieterse E 1978. Preliminary palynological results: Site 361, leg 40. Deep Sea Drilling Project. Initial Report of the Deep Sea Drilling Project 4, 857-881.

Morgan R 1978. Albanian to Senonian palynology of Site 364, Angola Basin. Initial Report of the Deep Sea Drilling Project 40, 915-951.

Muller J 1979. Form and function in angiosperm pollen. Annals of the Missouri Botanical Gardens 66, 593-632.

Muller J 1984. Significance of fossil pollen for angiosperm history. Annals of the Missouri Botanical Gardens 71, 419-443.

Muller-Stoll W R and Madel E 1962. Fossil woods of Monimiaceae and Euphorbiaceae from the Upper Cretaceous Umzamba Beds of East Pondoland, Cape Province. Transactions of the Geological Society of South Africa 65, 93-104.

Parkington J E and Poggenpoel C 1971. Excavations at De Hangen 1968. South African Archaeological Bulletin 26, 3-36.

Phillips J F V 1927. Fossil Widdringtonia in lignite of the Knysna Series, with a note on fossil leaves of several other species. South African Journal of Science 24, 188-197.

Rayner R J 1986. Conservation of an extinct ecosystem. Custos 15(7), 20-23.

Rennie J V L 1931. Note on fossil leaves from the Banke clays. Transactions of the Royal Society of South Africa 19, 251-253.

Rogers A W 1908. Notes on a journey to Knysna. Annual Report of the Geological Committee of the Cape of Good Hope 13, 129-134.

Schalke H J W G 1973. The upper Quaternary of the Cape Flats area (Cape Province, South Africa). Scripta Geologica 15, 1-57.

Scholtz A 1985. The palynology of the upper lacustrine sediments of the Arnot Pipe, Banke, Namaqualand. Annals of the South African Museum 95, 1-109.

Scholtz A 1986. Palynological and palaeobotanical studies in the southern Cape. Unpublished MA Thesis. University of Stellenbosch.

Scholtz A and Deacon H J 1982. Report on fossil pollens from sediments associated with a group of Kimberlite pipes in Botswana. Unpublished Report, University of Stellenbosch.

Scott L 1976. Palynology of Lower Cretaceous deposits from the Algoa basin (Republic of South Africa). Pollen et Spores 18, 563-609.

Scott L 1982a. A late Quaternary pollen record from the Transvaal bushveld, South Africa. Quaternary Research 17, 339-370.

Smith R M H 1986a. Sedimentation and palaeoenvironments of Late Cretaceous crater-lake deposits in Bushmanland, South Africa. Sedimentology 33.

Smith R M H 1986b. Crater lakes in the age of the dinosaurs. Sagittarius 1, 11-15.

Smoot E L and Taylor T N 1985. Palaeobotany: recent developments and future research directions. Palaeogeography, Palaeoclimatology and Palaeoecology 50, 149-162.

Stapelton R P and Beer E M 1977. Micropalaeontological age determination for the Brenton Beds. Bulletin of the Geological Survey of South Africa 60, 1-9.

Thiergart F, Frantz U and Raukopf K 1963. Palynologische untersuchungen von Tertiarkohlen und einer obserflachen prove nabe Knysna, Sud-Afrika. Advances in the Frontiers of Plant Science 4, 151-178.

Tschudy R H, Pilmore C L, Orth C J, Gilmore J S and Knight J D 1984. Disruption of the terrestrial plant ecosystem at the Cretaceous-Tertiary Boundary, Western Interior. Science 225, 1030-1032.

Tusenius M 1986. Charcoal analytical studies in the north eastern Cape. Unpublished MA Thesis. University of Stellenbosch.

Van Campo M 1976. Patterns of morphological variation within taxa. In: Ferguson I K and Muller J (editors) The evolutionary significance of the exine. Linnean Society Symposium Series Number 1.

Wells M J 1965. An analysis of plant remains from Scott's cave in the Gamtoos Valley. South African Archaeological Bulletin 20, 79-84.

Werger M J A 1983. Vegetation geographical patterns as a key to the past, with emphasis on the dry vegetation types of South Africa. Bothalia 14, 405-410.

Whitehead P H 1969. Evolution of wind pollination in the angiosperms. Evolution 23, 28-35.

Zavada M S 1984. The relation between pollen exine sculpturing and self-incompatibility mechanisms. Plant Systematics and Evolution 147, 63-78.

Zavada M S and Crepet W L 1981. Middle Eocene of North America: flowers of the Celtidoideae. American Journal of Botany 68, 924-933.

CHAPTER 2 BREEDING SYSTEMS IN THE CAPE FLORA

K E Steiner

Little work has been done on plant breeding systems in southern Africa. The objective of this contribution is to review the current theories on plant breeding systems in general and information from the Cape flora in particular.

INTRODUCTION

The sexual nature of plants has been recognized as important since Linneaus published his 'Systema Naturae' in 1735 (cf Stearn in Blunt 1971). Only after Darwin's (1876, 1877) experimental work was the significance of the variation in plant breeding systems recognized. Darwin (1876) found that progeny from cross-pollination were usually more vigorous than progeny from self-pollination. This led him and others to interpret the various types of sexual expression as mechanisms to promote outcrossing. Spatial and temporal separation of stamens and pistils, heterostyly, monoecism, andromonoecism, gynomonoecism, dioecism, androdioecism, gynodioecism and self-incompatibility were all viewed as mechanisms to promote outcrossing. Conversely, self-pollination or inbreeding was viewed as deleterious or only occasionally beneficial (cf Jain 1976). These views predominated and were developed further with the advent of the synthetic theory of evolution (Mather 1940; Lewis 1942; Darlington 1958; Grant 1975). It is now recognized that inbreeding, as well as outbreeding, can be adaptive depending on the selective regime (Jain 1976).

Wyatt (1983) defines breeding system (Bawa and Beach 1981 prefer the term sexual system) as "all aspects of sex expression in plants that affect the relative genetic contribution to the next generation of individuals within a species". Traditionally, sexual expression within a species has been determined on purely morphological grounds. This has involved an analysis of floral structure of individuals and populations in order to determine proper placement into one of the established categories (Table 2.1).

Classification of sexual systems using a strict morphological approach can lead to erroneous interpretations, where functional systems are not evident from morphological criteria alone. This is true both in cases where hermaphrodite flowers are functionally male (Arroyo and Raven 1975; Anderson 1979; Atsatt and Rundel 1982; Steiner 1985), and where they are functionally female (Charlesworth 1984; Haber and Bawa 1984; Lim 1984; Kevan and Lack 1985; Van Wyk 1985). The importance of a functional rather than morphological approach to plant breeding systems has been emphasized by Lloyd (1980), Ross (1982) and Charlesworth (1984).

Janzen (1977), Bawa (1980, 1982a), Bawa and Beach (1981), Beach (1981), Willson (1979, 1982), and Givnish (1980, 1982) argue that much of the variation in plant sexual systems is the result of selection to optimize paternal and maternal success in different ways (ie sexual selection). Sexual selection is defined by Stephenson and Bertin (1983) as 'the differential reproductive success of individuals of the same sex and species that survive to reproductive age and are capable of reproduction'.

TABLE 2.1 Classification of flowering plant sexual systems. Modified from Bawa and Beach (1981)

A. Systems based on the spatial distribution of male and female reproductive organs

- I. Individual plants
    1. Hermaphroditic: plants bear only bisexual flowers
    2. Monoecious: plants bear male and female flowers
    3. Andromonoecious: plants bear bisexual and male flowers
    4. Bynomonoecious: plants bear bisexual and female flowers
    5. Polygamonoecious: plants bear bisexual, male and female flowers
- II. Groups of plants
    1. Dioecious: plants bear either male or female flowers
    2. Androdioecious: plants bear either bisexual or male flowers
    3. Gynodioecious: plants bear either bisexual or female flowers
    4. Polygamodioecious (trioecious): plants bear either bisexual, male or female flowers

B. Systems based on temporal distribution of male and female organs within a flower or unisexual flowers within a plant (monoecious species)

- I. Protandry: pollen released from anthers before stigmas become receptive
- II. Protogyny: stigmas become receptive before pollen is released from anthers

C. Systems based on presence or absence of self-incompatibility alleles

- I. Self-incompatibility: plants polymorphic with respect to the presence of self-incompatibility alleles; pollinations involving pollen and stigma sharing the same self-incompatibility alleles, including self-pollinations result in no fruit set.
- II. Self compatibility

D. Systems based on variation in style and stamen length or style dimorphisms

- I. Heterostyly
    1. Distyly
    2. Tristyly
- II. Enantiomorphy

Footnote: Terminology can often be confusing in discussions of breeding systems because different terms are often used for the same phenomenon. One must be careful, as noted by Frankel and Galun (1977) and Wyatt (1983) to specify the level at which one is dealing. Thus a single plant may be andromonoecious (male and hermaphrodite flowers), or a population may be andromonoecious (eg with male and hermaphrodite plants). This is a problem particularly when working with flora descriptions, in which such distinctions are rarely made.

This theory was originally applied to animals to account for secondary sexual characteristics of males and females.

The basis for sexual selection theory is observed asymmetry in reproductive investment between males and females (Bateman 1948; Trivers 1972). In plants this is reflected in greater investment in female function (especially seeds and fruits) than in male function (stamens and pollen). Reproduction via female function (fruits and seeds) is likely to be limited by resources, and that via male function (pollen) by access to ovules. This should result in male competition for access to stigmas and ovaries (ie females) and female choice of potential mates (pollen grains). Female choice is presumably mediated through control over which pollen grains fertilize the ovules and which fertilized ovules mature into seed (Stephenson and Bertin 1983). Most discussions of sexual selection theory do not postulate the mechanism by which female choice occurs. Wiens et al (in press) is critical of the theory for this reason and suggests that spontaneous embryo abortion due to genetic lethals is a simpler way of viewing the mechanistically imprecise concept of female choice.

The application of sexual selection theory to plants has lagged behind its application to animals because the combination of both sexes in a single floral unit has obscured the separate roles played by male and female sexes. Only recently has an emphasis been placed on viewing these roles separately (Charnov 1979; Willson 1979). Application of sexual selection theory to plants is not always straight forward particularly with respect to the evolution of plant breeding systems (Stephenson and Bertin 1983). This is because predictions based on sexual selection are difficult to separate from those based on resource allocation (Ross 1982; Stephenson and Bertin 1983). Although recognizing differences in maternal and paternal patterns of reproduction, Lloyd (1982) maintains that enforced outcrossing of females has been the single most important selective force responsible for separate sexes.

SOURCES

In this review a number of sources were used when analysing the Cape flora in terms of current theories on plant breeding systems. The sexual expression of species listed by Bond and Goldblatt (1984) was initially determined from generic descriptions of Dyer (1975, 1976), but in many cases additional sources were consulted. These include:

- flora of the Cape Peninsula (Adamson and Salter 1950);
- flora Capensis (Harvey and Sonder 1859-1865);
- flora of southern Africa 10: part 1 (Wiens and Tölken 1979);
- flora of southern Africa 33: part 7, fascicle 2 (Hilliard 1983);
- Thiselton-Dyer (1896-1933);
- trees of southern Africa (Palgrave 1983);
- flora Zambesiaca (Exell 1966); and
- Killick (1969).

For certain genera (eg Agathosma and Euphorbia) monographers were consulted.

CONSTRAINTS

Five genera of Restionaceae (Ischyrolepis, Nevillea, Platycaulos, Restio and Rhodocoma) have been reported to be rarely monoecious (Dyer 1975). No clear indication could be found regarding the frequency of this occurrence within either populations, species or genera. Because of the rarity of monoecious individuals, all species of Restionaceae were considered to be dioecious.

Excluding the Restionaceae, the Cape flora has five genera, in addition to Euphorbia, that are reported to have both monoecious and dioecious species. One of these, Cliffortia, is considered to be entirely monoecious for the purpose of this analysis.

Criteria similar to those used by Freeman et al (1980) were used to categorize taxa as either wind or animal pollinated, while fruit type was obtained from flora accounts or by checking herbarium specimens. The proportion of woody species was obtained from Bond and Goldblatt (1984).

I calculated the total number of indigenous seed plants listed by Bond and Goldblatt (1984) to be 8 507 instead 8 504. It is the former figure that was used as the basis for all calculations.

COSEXUALITY AND OUTBREEDING

The overwhelming majority of flowering plants have male and female organs united into a single unit, the hermaphrodite flower. The percentage increases even more if one includes the various forms of monoecism (eg andromonoecism, gynomonoecism, polygamomonoecism) which together with hermaphroditism comprise the group referred to as cosexes (ie plants that function jointly as male and female) (Lloyd 1980). In the Cape flora, 79,5% of the species are hermaphroditic, while 93,3% are cosexual (Table 2.2).

Some of the advantages of simultaneous cosexuality according to Lloyd (1982) are:

- facilitation of mating;
- cost sharing;
- sex-differential fitness gains; and
- bet hedging.

The prime disadvantage of cosexuality is the reduction of heterosis among the progeny (Lloyd 1982).

The obvious importance of outcrossing among plants cannot be denied. Care should nevertheless be taken not to attribute all the facets of plant breeding systems to this factor alone (Bawa and Beach 1981; Lloyd 1982).

The most common mechanism found in plants to promote outcrossing is genetic self-incompatibility, or, the inability of pollen to fertilize ovules from the same flower or from flowers on the same plant. There are two basic categories of incompatibility: homomorphy and heteromorphy. Homomorphic systems can be either sporophytic, in which the factors preventing pollen germination on the stigma are derived from the parent sporophyte; or gametophytic, in which the incompatibility factors are produced by the pollen grain (young microgametophyte) itself. Associated with sporophytic incompatibility are trinucleate pollen, dry stigmas and stigmatic inhibition of pollen germination. Plants with gametophytic incompatibility generally have wet stigmas (except grasses) and inhibition often occurs in the style (De Nettancourt 1977). Heteromorphic incompatibility is found among heterostylous plants and will be dealt with under that section.

TABLE 2.2 Breeding systems in the Cape flora

Sexual system	Number of species	Percentage of flora
Hermaphrodite		
monostylous	6 603	77,6
heterostylous	162	1,9
Gynomonoecious	605	7,1
Andromonoecious	334	3,9
Polygamomonoecious	1	0,01[a]
Monoecious	230	2,7
Polygamodioecious	1	0,01
Dioecious	571[b]	6,7
Total	8 507	

[a] Ocotea bullata - Phillips (1924)
[b] includes gymnosperms

Outcrossing in the Cape flora

Very little is known about the relative proportions of self-compatible and self-incompatible species in the Cape flora, particularly among the dominant woody plants. Although some Proteaceae have been examined, a more extensive survey needs to be done. Only 11 of 69 Protea species have been tested. Ten of these were self-compatible and one was self-incompatible (Horn 1962a; Wiens et al 1983). Leucospermum species are predominantly self-compatible and to a certain extent self-pollinating (Vogts 1958; Horn 1962a; Lamont 1985), but at least one species, L erubescens, may be self-incompatible. The only member of the Proteaceae examined which is self-compatible and capable of self-pollination is Serruria florida (Horn 1962a). Other woody plants that have been tested include a self-compatible Muraltia species (Levyns 1954) and the self-incompatible Plumbago capensis (Fryxell 1957).

Among geophytes, Agapanthus (Alliaceae) (Leighton 1965) and most members of the Iridaceae subfamily Iridoideae are predominantly self-incompatible (eg Homeria, Galaxia and Moraea - Goldblatt 1976, 1981, 1984a), however, members of subfamily Ixioideae (eg Hesperantha, Sparaxis, Ixia and Watsonia) are predominantly self-compatible (Goldblatt 1984b; Horn 1962b). Also self-compatible as well as autogamous are two south-western Cape orchid species, Monodenia micrantha and Amphigena tenuis (Schelpe 1970). Other monocots that have been reported to be self-incompatible in the Cape flora are Gasteria, Aloe and Haworthia (Asphodelaceae) (East 1940; Bayer 1982).

Of greater interest than the presence or absence of self-incompatibility in scattered genera and species in the Cape flora would be information on the extent of obligate outcrossing at the community level. The current absence of such information severely handicaps efforts to understand the reproductive dynamics of communities in the fynbos biome, particularly the question as to the importance of pollinators.

Few studies anywhere have addressed the importance of outcrossing at the community level. With two exceptions (Moldenke 1975; Simpson 1977), all have been in tropical forests (Bawa 1974; Ruiz and Arroyo 1978; Sobrevila and Arroyo 1982; Bawa et al 1985; Bullock 1985). Despite the high incidence of dioecism in tropical forests, approximately 70% of the obligate outcrossing trees, with one exception, are self-incompatible hermaphrodites. Only the cloud forest in Venezuela had a larger proportion of dioecious species (54%) than self-incompatible hermaphrodites (Sobrevila and Arroyo 1982).

Simpson (1977) found obligate outcrossing rates of 85% and 54% among desert scrub perennials in Arizona (USA) and Catamarca (Argentina) respectively, while Moldenke (1975) examined plant communities along an elevational transect in central California and found obligate outcrossing rates among the scrub communities of 56%, 51% and 39% at low (33 to 105 m), mid (1 500 to 1 825 m) and high (3 333 to 3 500 m) elevations respectively.

Although self-incompatibility and dioecism appear to be equivalent outcrossing mechanisms (East 1940), the frequency of self-incompatibility breakdowns within predominantly self-incompatible species (De Nettancourt 1977) may be much greater than corresponding breakdowns among dioecious species (but cf Baker and Cox 1984). Outcrossing may be less strictly enforced in self-incompatibility systems, than in dioecism.

DIOECISM

Until relatively recently, the main force behind the evolution of dioecism (male and female organs borne on separate plants) has been assumed to be selection for outcrossing (Darwin 1877; Baker 1959, 1967; references in Bawa 1980). As a result of breeding systems surveys, especially in the tropics (Bawa 1974; Bawa and Opler 1975; Ruiz and Arroyo 1978; Sobrevila and Arroyo 1982; Bullock 1985), the dioecious habit is now recognized to be much more common than surveys from temperate areas previously suggested (cf Table 2.3). This is particularly evident among tropical trees, where up to 27% may be dioecious (Bawa et al 1985). Hermaphrodite species, however, greatly outnumber dioecious species even in the tropics (Bawa 1974; Croat 1979; Sobrevila and Arroyo 1982; Bullock 1985; Bawa et al 1985).

TABLE 2.3 Incidence of dioecy among various floras

Flora	Per cent dioecious	Total species	Author
Mediterranean regions			
California	2,8[d]	4 652	Fox 1985
Australia, South Australia	3,9	2 102	Parsons 1958
Australia, S W of W Australia	4,4	3 886	McComb 1966
South Africa, Cape flora	6,6[c]	8 497	
Islands - temperate			
British Isles	4,3[a]	1 377	Kay and Stevens 1986
New Zealand	12-13[b]	1 830	Godley 1979
Islands - tropical			
Puerto Rico, Virgin Islands	6,1	2 307	Flores and Schemske 1984
Panama, Barro Colorado Island	9,0[b]	1 212	Croat 1979
Hawaii	27,7	1 488	Carlquist 1974
Mainland - tropics			
India	6,7[b]	13 988	Roy 1974
Mexico, Chamela	12,3[b]	708	Bullock 1985
Mainland - temperate			
North and South Carolina	3,7[b]	2 717	Conn et al 1980
Alaska	3,9[d]	1 343	Fox 1985
North-east USA	5,4[e]	2 450	Fox 1985
Alaska Arctic Slope	5,8	367	Fox 1985

[a] 4,4% if gymnosperms included
[b] excluding gymnosperms
[c] 6,7% if gymnosperms included
[d] includes introduced species
[e] excluding monocotyledons

Three main ecological correlates of the dioecious habit have been identified, primarily as a result of breeding system surveys. These are:

- pollination by small generalist insects (Bawa 1980; Beach 1981; Bawa and Beach 1981; Sobrevila and Arroyo 1982; Fox 1985);
- fleshy animal dispersed fruits (Bawa 1980, 1982a; Givnish 1980, 1982, but see Fox 1985; Herrera 1982); and

- woody habit (Bawa and Opler 1975; Bawa 1980; Sobrevila and Arroyo 1982; Bawa et al 1985; Fox 1985).

These correlates have led to ecological hypotheses for the evolution of dioecism (Willson 1979, 1982; Bawa 1980, 1982a; Beach 1981; Bawa and Beach 1981; Givnish 1980; cf Baker 1984), but they do not entirely eliminate outcrossing as a selective factor. They simply suggest that other factors may be as, or more, important.

Controversy exists as to whether proponents of ecological hypotheses for the evolution of dioecism have understated or overstated the importance of outcrossing (Thomson and Barrett 1981; Bawa 1982; Givnish 1982; Willson 1982). Correlations between self-compatibility and dioecism in taxonomically related groups and in island floras form the basis of the argument (Baker 1959, 1967; Baker and Cox 1984).

Baker and Cox (1984) suggest that the high incidence of dioecism in island floras is probably due to several factors including autochthonous evolution from self-compatible island colonists, establishment of dioecious species from multiple propagules and "leaky dioecism" among dioecious colonists. They also showed that the incidence of dioecism on islands was no different from comparable mainland areas at similar latitudes although there was a correlation between dioecism and both island height and proximity to the equator.

In small populations dioecy is perhaps more efficient at enforcing outbreeding than gametophytic self-incompatibility and may explain the evolution of dioecism from small populations of self-incompatible species. (Anderson and Stebbins 1984).

Dioecism in the Cape flora

Approximately 6,6% (564 species) of the flowering plants in the Cape flora are dioecious, a figure higher than for any other mainland temperate flora (Table 2.3). Particularly noteworthy is the high percentage relative to other Mediterranean type floras (eg California and south-western Western Australia). In the Cape flora, 18,4% of the angiosperm families and seven per cent of the angiosperm genera contain dioecious species, while two of the three native gymnosperm genera and families contain dioecious species (Table 2.4).

An analysis of those families and genera containing dioecious species in the Cape flora reveals a disproportionate representation of species belonging to the Proteaceae and Restionaceae (Table 2.4). These two families together comprise 69% (394 species) of the dioecious species in the Cape.

Only two of the fourteen genera of Proteaceae (Leucadendron and Aulax) contain dioecious species and both of these are endemic to southern Africa. Aulax contains three species, while Leucadendron, with 80 species, accounts for 14% of all dioecious taxa in the Cape flora. The Restionaceae are the seventh largest family in the Cape Region and account for about half (54,4%) of all the dioecious species in the flora. It is doubtful that dioecism originated among the Cape Restionaceae, since Australian Restionaceae, from which the Cape members appear to be derived (Cutler 1972; Raven and Axelrod 1974; Dahlgren et al 1985), are mostly dioecious. Even less is known about the origins of Leucadendron (see

TABLE 2.4 Dioecious families and genera in the Cape flora

Family	Genus	Number of species	Habit	Flower size	Pollination agent	Dispersal
DICOTYLEDONS						
Anacardiaceae	Laurophyllus	1	woody	small	insect	non-fleshy
	Loxostylis	1	woody	small	insect	fleshy
	Rhus	25	woody	small	insect	fleshy
Apiaceae	Arctopus	3	herbaceous	small	insect	fleshy
Asteraceae	Brachylaena	4	woody	small	insect	non-fleshy
	Tarchonanthus	1	woody	small	insect	non-fleshy
Aquifoliaceae	Ilex	1	woody	small	insect	fleshy
Balanophoraceae	Sarcophyte	1	herbaceous	small	insect	fleshy
Cucurbitaceae	Coccinia	1	herbaceous	large	insect	fleshy
	Kedrostis[1]	1	herbaceous	small	insect	fleshy
	Lagenaria	1	herbaceous	large	insect	fleshy
	Zehneria	1	herbaceous	small	insect	fleshy
Euphorbiaceae	Acalypha[1]	1	1(w) 5(h)	small	wind	non-fleshy
	Adenocline[1]	6	woody	small	wind	non-fleshy
	Clutia	17	woody	small	insect	non-fleshy
	Euphorbia[1]	28*	17(w)11(h)	small	insect	non-fleshy
	Hyaenanche	1	woody	small	insect	non-fleshy
	Lachnostylis	2	woody	small to large	insect	non-fleshy
Ebenaceae	Diospyros	7	woody	small	insect	fleshy
	Euclea	10	woody	small	insect	fleshy
Flatcourtiaceae	Dovyalis	2	woody	small	insect	fleshy
	Kiggelaria	1	woody	small to large	insect	fleshy
	Trimeria	2	woody	small	insect	non-fleshy
Menispermaceae	Antizoma	1	woody	small	insect	fleshy
	Cissampelos	2	woody	small	insect	fleshy
Montiniaceae	Montinia	1	woody	small	insect	non-fleshy
Myricaceae	Myrica	6	woody	small	wind	fleshy
Myrsinaceae	Myrsine	2	woody	small	insect	fleshy
Myrtaceae	Eugenia	1	woody	large	insect	fleshy
Ptaeroxylaceae	Ptaeroxylon	1	woody	small	insect	non-fleshy
Polygonaceae	Rumex	1	herbaceous	small	wind	non-fleshy
Proteaceae	Leucadendron	80	woody	small	insect/wind	non-fleshy
	Aulax	3	woody	small	insect	non-fleshy
Rafflesiaceae	Cytinus	2	herbaceous	small	insect	non-fleshy
Rubiaceae	Anthospermum	6	woody	small	wind	non-fleshy
	Nenax	7	woody	small	wind	non-fleshy
	Galium	1	herbaceous	small	insect	non-fleshy
Salicaceae	Salix	2	woody	small	insect	non-fleshy
Salvadoraceae	Azima	1	woody	small	wind	non-fleshy
Santalaceae	Thesidium	7	6(w) 1(h)	small	wind	non-fleshy
Sapindaceae	Dondonaea	1	woody	small	insect	non-fleshy
	Papoea	1	woody	small	insect	fleshy
Viscaceae	Viscum[1]	2	woody	small	insect	fleshy
TOTALS 24 Families	43 Genera	246 Species	224 woody 22 herbs		200 insect 46 wind	176 n-fleshy 70 fleshy

TABLE 2.4 (continued)

Family	Genus	Number of species	Habit	Flower size	Pollination agent	Dispersal
MONOCOTYLEDONS						
Cyperaceae	Scirpus	1	herbaceous	small	wind	non-fleshy
Dioscoreaceae	Dioscorea	5	herbaceous	small	insect	non-fleshy
Hydrocharitaceae	Lagarosiphon	1	herbaceous	small	water	non-fleshy
Najadaceae	Najas	1	herbaceous	small	water	non-fleshy
Restionaceae	Anthochortus	6	herbaceous	small	wind	non-fleshy
	Askidiosperma	10	herbaceous	small	wind	non-fleshy
	Calopsis	23	herbaceous	small	wind	non-fleshy
	Cannomois	6	herbaceous	small	wind	non-fleshy
	Ceratocaryum	5	herbaceous	small	wind	non-fleshy
	Chondropetalum	12	herbaceous	small	wind	non-fleshy
	Dovea	1	herbaceous	small	wind	non-fleshy
	Elegia	32	herbaceous	small	wind	non-fleshy
	Hydrophilos	1	herbaceous	small	wind	non-fleshy
	Hypodiscus	16	herbaceous	small	wind	non-fleshy
	Ischryolepis	46	herbaceous	small	wind	non-fleshy
	Mastersiella	3	herbaceous	small	wind	non-fleshy
	Nevillea	2	herbaceous	small	wind	non-fleshy
	Platycaulos	8	herbaceous	small	wind	non-fleshy
	Restio	85	herbaceous	small	wind	non-fleshy
	Rhodocoma	3	herbaceous	small	wind	non-fleshy
	Staberoha	9	herbaceous	small	wind	non-fleshy
	Thamnochortus	31	herbaceous	small	wind	non-fleshy
	Willdenowia	11	herbaceous	small	wind	non-fleshy
TOTALS 5 Families	23 Genera	318 Species	318 herbs		311 wind 2 water 5 insect	318 n-fleshy

GYMNOSPERMS						
Podocarpaceae	Podocarpus	3	woody		wind	fleshy
Zamiacea	Encephalartus	4	woody		insect	fleshy
TOTALS 2 Families	2 Genera	7 Species	2 woody		1 wind 1 insect	2 fleshy

[1] Genera also containing monoecious species

SUMMARY INFORMATION

Total dioecious taxa of flowering plants = 564

Per cent dioecious = 564/8 507 = 6,6

below), but irrespective of where or how dioecism arose in these two groups, the extensive diversification that they have undergone has not apparently been restricted by the dioecious breeding system.

Leucadendron and the Restionaceae have diversified within the confines of quite different pollination systems. Most (87,5%) Leucadendron species are adapted to pollination by small generalist insects, although approximately ten species are wind pollinated and presumed to be derived from entomophilous ancestors (Williams 1972). The primarily entomophilous nature of Leucadendron in contrast to the Restionaceae, which are all wind pollinated, suggests a tropical rather than temperate origin for the genus, since the evolution of dioecism in the tropics is almost exclusively associated with species pollinated by small generalist insects (Bawa 1980). The Restionaceae, in contrast, probably originated in a more open subtropical or temperate environment.

The incidence of wind pollination in the Cape flora is about 12%. However, the incidence of wind pollination among dioecious species is over five times higher at 63%. This is due primarily to the success of the Restionaceae which constitute 91% of all wind pollinated species (Koutnik this volume). Wind pollination is also dominant among dioecious taxa in the arid western region of the United States of America (Freeman et al 1980), but in tropical forests, as well as temperate floras of New Zealand and the British Isles, the largest proportion of dioecious species are insect pollinated (McComb 1966; Bawa 1980).

Among dioecious species, the incidence of woodiness is about 37%, which is significantly lower (P less than 0,001) than the incidence of 50% which one finds in the flora as a whole. This is due to the dominance of nonwoody Restionaceae among dioecious species. If one removes the Restionaceae from consideration, the incidence of woodiness becomes 83% which is significantly greater (P greater than 0,001) than the incidence in the entire flora.

Although the fruits of dioecious species in the Cape flora, both in terms of genera and total species, are predominantly nonfleshy, the incidence of fleshiness is greater among dioecious species than among the flora as a whole. Thus, the pattern that one would expect based on Givnish's (1980, 1982) arguments, holds for the Cape flora despite the dominance of dioecious species by dry-fruited Restionaceae.

Despite the presence of dry fruits, the seeds of many dioecious species in the Cape are apparently animal dispersed. Based on Bond and Slingsby (1983) and Linder (1984), it is estimated that 41% (230 species) of the dioecious angiosperms produce elaiosomes and are dispersed by ants. This is more than twice the incidence of 15,3% (1 300 species that one finds in the flora as a whole. The Restionaceae comprise about 75% (172 species) of the dioecious species that produce elaisomes. However, even after exclusion of the Restionaceae from the analysis, the incidence of seeds with eliasomes among dioecous species is still significantly higher (P greater than 0,05) than it is for the flora as a whole. Seeds bearing eliasomes, although animal dispersed, should not be considered in the same category with fleshy endozoochorous, because of the relatively small energy expenditure for an elaisome relative to a fleshy fruit (cf Givinish 1980, 1982).

MONOECISM

Monoecism (male and female flowers on the same plant) has traditionally been viewed as an outbreeding mechanism (Darwin 1877), but sexual selection theory has been invoked as an important or even overriding factor in its evolution, as it has been for other types of sexual expression (Willson 1979; Bawa and Beach 1981; Bawa et al 1982). Thomson and Barrett (1981) cling to a predominantly outcrossing view of monoecism, because of its association with self-compatibility (East 1940; Godley 1955). Their fairly long list of exceptions, to which Mabea (Euphorbiaceae) may be added (Steiner 1983), seems sufficient to cast doubt on the universality of the outcrossing view. Bawa et al (1982) suggest that any outcrossing advantage of monoecism is probably due to the greater temporal, rather than spatial, separation that unisexual flowers allow. Spatial separation of the sexes may be a consequence of selection to reduce interference between pollen and stigmas in the same flower (Lloyd and Yates 1982), but this alone is more liable to be the result of sexual selection than selection for outcrossing, since spatial separation should do little to reduce geitonogamy.

The separation of male and female organs into separate flowers is also consistent with sexual selection theory, since it allows greater specialization of sexual functions. Sexual selection theory predicts competition between males for access to ovules. This can be divided into two components: prepollination competition for access to conspecific stigmas and postpollination competition within the stigma, style and ovary for access to ovules (Stephenson and Bertin 1983). Sexual selection arguments for monoecism have been used generally in relation to prepollination factors which increase the number of different stigmas that pollen from a given individual reaches. These factors include the number of male flowers, their arrangement, and the timing of pollen release, and the duration of the male phase (Willson 1979; Bawa et al 1982). In most monoecious species, male flowers are produced in excess of female flowers, the predicted outcome of male competition (Willson 1979; Stephenson and Bertin 1983). One might also expect the male phase to last longer than the female phase as was found by Bawa et al (1982) for Cnidoscolus, however, in other Euphorbiaceae the female phase is longer than the male phase (Armbruster and Webster 1979; Steiner 1983).

Although there are obviously selective advantages to a separation of the sexes as exhibited by monoecious species, the numerous parallel reversions to a single floral unit (pseudanthium) in a unisexual family such as the Euphorbiaceae (eg Pedilanthus, Euphorbia, Dalechampia and Mabea), reaffirms the advantages of cosexuality for the majority of angiosperms (cf Lloyd 1982).

Monoecism in the Cape flora

The incidence of monoecism in the Cape flora (2,7%) is much lower than in other floras both temperate and tropical with the exception of south-west Western Australia (Table 2.5). Unfortunately values for other mediterranean climates have not been published, making it difficult to judge whether a low incidence of monoecism is peculiar to this type of climate.

TABLE 2.5 Incidence of monoecy among various floras

Flora	Per cent monoecious	Total species	Reference
Mediterranean regions			
Cape flora	2,7	8 497	
SW of W Australia	2,6	3 886	McComb 1966
South Australia	5,8	2 101	Parsons 1958
Islands			
British Isles	8,7	1 594	McComb 1966
New Zealand	9,0	1 830	Godley 1979
Puerto Rico and Virgin Islands	10,5	2 037	Flores and Schemske 1984
Panama, Barro Colorado Island	11,0	1 212	Croat 1979
Mainland			
Mexico, Chamela	13,0	708	Bullock 1985
India	13,9	13 988	Roy 1974

Although the number of angiosperm families with monoecious species in the Cape flora is the same as the number with dioecious species (ie 28), the number of monoecious genera and species is considerably less (55 and 227 versus 65 and 558 respectively - cf Table 2.6).

Cliffortia with 106 species in the Cape flora, has been reported to have both monoecious and dioecious species (Weimark 1934). Because the genus is so poorly known, however, it is difficult to accurately determine the proportion of each type. Weimark (1934, 1946, 1948, 1959) cited at least one monoecious specimen for 50 (40%) of the 106 species. Of the remaining species, 26 were represented by male and female specimens, 25 were represented by only one sex, one was andromonoecious (Weimark 1948) and four had no sexual system information provided. Sixty-nine per cent of the species for which both male and female, but not monoecious specimens were cited, were represented by fewer than 10 collections, while of the 25 species known from only one sex, 17 were known from only female flowers and eight from only male flowers. For this last group, not more than three specimens were cited by Weimark (1934).

Cliffortia species, being wind pollinated (Koutnik this volume), are probably strongly dichogamous (Faegri and van der Pijl 1979). It is likely, therefore, that in most cases flowers of only one sex are present on an individual or group of individuals at a given time. This could very easily explain the patterns noted above, as there may be only a very short period in which male and female stages overlap on any one individual. This would explain why most collections are either male or female but not both. Variation in the degree to which the stages overlap could also explain the variation among species in the number of monoecious collections. I prefer to take a conservative view and therefore consider the entire genus, with the exception of C hermaphroditica, to be monoecious. If, however, the 51 species for which monoecious collections are unknown prove to be dioecious, the overall percentage of dioecious species in the Cape Flora would increase to 7,3%.

ANDROMONOECISM

Although the production of hermaphrodite and male flowers on the same plant (andromonoecism) has often been viewed as an outbreeding device (eg Heithaus et al 1974), many andromonoecious species have other outbreeding devices such as self-incompatibility (Ruiz and Arroyo 1978) or protandrous dichogamy (Webb 1981). Alternative hypotheses to account for the evolution of andromonoecism generally involve resource allocation, pollinator attraction and/or male fitness arguments. Male flowers represent a means of increasing the floral display above levels that, due to resource limitations, could be achieved by hermaphrodite flowers alone. Larger floral displays generally result in increased pollinator visitation rates which in turn increase fitness, particularly the male component (Willson and Price 1977; Lloyd 1979; Primack and Lloyd 1980; Webb 1981; Solomon 1985).

Most hermaphroditic plants produce many more flowers than ever set fruit (Stephenson 1980, 1981). Thus many bisexual flowers function solely as pollen donors or males. Primack and Lloyd (1980) have shown that a hermaphroditic species can have an effective gender (contribution of ovules and pollen to the next generation) similar to that of an andromonoecious species. The major difference between hermaphrodite and andromonoecious species, however, is that hermaphrodite flowers that function as males still retain the potential to act as females. This may be important for progeny selection by the pistil through pollen-stigma or pollen tube style interactions or via embryo or fruit abortion (Bawa and Beach 1981; Stephenson and Bertin 1983).

Production of male flowers may also be an important means of increasing male fecundity by boosting the pollen/ovule ratio (Webb 1981; Solomon 1985) or by allowing spatial or temporal strategies or pollen dispersal (Primack and Lloyd 1980; Lloyd and Yates 1982; Solomon 1985).

Andromonoecism in the Cape flora

The number of andromonoecious species in the Cape flora is 334 (3,9%) and most (60%) are either grasses or sedges (Table 2.7). Since these species are all wind pollinated, the production of male flowers must be the result of selection for increased male fecundity and/or optimal resource allocation, rather than enhancement of the floraldisplay.

Among the 11 genera in seven dicotyledonous families with andromonoecious species, only Tetragonia (Adamson 1955) and Agathosma contain appreciable numbers with 29 and 65 respectively. Approximately half of all Agathosma species are andromonoecious, a condition associated with a trend towards

TABLE 2.6 Monoecious families and genera in the Cape flora

Family	Genus	Number of species
DICOTYLEDONS		
Achariaceae	Acharia	1
	Ceratiosicyos	1
Amaranthaceae	Amaranthus	2
Anacardiaceae	Heeria	1
Apiaceae	Annesorrhiza	5
Asteraceae	Cadiscus	1
	Euryops	2
	Hertia	2
	Phaenocoma	1
	Polyarrhena	3
	Relhania	4
Balanophoraceae	Mystropetalon	2
Ceratophyllaceae	Ceratophyllum	1
Chenopodiaceae	Atriplex	2
	Manochlamys	1
Cucurbitaceae	Citrullus	1
	Kedrostis	2
Euphorbiaceae	Acalypha	3
	Adenocline	1
	Andrachne	1
	Ctenomeria	1
	Dalechampia	1
	Euphorbia	18
	Excoecaria	1
	Jatropha	1
	Leidesia	2
	Phyllanthus	3
	Seidelia	1
Hamamelidaceae	Trichocladus	1
Haloragidaceae	Laurembergia	1
	Myriophyllum	1
Moraceae	Ficus	4

Family	Genus	Number of species
DICOTYLEDONS (continued)		
Myricaceae	Myrica	7
Polygonaceae	Emex	1
	Rumex	2
Rosaceae	Cliffortia	105
Rutaceae	Vepris	1
Sapindaceae	Allophylus	1
Ulmaceae	Celtis	1
Urticaceae	Australina	5
	Forsskaolea	1
	Laportea	3
Viscaceae	Viscum	4
21	43	203

MONOCOTYLEDONS		
Araceae	Zantedeschia	1
Cyperaceae	Chrysithrix	3
	Carex	5
	Schoenoxiphium	5
Hydrocharitaceae	Halophila	1
Lemnaceae	Lemna	2
	Spirodela	1
	Wolffia	1
Typhaceae	Typha	1
Zannichelliaceae	Zannichellia	2
	Althenia	1
Zosteraceae	Zostera	1
7	12	24

GYMNOSPERMS		
Cupressaceae	Widdringtonia	3

SUMMARY INFORMATION
Total monoecious taxa (flowering plants only) = 227
Per cent of flora that is monoecious = 2,7

TABLE 2.7 Andromonoecious families and genera in the Cape flora

Family	Genus	Number of species
DICOTYLEDONS		
Aizoaceae	Tetragonia	29
Apiaceae	Capnophyllum	1
	Conium	2
	Hermas	9
	Sanicula	1
Chenopodiaceae	Suaeda	2
Fabaceae	Acacia	2
Rutaceae	Agathosma	c 65
	Empleurum	2
Sterculiaceae	Sterculia	1
Rosaceae	Cliffortia	1
7	11	115
MONOCOTYLEDONS		
Cyperaceae	Bulbostylis	2
	Carpha	2
	Costularia	1
	Cyperus	11
	Eleocharis	2
	Epischoenus	8
	Ficinia	57
	Fimbristylis	3
	Fuirena	3
	Hellmuthia	1
	Isolepis	18
	Juncellus	1
	Kyllinga	3
MONOCOTYLEDONS (continued)		
	Macrochaetium	2
	Mariscus	4
	Neesenbeckia	1
	Pycreus	3
	Rhynchospora	1
	Schoenus	1
	Scirpus	20
	Tetraria	41
Poaceae	Andropogon	2
	Anthoxanthum	2
	Cymbopogon	2
	Diheteropogon	1
	Enneapogon	2
	Eustachys	1
	Harpochloa	1
	Helictotrichon	6
	Holcus	1
	Pennisetum	2
	Phragmites	1
	Plagiochloa	6
	Rhynchelytrum	2
	Setaria	2
	Stenotaphrum	2
	Trachypogon	1
	Tristachya	1
2	38	220

SUMMARY INFORMATION
Total andromonoecious taxa = 334
Andromonoecism in the flora = 3,9 per cent

more compact capitate inflorescences (A Bean personal communication). Andromonoecism is a common feature of the Apiaceae (Webb 1981), but due to the relatively small size of this family in the Cape flora, its contribution (13 species in four genera) is relatively minor. Some Asteraceae may also be andromonoecious (D Wiens personal communication). In Gorteria and most Gorteriidae central disc flowers are functionally male, outer disc flowers are hermaphrodite and ray flowers are sterile (D Wiens personal communication). Hermaphroditic Proteaceae genera have been tentatively considered as functionally andromonoecious by Rebelo and Rourke (1986) and Wiens et al (1983), due to the low seed set observed (0 to 50%).

GYNOMONOECISM

Gynomonoecism (the presence of female and bisexual flowers on the same plants) is a relatively rare phenomenon outside of the Asteraceae and little is known about its evolution and adaptive significance. However, Bawa and Beach (1981) suggest that it should be viewed as a pollination rather than an outbreeding system.

In the Asteraceae, gynomonoecism is the result of sterilization of the stamens of the ray florets, a possible consequence of selection for increased pollinator attraction (cf Stuessy 1986). This selective pressure may have required a shift in resource allocation from stamens and pollen to showy corollas (Bawa and Beach 1981). Lloyd (1979) suggests that since the unit of attraction in the Asteraceae is the whole head or capitulum and not the individual floret, an increase in pollen-producing flowers (ie hermaphrodites) would have a relatively small impact on overall male fitness.

Gynomonoecism in the Cape flora is restricted almost exclusively to the Asteraceae which contain 98% of all gynomonoecious taxa (Table 2.8). The Asteraceae, with 986 species, is the largest family in the Cape flora (Bond and Goldblatt 1984) and since the majority (61%) of its members are gynomonoecious, it is not surprising to find a relatively large percentage of species (7,1) in the flora that are gynomonoecious.

HETEROSTYLY

Heterostyly is a condition in which plants within a population have one of two or three distinct floral forms. In distyly, the most common type of heterostyly, there are two distinct forms or morphs:

- a long styled form with anthers positioned below the stigma; and

- a short-styled form with anthers positioned above the stigma.

The stigma position of each morph corresponds to the anther position of the other morph (Figure 2.1). There are often differences in pollen grain number and size (smaller, but more numerous in long-styled flowers) and occasionally differences in pollen grain shape and sculpturing, stigma size and shape, size of stigmatic papillae and corolla size and shape (Ganders 1979).

These floral dimorphisms are genetically linked to a diallelic sporophytic self-incompatibility system. This is more limiting than the typical

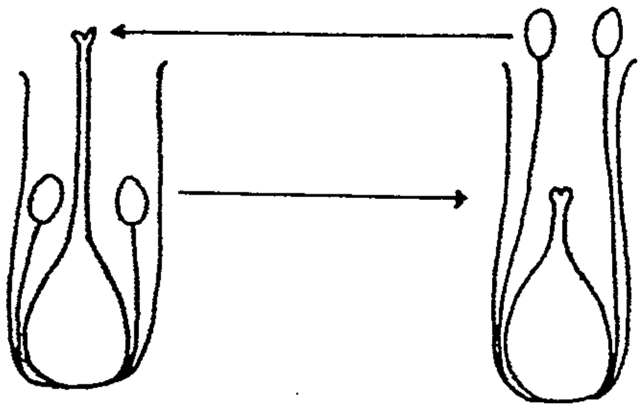


FIGURE 2.1 Distyly, arrows indicate direction of compatible crosses.

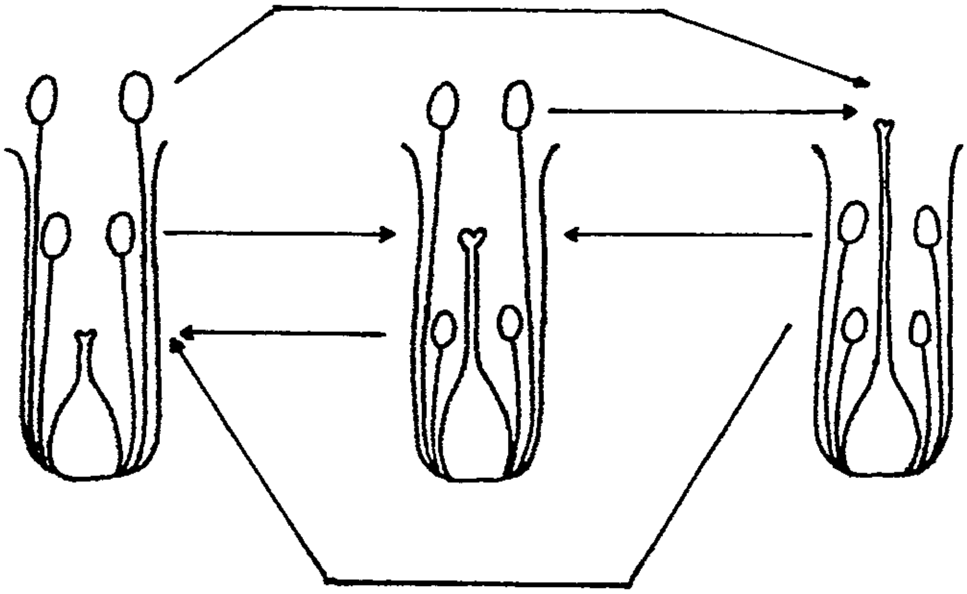


FIGURE 2.2 Tristyly, arrows indicate direction of compatible crosses.

multiallelic incompatibility system found in homomorphic angiosperms because only half of the individuals in a population are cross compatible. In distylous species, successful pollination only occurs when pollen from a different floral morph lands on the stigma (ie pollen from long-styled flowers on flowers with short styles and vice versa). In the diallelic self-incompatibiilty system, one morph (usually the short-styled form) is heterozygous while the other morph is homozygous recessive (usually the long-styled form). Compatible crosses, therefore, result in a population in which the two morphs occur in equal proportions (ie 1:1).

The presence of heterostyly in many unrelated groups indicates that it has arisen independently numerous times during the course of angiosperm evolution (Ganders 1979). This explains much of the variation one finds in secondary characters associated with heterostyly, but despite these differences, the starting point for the evolution of heterostyly is considered to have been the same in all cases (Ganders 1979).

In the Plumbaginaceae the first stage in the evolution of heterostyly was shown to be development of the diallelic sporophytic self-incompatibility system (Baker 1966; Charlesworth and Charlesworth 1979). Opinion on how the diallelic system became established varies. It may have originated from self-compatible ancestors faced with strong selection for outcrossing (Vuilleumier 1967; Ganders 1979), or through loss of alleles from a single locus multiallelic incompatibility system via genetic drift (Crowe 1964; Wyatt 1983).

After establishment of sporophytic diallelic self-incompatibility, floral polymorphisms were presumably selected in order to increase the chance of disassortative pollination (ie pollination between compatible morphs) (Ganders 1979). The efficacy of heterostyly in this respect was first proposed by Darwin (1877) and although there are difficulties in testing his hypothesis, evidence for disassortative mating among heterostylous species does exist (Ganders 1979; Nicholls 1986).

Tristyly is a more complicated form of heteromorphy in which there are three sets of stamen lengths and three style lengths. Plants have flowers with:

- short styles and anthers borne at two levels (intermediate and high) above the stigma;

- flowers with medium length styles and a set of anthers above (high) and below (low) the stigma; or

- flowers with long styles and anthers borne at two levels below the stigma (low and intermediate) (Figure 2.2).

Pollen grain size often varies with anther position, with anthers from the shortest stamens producing the smallest pollen grains, intermediate pollen grains from mid-stamens and large pollen grains from the longest stamens (Darwin 1877; Ornduff 1974; Barrett 1977, 1978; Ganders 1979; Price and Barrett 1984). In some tristylous plants, however, pollen grains from the intermediate level anthers can be intermediate in size or similar to pollen grains from upper or lower anthers (Ganders 1979). Successful pollination occurs only with pollen from anthers that are at the same level as the stigma being pollinated (cf Figure 2.2). The genetics of the self-incompatibilty system is more complicated for tristylous plants

TABLE 2.8 Gynomonoecious families and genera in the Cape flora

Family	Genus	Number of species
DICOTYLEDONS		
Asteraceae	Alciope	3
	Amellus	6
	Amphiglossa	2
	Anaxeton	9
	Arctotus	29
	Artemesia	1
	Aster	3
	Athrixia	3
	Atrichantha	2
	Bryomorphe	1
	Chrysanthemoides	2
	Cineraria	11
	Conyza	3
	Cotula	20
	Dimorphotheca	1
	Disparago	7
	Dolichothrix	1
	Dymondia	1
	Edmondia	3
	Erigeron	1
	Eriocephaulus	10
	Euryops	44
	Felicia	55
	Gerbera	9
	Gibbaria	2
	Gnaphalium	5
	Gymnodiscus	1
	Gymnostephium	7
	Haplocarpha	3
	Helichrysum	76
	Heterolepis	3
	Hippia	7
	Ifloga	9
	Lasiopogon	1
	Lasiospermum	2
	Leucoptera	1
	Leysera	3
DICOTYLEDONS		
Asteraceae (continued)	Mairea	14
	Matricaria	6
	Microglossa	1
	Minurothamnus	1
	Oreoleysera	1
	Osteospermum	41
	Othonna	47
	Perdicium	2
	Petalacte	3
	Phaneroglossa	1
	Phymaspermum	2
	Plecostachys	2
	Poecilolepis	2
	Polyarrhena	1
	Printzia	2
	Pseudognaphalium	1
	Relhania	18
	Rosenia	1
	Senecio	91
	Steirodiscus	4
	Stilpnogyne	1
	Troglophyton	2
	Vellereophyton	2
Chenopodiaceae	Chenolea	1
2	64	601

MONOCOTYLEDONS		
Aponogetonaceae	Aponogeton	1
Cyperaceae	Trianoptiles	3
2	2	4

SUMMARY INFORMATION
Total number of gynomonoecious taxa = 605
Per cent gynomonoecism in the flora = 7,1

since there are two alleles at each of two loci (Ganders 1979). Crosses between compatible morphs result in equal proportions of three floral morphs within a population. A model for the evolution of tristyly is presented by Charlesworth (1979).

Tristyly is relatively rare, known from only three of the approximately 23 families containing heterostylous species (Vuilleumier 1967), but it is the most prevalent form of heterostyly in southern Africa. This is due to Oxalis, the sixth largest genus (126 species) within the Cape flora (Bond and Goldblatt 1984). All Oxalis species are considered to be morphologically tristylous (Marloth 1925; Salter 1944), however, the physiological control of outbreeding (ie self-compatibilty) has broken down in some species even to the point of autogamy (Ornduff 1974).

Heterostyly in the Cape flora

There are five, possibly six families, besides Oxalidaceae, in the Cape flora that are heterostylous (Ornduff 1974). These include:

- Gentianaceae (Sebaea, Villarsia and Nymphoides);
- Iridaceae (Nivenia);
- Oleaceae (Jasminum);
- Plumbaginaceae (Plumbago, Limonium);
- Rubiaceae (Oldenlandia); and possibly
- Boraginaceae (Anchusia and Cordia).

In most of the above cases, only a portion of the species in the genus are heterostylous and only in the Iridaceae is heterostyly unique to the Cape for the family. The total number of heterostylous species in the Cape flora is about 161 or 1,9%. Seventy-seven per cent of these are tristylous (Oxalis species) while the rest are distylous. Comparable data from temperate areas are unavailable except for New Zealand where there are no confirmed examples of heterostyly (Godley 1979), but in a tropical deciduous forest in Mexico the proportion was three per cent (Bullock 1985). In a survey of 333 trees in a tropical rainforest in Costa Rica, Bawa et al (1985) found that 3,6% were heterostylous.

Despite Ornduff's (1974, 1983, 1985) studies of heterostyly in South Africa, there is still much to be done. No observations of pollinators nor assessments of pollen flow have been made on any heterostylous species in southern Africa. The genus Nivenia, currently under study (P Goldblatt personal communication), seems particularly interesting as a result of Ornduff's (1974, 1983) preliminary studies. This genus of nine species (P Goldblatt personal communication) has both homomorphic and distylous species. Within those known to be heterostylous, there is N binata which has the typical pollen dimorphism (Mulcahy 1965) and N corymbosa which does not (Ornduff 1974). The presence of self-compatibility in both homomorphic (N stokoei) and distylous species (N binata) in the same genus is quite unusual (Ornduff 1974). Ornduff (1983) has recently suggested that N corymbosa, although morphologically distylous, is functionally androdioecious.

ENANTIOMORPHY

A much rarer type of heteromorphy (known from only ten genera in five families) is enantiomorphy (enantiostyly) a situation where plants have flowers with left and right hand forms (ie flowers have the style deflected either to the right or to the left of centre. Some species have flowers with only one style orientation on a given plant, but both orientations within a population, while in other cases both types may be present within a single inflorescence (Ornduff 1974; Bowers 1975; Dulberger and Ornduff 1980; Dulberger 1981). Dulberger (1981) lists eight floral characteristics besides the style deflection that are often associated with enantiostyly. These include:

- nectarless flowers with upper feeding and lower pollinating anthers;
- poricidal anther dehiscence (pollen released by "buzz" pollination)(cf Buchmann 1983);
- pollen from pollinating anthers deposited on side or back of pollinator while pollen from feeding anthers deposited ventrally;
- curved styles and stigmas to touch the side or back of pollinators;
- minute stigmas;
- arching of anthers - upper, lower or both;
- lower anthers which function as a lever or catapult; and
- deflection of one or more stamens in the opposite direction from the style.

Enantiomorphy has been seen as:

- an outbreeding mechanism (Todd 1882; Wilson 1887; Robertson 1890; Knuth 1906; Ornduff and Dulberger 1978; Dulberger and Ornduff 1980);
- as a means for reducing pollen wastage (Dulberger and Ornduff 1980); or
- for providing easy access to the feeding anthers while preventing injury to the gynoecium that could be caused by the "buzzing"vibrations utilized by pollinating bees to extract pollen (Dulberger 1981).

Enantiomorphy in the Cape flora

There are four genera in three families in the Cape flora that contain enantiostylous species. These include:
- _Wachendorfia_ (five species) and _Dilatris corymbosa_ (Haemadoraceae);
- _Cyanella_ (two of five species) (Tecophilaeaceae); and
- _Tenicroa_ (three species) (Hyacinthaceae).

Dilatris corymbosa and _Wachendorfia_ species exhibit stylar dimorphism (Ornduff 1974; Ornduff and Dulbergher 1978), but they deviate in two respects from enantiostyly as outlined by Dulbergher (1981). They produce nectar and they do not have heteranthery or apical anther dehiscence.

Although only two of the four species of _Cyanella_ in the Cape flora (_C alba_ and _C lutea_) are enantiostylous (Dulbergher and Ornduff 1980;

Dulberghe r 1981), the other three species, *C orchidiformis*, *C pentheri* and and *C hyacinthoides*, while lacking the stigma deflection, do possess dimorphic stamens and apically dehiscent anthers.

In her revision of *Sypharissa* (now *Tenicroa*) Obermeyer (1980) noted that flowers had declinate styles, but not whether they were deflected to the right or left (ie entantiostylous). From illustrations in Mason (1972), however, it is obvious that *T filifolia* (Jacq.) Raf. and *T exuviata* (Jacq.) Speta (both as *Urginea*) are enantiostylous, with both right and left flowers opening simultaneously on the same plant. *Tenicroa nana*, occurring just outside the Cape floral region in the western Cape, has nectarless flowers, deflected styles and apically dehiscent anthers, but the stamens are not dimorphic nor are the stigmas minute (cf Snijman 1985). In this species, flowers with right and left deflected styles can be open on a given plant at the same time.

A big gap in our knowledge of enanatiostyly relates to the behaviour of pollinators, since this can strongly influence the degree of outcrossing within a population (Bowers 1975). No pollinator observations have been made on any of the South African enantiomorphic species. *Cyanella*, because it has both species with and without enantiomorphic flowers, seems particularly well suited for comparative field studies, emphasizing pollinator behaviour, to complement the observations of Dulberger and Ornduff (1980) and to provide insights into the selective factors responsible for the evolution of enantiomorphy. It would also be interesting to compare the reproductive biology of *Tenicroa* species with *Ixia scilliaris* (Iridaceae), since the flowers are superficially similar except for the style and stigmas. *Ixia scilliaris* has a three-lobed style that is included in the throat rather than the exerted and deflected style of *Tenicroa*. Pollinator observations and population studies of *Wachendorfia* are also sorely needed to determine whether enantiostyly in this case, despite its departure from the more common cases, is the result of similar selection pressures.

CLEISTOGAMY AND APOMIXIS

Cleistogamy in the Cape Flora has been reported by Fries (1909) for *Argyrolobium tomentosum* (=*A andrewsianum* (Fabaceae) and by Bolus (1896) for *Pterygodium newdigatae* (Orchidaceae)). *Pterygodium newdigatae* consists of two genetic varieties which can occur in mixed populations (Duthie 1915; Stewart et al 1982). The cleistogamous variety, (variety *cleistogamum*) would be characterized as "completely cleistogamous" within Lord's (1981) classification scheme and unlike most cleistogamous species (Lord 1981), *P* var *cleistogamum* is apomictic (Duthie 1915).

Apomixis within the Cape flora has also been reported for six grass species (Brown and Emery 1957; Brown 1958) and suggested for *Hypoxis* (Wilsenach 1967; Wilsenach and Papenfus 1967; Wilsenach and Warren 1967) and *Ledebouria* (Jessop 1970). Vegetative apomixis is found in a variety of Iridaceae including *Homeria bulbilifera*, *Watson bulbifera*, *W vivipara*, *Sparaxis bulbifera* and *Geissorhiza bolusii* (Goldblatt 1971, 1978).

CONCLUSION

Despite the absence of information on plant breeding systems in the Cape flora, a few features are already apparent. These include:

- the relatively high incidence of dioecism;
- a higher incidence of wind pollination among dioecious species than for the flora as a whole;
- a lower incidence of woodiness among dioecious species than for the flora as a whole; and
- a higher incidence of fleshy fruits among dioecious species than for the flora as a whole.

Two of the three ecological correlates of dioecism listed above (ie nonwoodiness and wind pollination) differ from trends seen in other floras where woodiness and insect pollination are associated with dioecy. This is a result of the large number of Restionaceae in the flora. If Restionaceae are excluded from consideration, both of these correlates change and dioecy becomes associated with woodiness and insect pollination. Because of this impact on breeding systems of the Cape flora, as well as on general fynbos ecology, a greater emphasis should be placed on understanding the autecology of the Restionaceae.

The genus Clifffortia is an important component of many communities in the flora, yet it is still very poorly known. Sex expression studies among species in this genus would help clarify the confusion that exists regarding monoecy and dioecy and might contribute to our understanding of the selective factors that promote the evolution of dioecism from monoecism in general. Sex ratios and dispersion patterns within natural populations of Cliffortia and other dioecious genera should be examined as well.

Reports of compatibility levels in the Cape flora are still too fragmented to indicate any trends in the extent of outbreeding. Community analyses of outbreeding levels are sorely needed in all of the communities that comprise the Cape flora, but especially in those with species rich fynbos vegetation. Until this information is obtained, the reproductive dynamics of these communities will remain a mystery that will seriously hamper efforts at enlightened management.

REFERENCES

Adamson R S 1955. The South African species of Aizoaceae. Journal of South African Botany 21, 109-154.

Adamson R S and Salter T M 1950. Flora of the Cape Peninsula. Juta, Cape Town.

Anderson G J 1979. Dioecious Solanum species of hermaphroditic origin is an example of broad convergence. Nature (London) 282, 836-838.

Anderson G J and Stebbins G L 1984. Dioecy versus gametophytic self-incompatibility: a test. American Naturalist 124, 423-428.

Armbuster R W S and Webster G L 1979. Pollination of two species of Dalecampia (Euphorbiaceae) in Mexico by euglossine bees. Biotropica 11, 278-283.

Arroyo M T K and Raven P H 1975. The evolution of subdioecy in morphologically gynodioecious species of *Fuchsia* section Encliandra (Onagraceae). Evolution 29, 500-511.

Atsatt P R and Rundel P 1982. Pollinator maintenance versus fruit production: partitioned reproductive effort in subdioecious *Fuchsia lycioides*. Annals of the Missouri Botanic Gardens 69, 199-208.

Baker H G 1959. Reproductive methods as factors in speciation in flowering plants. Cold Spring Harbor Symposium on Quantitative Biology 24, 177-191.

Baker H G 1966. The evolution, functioning and breakdown of heteromorphic incompatibility systems. I. The Plumbaginaceae. Evolution 20, 349-68.

Baker H G 1967. Support for Baker's Law as a rule. Evolution 21, 853-856.

Baker H G 1984. Some functions of dioecy in seed plants. American Naturalist 124, 149-158.

Baker H G and Cox P A 1984. Further thoughts on dioecism and oceanic islands. Annals of the Missouri Botanic Gardens 71, 244-253.

Barrett S C H 1977. The breeding system of *Pontederia rotundifolia* L., a tristylous species. The New Phytologist 78, 209-220.

Barrett S C 1978. Floral biology of the water hyacinth, *Eichornia azurea* (Sw.) Knuth. (Pontederiaceae). Aquatic Botany 5, 217-228.

Bateman A J 1948. Intrasexual selection in *Drosophila*. Heredity 2, 349-369.

Bawa K S 1974. Breeding systems of tree species in a tropical lowland community. Evolution 28, 85-92.

Bawa K S 1980. Evolution of dioecy in flowering plants. Annual Review of Ecology and Systematics 11, 15-19.

Bawa K S 1982a. Seed dispersal and the evolution of dioecism in flowering plants - A response to Herrera. Evolution 36: 1322-1325.

Bawa K S 1982b. Outcrossing and the incidence of dioecism in island floras. American Naturalist 119, 866-871.

Bawa K S and Beach J H 1981. Evolution of sexual systems in flowering plants. Annals of the Missouri Botanic Gardens 68, 254-274.

Bawa K S and Opler P A 1975. Dioecism in tropical forest trees. Evolution 29, 167-179.

Bawa K S, Webb C J and Tuttle A F 1982. The adaptive significance of monoecism in *Cnidoscolus urens* (L.) Arthur (Euphorbiaceae). Botanical Journal of the Linnean Society 85, 213-223.

Bawa K S, Opler P A, Perry D R and Beach J H 1985. Reproductive biology of tropical lowland rain forest trees. I. Sexual systems and incompatibility mechanisms. American Journal of Botany 72, 331-345.

Bayer M B 1982. The New *Haworthia* Handbook. National Botanic Gardens of South Africa, Kirstenbosch.

Beach J H 1981. Pollinator foraging and the evolution of dioecy. American Naturalist 118, 572-577.

Blunt W 1971. The compleat naturalist. Collins, London.

Bolus H 1896. Orchids of South Africa. Volume 1, Part II, Table 99.

Bond P and Goldblatt P 1984. Plants of the Cape flora: a descriptive catalogue. Journal of South African Botany, Supplementary Volume 13.

Bond W J and Slingsby P 1983. Seed dispersal by ants in shrublands of the Cape Province and its evolutionary implications. South African Journal of Science 79, 231-233.

Bowers K A 1975. The pollination ecology of *Solanum rostratum* (Solanaceae). American Journal ofBotany 62, 633-638.

Brown W V 1958. Apomixis as related to geographical distribution in the Panicoid grass tribes. Journal of South African Botany 24, 191-200.

Brown W V and Emery H P 1957. Some South African apomictic grasses. Journal of South African Botany 23, 123-125.

Buchmann S L 1983. Buzz pollination in angiosperms. In: Jones C E and Little R J (editors) Handbook of experimental pollination biology. Van Nostrand-Reinhold, New York. pp 73-113.

Bullock S H 1985. Breeding systems in the flora of a tropical deciduous forest in Mexico. Biotropica 17, 287-301.

Carlquist S 1974. Island biology. Columbia University Press, New York.

Charlesworth D 1979. The evolution and breakdown of tristyly. Evolution 33, 489-498.

Charlesworth 1984. Androdioecy and the evolution of dioecy. Biological Journal of the Linnean Society 23, 333-348.

Charlesworth D and Charlesworth B 1979. A model for the evolution of heterostyly. American Naturalist 114, 467-498.

Charnov E L 1979. Simultaneous hermaphroditism and sexual selection. Proceedings of the National Academy of the United States of America 76, 2480-2484.

Conn J S, Wentworth T R and Blum U 1980. Patterns of dioecism in the flora of the Carolinas. American Midland Naturalist 103,310-315.

Croat T B 1979. The sexuality of the Barro Colorado Island flora (Panama). Phytologia 42, 319-348.

Crowe L K 1964. The evolution of outbreeding in plants. I. The angiosperms. Heredity 27, 111-118.

Cutler D F 1972. Vicarious species of Restionaceae in Africa, Australia and South America. In: Valentine D H (editor) Taxonomy, phytogeography and evolution. Academic Press, London. pp 73-78.

Dahlgren R M T, Clifford H T and Yeo P F 1985. The families of monocotyledons. Springer-Verlag, Berlin.

Darlington C D 1958. The evolution of genetic systems. Cambridge University Press, London.

Darwin C 1876. Cross and self fertilization in the vegetable kingdom. John Murray, London.

Darwin C 1877. The different forms of flowers and plants on the same species. John Murray, London.

De Nettancourt D 1977. Incompatibility in angiosperms. Springer-Verlag, Berlin.

Dulberger R 1981. The floral biology of *Cassia didymobotrya* and *C auriculata* (Caesalpiniaceae). American Journal of Botany 68, 1350-1360.

Dulberger R and Ornduff R 1980. Floral morphology and reproductive biology of four species of Cyanella(Tecophilaeaceae). The New Phytologist 86, 45-46.

Duthie A V 1915. Note on apparent apogamy in Pterygodium newdigatae. Transactions of the Royal Society of South Africa 5, 593-598.

Dyer R A 1975. The genera of southern African flowering plants. Volume 1: Dicotyledons. Department of Agricultural Technical Services, Pretoria.

Dyer R A 1976. The genera of southern African flowering plants. Volume 2: Monocotyledons. Department of Agricultural Technical Services, Pretoria.

East E M 1940. The distribution of self-sterility in the flowering plants. Proceedings of the American Philosophical Society 82, 449-518.

Exell A W 1966. Sapindaceae. In: Exell W A, Fernandes A and Wild H (editors) Flora Zambesiaca, Volume 2, Part 2.

Faegri K and van der Pijl L 1979. The principles of pollination ecology. Pergamon, Oxford.

Flores S and Schemske D W 1984. Dioecy and monoecy in the flora of Puerto Rico and the Virgin Islands: ecological correlates. Biotropica 16, 132-139.

Fox J 1985. Incidents of dioecy in relation to growth form, pollination and dispersal. Oecologia 67, 244-249.

Frankel R and Galun E 1977. Pollination mechanisms, reproduction and plant breeding. Springer-Verlag, Berlin.

Freeman D C, Harper K T and Ostler W K 1980. Ecology of plant dioecy in the intermountain region of western North America. Oecologia 44, 410-417.

Fries R E 1909. Über kleistogamie bei Argyrolobiumandrewsianum Steudel. Arkiv för botanik 8, 14.

Fryxell P A 1957. Mode of reproduction of higher plants. Botanical Review 23, 135-233.

Ganders F R 1979. The biology of heterostyly. New Zealand Journal of Botany 17, 607-635.

Givnish T J 1980. Ecological constraints on the evolution of breeding systems in seed plants: dioecy and dispersal in gymnosperms. Evolution 34, 959-972.

Givnish T J 1982. Outcrossing versus ecological constraints in the evolution of dioecy. American Naturalist 119, 849-865.

Godley E J 1955. Monoecy and incompatibility. Nature 176, 1176-1177.

Godley E J 1979. Flower biology in New Zealand. New Zealand Journal of Botany.

Goldblatt P 1971. Cytological and morphological studies in the southern African Iridaceae. Journal of South African Botany 37, 317-460.

Goldblatt P 1976. The genus Moraea in the winter rainfall region of southern Africa. Annals of the Missouri Botanic Gardens 63, 657-786.

Goldblatt P 1978. An analysis of the flora of southern Africa: its characteristics, relationships and origins. Annals of the Missouri Botanic Gardens 65, 369-436.

Goldblatt P 1981. Systematics and biology of Homeria (Iridaceae). Annals of the Missouri Botanic Gardens 68, 413-503.

Goldblatt P 1984a. New species of Galaxia (Iridaceae) and notes on the cytology and evolution of the genus. Annals of the Missouri Botanic Gardens 71, 1082-1087.

Goldblatt P 1984b. A revision of Hesperantha (Iridaceae) in the winter rainfall area of southern Africa. Journal of South African Botany 50, 15-141.

Grant V 1975. Genetics of flowering plants. Columbia University Press, New York.

Haber W A and Bawa K S 1984. Evolution of dioecy in Saurania (Dilleniaceae). Annals of the Missouri Botanic Gardens 71, 289-293.

Harvey W H and Sonder O W 1859-1865. Flora Capensis. Volumes 1-3. Hodges, Smith and Company, London.

Heithaus E R, Opler P A and Baker H G 1974. Bat activity and pollination of Bauhinia pauletia: plant-pollinator coevolution. Ecology 55, 412-419.

Herrera C M 1982. Breeding systems and dispersal-related maternal reproductive effort of southern Spanish bird-dispersed plants. Evolution 36, 1299-1314.

Hilliard O M 1983. Asteraceae, Inuleae, Gnaphaliinae in part. Flora of Southern Africa 33: Part 7, fascile 2, 1-325.

Horn W 1962a. Breeding research in South African plants: II. Fertility of Proteaceae. Journal of South African Botany 28, 259-268.

Horn W 1962b. Breeding research on South African plants. III. Intra- and interspecific compatibility in Ixia L., Sparaxis Ker., Watsonia Mill and Zantedischia Spreng. Journal of South African Botany 28, 269-278.

Jain S K 1976. The evolution of inbreeding in plants. Annual Review of Ecology and Systematics 7, 469-495.

Janzen D H 1977. A note on optimal mate selection by plants. American Naturalist 111, 365-371.

Jessop J P 1970. Studies in the bulbous Liliaceae. I. Scilla, Schizocarpus and Ledebouria. Journal of South African Botany 36, 233-266.

Kay Q O N and Stevens D P 1986. The frequency, distribution and reproductive biology of dioecious species in the native flora of Britain and Ireland. Botanical Journal of the Linnean Society 92, 39-64.

Kevan P G and Lack A J 1985. Pollination in a cryptically dioecious plant *Decaspermum parviflorum* (Lam) Scott A J (Myrtaceae) by pollen-collecting bees in Sulawesi, Indonesia. Biological Journal of the Linnean Society 25, 319-330.

Killick D J 1969. The South African species of *Myrica*. Bothalia 10, 5-17.

Knuth P 1906. Handbook of flower pollination. Volume I. (Translated by Aimsworth Davis J R). Clarendon Press, Oxford.

Lamont B B 1985. The comparative reproductive biology of three *Leucospermum* species (Proteaceae) in relation to fire responses and breeding systems. Australian Journal of Botany 33, 139-145.

Leighton F M 1965. The genus *Agapanthus* L. Heriter. Journal of South African Botany, Supplementary Volume IV.

Levyns M R 1954. The genus *Muraltia*. Journal of South African Botany, Supplementary Volume II.

Lewis D 1942. The evolution of sex in flowering plants. Biological Review 17, 46-67.

Lim A L 1984. The reproductive biology of rambutan, *Nephelium lappaceum* L. (Sapindaceae). The Garden's Bulletin, Singapore 37, 181-192.

Linder H P 1984. A phylogenetic classification of the genera of the African Restionaceae. Bothalia 1 & 2, 11-76.

Lloyd D G 1979. Parental strategies of angiosperms. New Zealand Journal of Botany 17, 595-606.

Lloyd D G 1980. Sexual strategies in plants. III. A quantitative method for describing the gender of plants. New Zealand Journal of Botany 18, 103-108.

Lloyd D G 1982. Selection of combined versus separate sexes in seed plants. American Naturalist 120, 571-585.

Lloyd D G and Yates J M A 1982. Intrasexual selection and the segregation of pollen and stigmas in hermaphrodite plants, exemplified by *Wahlenbergia albomarginata* (Campanulaceae). Evolution 36, 903-913.

Lord E M 1981. Cleistogamy: a tool for the study of floral morphogenesis, function and evolution. Botanical Review 47, 421-449.

Marloth R 1925. Oxalidaceae. In: Flora of South Africa 2, 92-96.

Mason H J 1972. Western Cape Sandveld Flowers. Struik, Cape Town.

Mather K 1940. Outbreeding and separation of sexes. Nature 145, 484-486.

McComb J A 1966. The sex forms of species in the flora of the south west of Western Australia. Australian Journal of Botany 14,303-316.

Moldenke A R 1975. Niche specialization and species diversity along a California transect. Oecologia 21, 219-242.

Mulcahy D 1965. Heterostyly within *Nivenia* (Iridaceae). Brittonia 17, 349-351.

Nicholls M S 1986. Population composition, gender specialization and the adaptive significance of distyly in *Linum perenne* (Linaceae). The New Phytologist 102, 209-217.

Obermeyer A A 1980. The genus *Sypharisa* (Liliaceae). Bothalia 13, 111-114.

Ornduff R 1974. Heterostyly in South African plants: A conspectus. Journal of South African Botany 40, 169-187.

Ornduff R 1983. Studies on the reproductive system of Nivenia corymbosa (Iridaceae), an apparently androdioecious species. Annals of the Missouri Botanic Gardens 70, 146-148.

Ornduff R 1985. Reproductive ecology and chromosome numbers of native and exotic races of *Oxalis pes caprae* L. and their bearing on the genesis of a noxious weed. Abstract II AETFAT: 8.

Ornduff R and Dulberger R 1978. Floral enantiomorphy and the reproductive system of Wachendorfia paniculata (Haemodoraceae). New Phytologist 80, 427-434.

Palgrave K C 1983. Trees of Southern Africa. Second Edition, Struik, Cape Town.

Parsons P A 1958. Evolution of sex in the flowering plants of South Australia. Nature 181, 1673-1674.

Phillips J F V 1924. The biology, ecology and sylviculture of "stinkwood" Ocotea bullata E Mey: introductory studies. South African Journal of Science 21, 275-292.

Price S D and Barrett C H 1984. The function and adaptive significance of tristyly in Pontederia cordata L. (Pontederiaceae). Biological Journal of the Linnean Society 21, 315-329.

Primack R B and Lloyd D G 1980. Sexual strategiesin plants IV. The distributions of gender in two monomorphic shrub populations. New Zealand Journal of Botany 18, 109-114.

Primack R B and Lloyd D G 1980a. Andromonoecy in the New Zealand montane shrub manuka, Leptospermum scoparium (Myrtaceae). American Journal of Botany 67, 361-368.

Raven P H and Axelrod D I 1974. Angiosperm biogeography and past continental movements. Annalsof the Missouri Botanic Gardens 61, 539-673.

Rebelo A G and Rourke J P 1986. Seed germination and seed set in southern African Proteaceae: ecological determinants and horticultural problems. Acta Horticulturae 185, 75-88.

Robertson C 1890. Flowers and insects. V Botanic Gazette 115, 119-204.

Ross M D 1982. Five evolutionary pathways to subdioecy. American Naturalist 119, 297-318.

Roy R P 1974. Sex mechanism in higher plants. Journal of the Indian Botanical Society 53, 141-155.

Ruiz T Z and Arroyo M T K 1978. Plant reproductive ecology of a secondary deciduous forest in Venezuela. Biotropica 10, 221-230.

Salter T M 1944. The genus Oxalis in South Africa. Journal of South African Botany Supplementary Volume 1, 1-355.

Schelpe E A 1970. Self-pollination, cleistogamy and apomixis among South African orchids. South African Orchid Journal 1, 9-10.

Simpson B 1977. Breeding systems of dominant perennial plants in two disjunct warm desert ecosystems. Oecologia 27, 203-336.

Snijman D 1985. A new species of Tenicroa (Liliaceae-Scilleae) from Namaqualand. South African Journal of Botany 51, 284-286.

Sobrevila C and Arroyo M T K 1982. Breeding systems in a montane tropical cloud forest in Venezuela. Plant Systematics and Evolution 140, 19-37.

Solomon B P 1985. Environmentally influenced changes in sex expression in an andromonoecious plant. Ecology 66, 1321-1332.

Steiner K E 1983. Pollination of Mabea occidentalis (Euphorbiaceae) in Panama. Systematic Botany 8, 105-117.

Steiner K E 1985. Functional dioecism in the Malpighiaceae: the breeding system of Spachea membranacea Cuatr. American Journal of Botany 72, 1537-1543.

Stephenson A G 1980. Fruit set, herbivory, fruit reduction, and the fruiting strategy of Catalpa speciosa (Bignoniaceae). Evolution 33, 1200-1209.

Stephenson A G 1981. Flower and fruit abortion: proximate causes and ultimate functions. Annual Review of Ecology and Systematics 12, 253-279.

Stephenson A J and Bertin R 1983. Male competition, female choice, and sexual selection in plants. In: Real L (editor) Pollination biology. Academic Press, Orlando. pp 109-149.

Steussy T 1986. Adaptive significance of ray corollas in *Helianthus grosseserratus* (Compositae). American Midland Naturalist 115, 191-197.

Stewart J, Linder H P, Schelpe E A and Hall A V 1982. Wild Orchids of Southern Africa. Macmillan, Johannesburg.

Thiselton-Dyer W T 1896-1933. Flora Capensis. Volume 4-7. Reeve and Company, London.

Thomson J D and Barrett S C H 1981. Selection for outcrossing, sexual selection, and the evolution of dioecy in plants. American Naturalist 118, 443-449.

Todd J E 1882. On the flowers of *Solanum rostratum* and *Cassia chamaecrista*. American Naturalist 16, 281-287.

Trivers R L 1972. Parental investment and sexual selection. In: Campbell B (editor) Sexual selection and the descent of man, 1871-1971. Aldine, Chicago. pp 136-179.

Van Wyk A E 1985. Studies on the reproductive biology of *Eugenia* L. (Myrtaceae) in southern Africa. Abstract AETFAT XI. pp 9-10.

Vogts M M 1958. Proteas, ken en kweek hulle. Afrikaane-Pers Boekhandel, Johannesburg.

Vuilleumier B S 1967. The origin and evolutionary development of heterostyly in the angiosperms. Evolution 21, 210-226.

Webb C J 1981. Andromonoecism, protandry and sexual selection in Umbelliferae. New Zealand Journal of Botany 19, 335-338.

Weimark H 1934. Monograph of the genus *Cliffortia*. Ohhlsson, Lund.

Weimark H 1946. Further notes on the genus *Cliffortia*. Botanika Notiser 99, 407-420.

Weimark H 1948. The genus *Cliffortia*, a taxonomical survey. Botanika Notiser 101,167-208.

Weimark H 1959. Four new *Cliffortia* species. Botanika Notiser 12, 73-79.

Wiens D, Calvin C L, Wilson C A, Davern C I, Frank D and Seavey S R (in press). Reproductive success, spontaneous embryo abortion, and genetic load in flowering plants. Oecologia.

Wiens D, Rourke J P, Casper B B, Rickart E A, Lapine T R, Peterson C J and Channing A 1983. Nonflying mammal pollination of southern African Proteas: a non-coevolved system. Annals of the Missouri Botanic Gardens 70, 1-31.

Wiens D and Tölken H R 1979. Viscaceae. Flora of southern Africa 10: part 1, 43-56.

Williams I J M 1972. A revision of the genus *Leucadendron* (Proteaceae). Contributions to the Bolus Herbarium. University of Cape Town, Rondebosch.

Willson M F 1979. Sexual selection in plants. American Naturalist 113, 777-790.

Willson M F 1982. Sexual selection and dicliny in angiosperms. American Naturalist 119, 79-583.

Willson M F and Price P W 1977. The evolution of inflorescence size in *Asclepias* (Asclepiadaceae). Evolution 31, 495-511.

Wilsenach R 1967. Cytological observations on *Hypoxis*: I. Journal of South African Botany 33, 75-84.

Wilsenach R and Papenfus J N 1967. Cytological observations on *Hypoxis*: II. Journal of South African Botany 33, 111-116.

Wilsenach R and Warren J L 1967. Cytological observations on *Hypoxis* III. Journal of South African Botany 33, 133-140.

Wilson J 1887. On the dimorphism of flowers of *Wachendorfia paniculata*. Transactions of the Proceedings of the Botanical Society of Edinburgh 17, 73-77.

Wyatt R 1983. Pollinator-plant interactions and the evolution of breeding systems. In: Real L (editor) Pollination Biology. Academic Press, Orlando. pp 51-95.

CHAPTER 3 INSECT POLLINATION IN THE CAPE FLORA

V B Whitehead, J H Giliomee and A G Rebelo

Insect pollination is by far the most intricate and diverse of the pollination systems, primarily because of the variety of anthophilous insect families, each imposing different constraints on their associated pollination syndromes.

Nevertheless, probably because of the diversity of insect species, research on insect pollination in the Cape flora has been seriously neglected. None of the management practices applied to preserve the vegetation within the Cape flora have ever been evaluated as to their possible effects on insects.

INTRODUCTION

The mechanisms by which pollen grains reach stigmas to fertilize flowers and produce seeds are many, varied, and sometimes bizarre. Pollination relationships between plants and animals may have begun before angiosperms were in existence. Early gymnosperms, although not ancestral to the angiosperms, were probably pollinated by insects. They could have provided the necessary pollinators for angiosperm progenitors (Baker and Hurd 1968).

Specialization in plants takes many forms, and for various reasons. The loss of stamens for example is correlated with the provision of nectar and the reduction of perianth members changes the flower shape and results in better recognition by pollinators. Flower constancy by pollinators indicates greater evolutionary interdependency between flower and pollinator.

The ability of pollinators to recognize and discriminate between flowers, and their ability to reach hidden attractants must have had a profound effect on the evolution of floral characters. Conversely, the development of new floral characters would provide opportunity for increased pollinator evolution. These changes could be step wise, or contemporaneous, and could be initiated by either plant or pollinator. This interdependency can potentially be disadvantageous as plants can be restricted by the absence of suitable pollinators, or pollinators limited by the lack of suitable host plants. The microevolutionary events leading to change show up more readily in plants, with their more easily modifiable flower colour and morphology, than in the pollinators, which often have complex morphology and behaviour patterns (Baker and Hurd 1968).

Very little is known about how flowers and pollinators influenced each other during the last 150 My. Much can be gained from the study of contemporary relationships between flowers and their visitors, from which it may be possible to distinguish the roles of morphology, physiology and ethology in the evolution of pollination.

Discussion of various pollen vectors from the most primitive (beetles) to the more specialized butterflies and moths and finally the highly specialized bee pollinators shows the latter to be highly coadapted with their host plants (Kevin and Baker 1983). There appears to be a close correlation between pollinator needs (nectar, pollen and oil) and floral attraction (colour, shape and odour). These are defined as primary and secondary attractants respectively (Faegri and van der Pijl 1979).

Nectar is highly variable both in volume and composition; not only between species but also between individual plants. It is also affected by the physiological state of the plant and time of the day. Pollen is the next most sought after resource and is a vital food for many insects. The whole economy of bees is centered on pollen and nectar and results in very close relationships with plants.

Scent can be a guide from a distance for beetles. It also stimulates some butterflies and flies to seek food. However, hawkmoths, some butterflies and bee flies do not respond to scent. Colour blindness is evident in some flies, beeflies and hawkmoths, but the last sometimes use guide marks. The ability to develop constancy to colour and scent occurs in some flies and many moths, and flower shape is perceived by some butterflies, but the importance of shape and scent increases when the colour of the flower is not optimal (Proctor and Yeo 1973). Night flying moth pollinators have been shown to orientate to odours, but to also use visual clues (Brantjes 1978).

Flower visitation is not only affected by the attractants offered, but also by physical factors such as light intensity. Moths are mainly nocturnal, whereas most other visitors are diurnal often having preferential visitation times. Temperature and wind also restrict the activity of pollinators as does humidity, the latter through affecting the concentration of nectar (Faegri and van der Pijl 1979).

Different pollinators occur in and assume a dominant role in different climatic zones:

- flies and butterflies are important in the alpine zones in Europe;
- bumblebees in the alpine zone of California;
- and in the Andes butterflies are the main pollinators.

In all evolutionary processes there is selection for specialization, but at the same time genetic and behavioural flexibility is retained. Pollination communities may be regarded as dynamic entities based on mutualism between plant and pollinator, or, as competing interacting systems with flowers competing for pollinators and pollinators for floral resources.

For recent reviews of the state of pollination biology see the following:

- Proctor and Yeo (1973) 'The pollination of flowers';
- Richards (1978) 'The pollination of flowers by insects';
- Anon (1979) 'Reproduction in flowering plants';
- Faegri and van der Pijl (1979) 'Principles of pollination ecology';

- Armstrong et al (1982) 'Pollination and evolution';
- Real (1983) 'Pollination biology';
- Jones and Little (1983) 'Hand-book of experimental pollination biology';
- Bentley and Elias (1983) 'The biology of nectaries';
- Meeuse and Morris (1984) 'The sex life of flowers';
- Barth (1985) 'Insects and flowers: the biology of a partnership'; and
- Baker (1985) 'Trends in pollination biology'.

EARLY STUDIES IN THE CAPE FLORA

Although *Disa uniflora* (Orchidaceae) propagates extensively by vegetative means, occasional ripe fruits with seeds were recorded by several of the nineteenth century observers. Trimen (1864) investigated the floral structure and concluded that it could only be pollinated by a nectar-sipping lepidopteran. This was corroborated when Marloth (1896) showed that the mountain pride butterfly *Meneris tulbaghia* (Satyridae) visited *D uniflora* and carried the *Disa* pollinaria on its front legs.

While some cycads are wind pollinated, *Encephalartos altensteinii* and *E villosus* (Zamiaceae) are pollinated by a group of *Antliarhinus* (Curculionoidea; Antliothininae) snout beetles. Male cycad cones open first and emit a strong odour. Large numbers of male and female snout beetles are attracted to and copulate in the cones. As the male cones degenerate, the pollen-covered female beetles fly to the female cones and force their way in to lay their eggs in the developing seeds, effecting pollination in the process (Pearson 1907; Rattray 1913; Marloth 1913-1925).

Special albuminous organs in the flowers of the parasitic genus *Hydnora* (Hydnoraceae) emit a putrid odour which attracts carrion beetles. One species attracts the skin-and-hide beetle *Dermestes maculatus* (Demestoidea), while another attracts the nitidulid *Carpophilus binotata* (Marloth 1907, 1913-1925).

Marloth (1903) also described pollination of *Roridula* (Roridulaceae). In old flowers the stamens are erect, whereas in the newly opened flowers they are depressed. The swollen base of the anther flexes up, when stimulated, releasing a shower of pollen in the process. The pollen vector is a mirid bug with *Permeridea marlothi* (Eicocephaloidea) on *R dentata* and *P roridulea* on *R gorgonias*. These bugs are not affected by the sticky leaf exudate which traps insects landing on the foliage. The contents of the swollen base of the anthers are high in sugars. Many of the mirids found had pollen adhering to their body hairs and it was postulated that feeding on the highly nutritive base of the anthers by the mirid triggered the upward flexing of the anthers which released pollen on to the body of the mirid. Mirids are active insects and move readily between plants ensuring cross-pollination.

The period from 1920 to the present

After the 1920's very little in the form of detailed observations on pollinator's were made and the information gleaned is mostly incidental to the main research theme of the reporter. The only exception is the work of Vogel (1954) which is dealt with later.

Brauns (1926) and Michener (1970), both found the allodapine bees to be polylectic, collecting pollen and nectar from such diverse families as the Asteraceae, Scrophulariaceae, Labiateae and Fabaceae (Papilionoideae). Brauns (loc cit) mentions that they are also active during the winter months on Erica and Aloe.

Watmough (1974) states that Xylocopa (Anthophoridae) carpenter bees are the only pollinators robust enough to operate the flower mechanism of the local Papilionoideae. Phillips (1926) found Xylocopa caffra to be a poor pollinator of Virgilia (Fabaceae), as in most instances they robbed the flowers by biting an opening above the nectaries, and suggested that Anthophora (Anthoporidae) bees are more effective pollinators of this species. Van Wyk (1983), however, attributes this type of damage to beetles. His observations indicate that X flavorufa is the most important pollinator of Virgilia in the southern Cape while X caffra and X watmoughi probably play an important, but subordinate, role. In the south-western Cape, X capitata confines its visits exclusively to Virgilia divaricata and V oroboides. At least five flowers must be visited every minute to supply enough energy for flight (Nicholson 1981).

General writings of an ecological nature, both botanical and entomological often contain references to flower visitors. The work of Claassens and Dickson (1980), for example, contains numerous references to the feeding of adult butterflies. Many species of the Lycaenidae (Lepidoptera) whose adults take nectar, and presumably pollinate mainly Selago species (Scrophulariaceae) have larvae which feed on the foliage of the same plants.

Studies specifically aimed at pollination have recently been undertaken. A good example of this is the study of Robertson (1980) on pollination of selected Erica (Ericaceae) species in the Cape Peninsula. Of the six Erica species studied, E phylicifolia, E plunkeneti and E cerinthoides were visited by birds only. Erica viridipurpurae and E parvifolia on the other hand have open corollas and are visited by many insects, with bees and flies predominating. The activity and pollen transfer ability of two of the bees, Allodapula acutigera (Anthophoridae) and Apis mellifera (Apidae) were studied. Apis mellifera transfers more pollen per visit than Allodapula acutigera, but the latter is considered to be more effective as it occurs in much larger numbers on the flowers.

Hermann (1985) found Apis mellifera to be the most frequent visitor collecting pollen from Erica specimens, including those with tubular flowers such as E versicolor, E discolor and E densifolia. These flowers are also visited by sunbirds (Nectariniidae), in contrast to those with bell and funnel-shaped flowers. After honeybees, anthophorids and other small bees such as allodapines and halictids, are the most important insect pollinators of Erica species. Using the shape of flowers to determine the pollination syndromes in the 425 Erica species occurring in the south-western Cape. Rebelo et al (1985) found 80% of the species to be insect pollinated. Of these, nine per cent are considered to be fly pollinated, being visited by species with long proboscides such as Tabanidae, Bombyliidae and Nemestrinidae (Vogel 1954). The flowers differ from those of bird pollinated species in that the orifice is very small and the corolla lobes large, star-shaped and spreading. The rest of the insect pollinated species were difficult to categorize, but they are probably adapted for pollination by bees, flies and butterflies.

Gess (1968) found that *Protea* flowers were visited by a wide variety of insects, mainly beetles, which comprised an entire community, complete with predators and scavengers. *Pria cinerescens* (Nitidulidae) feeds on *Protea* pollen (and presumably could pollinate the flowers) and the distribution of the large scarabaeid beetle *Trichostetha fascicularis* (Cetoniinae), also a supposed pollinator of *Protea*, parallels that of the distribution of *Protea*. Mostert et al (1980) found over 2 200 insects in 20 *P repens* inflorescences, of which beetles accounted for nearly 70%.

Until recently, the Cape Sugarbird *Promerops capensis* (Promeropidae) was thought to be one of the major pollinating agents of *Protea*, but when birds are excluded from visiting, the fertile seed yield is not depressed (Coetzee and Giliomee 1985). In contrast, when insects are excluded, the production of seed drops dramatically. The major pollinators are apparently the small beetles of the families Halticidae, Nitidulidae and Staphylinidae. Where both birds and insects have access to inflorescences, fertile seed yield is slightly depressed in relation to yields where only insects have access. This is attributed to possible damage to the ovaries by probing bird (Coetzee and Giliomee 1985). As *Promerops*'s diet also includes insects (Mostert et al 1980), the decline in seed yield may also be due to predation of beetles by birds.

Whitehead (1984) showed that many species of the Fideliidae (Hymenoptera: Apoidea) are often restricted in the flowers they visit. *Fidelia paradoxa*, *F villosa* and *F kabrowi* obtain both nectar and pollen only from some of the genera in the Mesembryanthemaceae, and *F braunsiana* is restricted to members of the genus *Berkheya* (Asteraceae). *Parafidelia* species (Fideliidae) (undescribed) obtains pollen and nectar from three species of *Grielum* (Rosaceae) and the closely related *Neuradopsis* (Rosaceae). *Parafidelia major* on the other hand, although it obtains pollen and nectar from *Grielum humifusum*, also obtains nectar from whatever other flower sources are available. These include *Arctotheca* (Asteraceae), *Hermania* (Steculiaceae), *Lapeirousia* (Iridaceae) and some Mesembryanthemaceae genera (Table 3.1).

The pink to mauve *Diascia* (Scrophulariaceae) flowers do not produce nectar, but have two backward projecting spurs which produce a plant-oil (Vogel 1974). Whitehead et al (1984) and Vogel (1984) found, in Namaqualand, that *Diascia* flowers were visited by bees of the genus *Redivida* (Melittidae) which collect the oil presented in the spurs. Pollen collection takes place simultaneously and analysis of the pollen loads of *R longimanus* revealed that although most of pollen was that of *Diascia*, other pollen was also present. This was attributed to visits to nectar flowers, mainly *Arctotheca* and *Homeria* (Iridaceae) in the western Cape.

TABLE 3.1 Pollen and nectar plants of fideliid bees (Fideliidae) in South Africa

BEE SPECIES	PLANT FAMILY/PLANT NAME	N	P
Fidelia paradoxa	**Mesembryanthemaceae**		
	M querichianum	N	P
	M barklyi	N	P
	M magniflorum	N	P
	M crystallinum	N	P
n = 338	Psilocaulon ciliatum	N	P
	P cf pfeillii	N	P
	P arenosum	N	P
	P junceum	N	P
	Spalmanthus prasinus	N	P
	S vigilans	N	P
	S canaliculatus	N	P
	Prenia venrensbergii	N	P
	P pallens	N	P
	Aridaria dejagerae	N	P
	A compacta		P
	Ruschia hutchinsoni		P
	Delasperma littorale	N	P
	Opophytum aquosum	N	P
	Carpobrotus edulis	N	P
Fidelia villosa	**Mesembryanthemaceae**		
	Mesembryanthemum nodiflorum		P
	M crystallinum	N	P
n = 65	Brownanthus ciliatus	N	P
	Aridaria compacta		P
	Spalmanthus tetragonus	N	P
Fidelia kobrowi	**Mesembryanthemaceae**		
	Mesembryanthemum guerichianum		P
	M crystallinum	N	P
n = 98	M hypotropicum		P
	Malephora lutea	N	
	Aridaria tenuifolia	N	
	Opophytum aquosum	N	P
	Psicaulon simile	N	P
	Spalmanthus vigilans	N	P
Fidelia braunsiana	**Asteraceae**		
	Berkheya carlinifolia	N	P
	B orobromoides	N	P
n = 72	B schinzii	N	P
	B spinosa	N	P
	B viscosa	N	P
Parafidelia friesei	Pedaliacae	N	P
	Sesamum capense	N	P
	S rigidum	N	P
	S triphyllum		
n = 65	**Fabaceae**	N	
	Crotolaria podocarpa		
	Capparaceae	N	P
	Cleome hirta		
	Malvaceae	N	
	Sida hoepfneri		
Parafidelia major	**Rosaceae**		
	Grielum humifusum	N	P
	G sinuatum	N	P
	Neuradopsis austro-africana	N	P
	Mesembryanthemceae		
	Spalmanthus viridiflorus	N	
	Eberlanzia clausa	N	
	Asteraceae		
	Arctotheca calendula	N	
	Iridaceae		
	Lapeirousia barklyi	N	
	Sterculiaceae		
	Hermannia trifurca	N	
	H heterophylla	N	
	Zygophyllaceae		
	Zygophyllum prismatocarpum	N	
Parafidelia ornata	**Pedaliaceae**		
	Sesamum rigidum	N	
	Capparaceae		
n = 26	Cleome kalahariensis	N	
	Fabaceae		
	Tephrosia cf griseola	N	
	T oxygonum	N	
	Zygophyllaceae		
	Tribulus zeyheri		P
	T cristatus		P
	T pterophorus		P
	Polygonaceae		
	Oxygonum ornatum	N	
	Aizoaceae		
	Tribulocarpus dimorphanthus		P
	Fabaceae		
	Ptycholobum biflorum	N	
Parafidelia pallidula	**Zygophyllaceae**		
n = 79	Sisyndite spartea	N	P
Parafidelia sp nov A	**Rosaceae**		
	Grielum sinuatum	N	P
	G grandiflorum	N	P
n = 273	G humifusum	N	P
	Zygophyllaceae		
	Tribulus zeyheri	N	
Parafidelia sp nov B	**Rosaceae**		
n = 20	Neuradopsis austro-africana	N	P
Parafidelia sp nov c	?		
n = 3			

N = Nectar, P = Pollen

A large number of species of *Diascia* occur in the Drakensberg of Natal and north-eastern Cape, and are serviced by only four *Rediviva* species (Steiner and Whitehead 1985). *Rediviva neliana*, the most widespread and numerous oil-bee, has been found to collect oil from and pollinate at least nine *Diascia* species. Placement of the pollen occurs on various parts of the body of the bee, avoiding pollen wastage and ensuring effective cross-pollination of all co-occurring species.

Extensive work is also being done on the pollinators of *Diascia* and related genera in the western Cape and Namaqualand. To date, in a limited area of Namaqualand, 12 new species of oil-collecting bees have been discovered. Although there appear to be some geographic limits to their distribution, the species of oil-flowers utilized are determined by the accessibility of the oil-bearing areas in the flower and the length of the bees oil-collecting legs (Whitehead and Steiner unpublished data).

INSECT POLLINATORS

In a survey of the potential insect pollinators in South Africa, Vogel (1954) recognizes four pollinator categories grouped into two classes:

- 1a - the psychoidophilous group containing (mainly diurnal) long proboscid flies and butterflies;
- 1b - the psycophilous group containing moths and hovering moths which are largely nocturnal;
- 2a - the bee group containing Hymenoptera and bee-like flies (Syrphidae and Bombyliidae) and many beetle species;
- 2b - the carrion group containing flies and beetles which live off dung and carrion.

Despite the apparent validity of the groupings, the long-proboscid and bee flies have not received much attention in general pollination literature, even in such standard texts as Faegri and van der Pijl (1979), reviews by Jones and Little (1983), Real (1983) and Richards (1983), or popular accounts such as Meeuse and Morris (1984). Overall, the importance of flies as pollinators, especially in South Africa, has been underrated.

Coleoptera

Beetle-pollinated flowers are considered to be a primitive 'archetype' from which other pollination syndromes have developed (Faegri and van der Pijl 1979). In the south-west Cape beetles are frequent visitors to many Asteraceae, which may be considered as typical beetle flowers (eg *Arctotis*, *Euryops*, *Gazania*, *Didelta*, *Oldenburgia* and many others). Recent work has indicated that insects, mainly beetles, may play an important role in the pollination of the Proteaceae (Coetzee and Giliomee 1985). The genera *Protea*, *Berzelia* and *Brunia* (Bruniaceae) may be considered 'beetle flowers'. Faegri (1965) maintained that insects are unlikely to pollinate *Protea repens* because of the massed styles, but were probably important pollinators in the Protea species with open, bowl shaped inflorescences. By contrast, Gess (1968) reasoned that the deeper cuplike inflorescences (eg P repens) tended to have more insects than the open saucer-shaped species (eg P cynaroides, P arborea), and that beetles featured most prominantly as visitors to Protea inflorescences (90 species (30 of which were undescribed) out of 200 insect species). Visiting beetles include predators and scavengers, and some species spend their entire life cycles in Protea inflorescences. Female beetles, by using Protea inflorescences as a base for secreting sex pheromones ('rendezvous attraction'), may play an important role in determining patterns of pollen flow (Faegri and van der Pijl 1979). This 'Red Light Hypothesis' has been tested by Rebelo and Walboom (unpublished). They found that the sex ratio of beetles was identical for both beetles found individually on inflorescences and for the inflorescences containing over 50 beetles. This suggests that if sex pheromones are playing a role, they attract both sexes equally. The possibility that the aggregations of beetles was induced by the presence of resources in the inflorescences is counteracted by the apparent randomness of the associations with regard to flower age.

The factor attracting beetles to inflorescences is not visually cued since beetle aggregations occur in species with inflorescences in which beetles are not visible externally.

The major groups of coleopteran pollinators are:

- The Hopliini (Scarabaeidae, Rutelinae) largely endemic to southern Africa with a large western Cape component (Scoltz and Holm 1985). These fall into two pollination categories: the nectar feeders (eg Anisonyx) and the pollen and flower eaters (eg Dichelus, Heterochelus, Peritrichia, and Lepithrix) (Vogel 1954). These beetles are mainly visitors to annual Asteraceae, and may play an important role in pollination of the large annual Namaqualand flora displays. Some of these beetles are sluggish and remain for long periods in one position on one flower while others are as active as honeybees and probably are very effective pollinators (Giliomee 1986). Despite the passing of 41 years since Vogel (loc cit) suggested that a close relationship must exist between the annual occurrence of monkey beetles and composite flowers, no further work in this field has been undertaken.

- The Cetoniinae, another group of flower eaters and nectar feeders belonging to the Scarabaeidae. Included in the group is the large Green Protea Beetle Trichostheta fascicularis whose distribution range is determined by the occurrence of the plant genus Protea (Gess 1968), although it has been observed to feed on Leucospermum (Proteacea), Brunia and Berzelia as well (A G Rebelo personal observation). Other members of the Scarabaeidae include the dung and carrion beetles which may be important in the pollination of carrion flowers, but no modern studies on pollinating roles of these beetles have been undertaken in the region.

Other groups potentially important in pollination include the Halticidae, Nitidulidae and Staphylinidae (all reported to occur on Protea by Gess (1968) and Coetzee and Giliomee (1985)), Phalacridae (on Asteraceae), Melyridae (on Bruniaceae and Asteraceae) and Chrysomelidae (on Asteraceae and Bruniaceae) (Giliomee 1986 and personal observation). The Meloidae (blister, oil and CMR beetles) include the Mylabrini which forage off petals and the Zonitinae which have maxilla modified for feeding on floral nectar (Moor de 1985). Nemognathus (Zonitinae) includes presumably eutrophic species with maxillae approaching body length (Faegri and van der Pijl 1979).

Diptera

The Diptera are highly diversified pollinating agents in the south western Cape, and comprise four main groups:

- generalized flies and midges which visit myiophilous flowers;
- muscoid flies which pollinate carrion and dung flowers;
- bee flies which parallel bee behaviour at flowers; and
- long proboscid-flies which form a pollinator category (rhinomyiophily, sensu Rebelo et al 1985) closely allied to moths and butterflies.

The anthophilous diptera in southern Africa have not received the attention that they merit (Bowden 1978).

The generalized fly pollinator category includes a wide variety of species which occur on flowers as adults. Fly pollination appears to be very important in the Strandveld communities near the coast where seaweed flies (Coelopidae) may be extremely plentiful (Rebelo 1987). Virtually nothing is known about the ecology of many of these flies. Flies recorded in the taxonomic literature (Barraclough and Londt 1985) as usually collected on flowers include members of the following families:

- Nematocera - Ceratopogonidae (midges) and Bibionidae (march flies);
- Brachycera - Rhagionidae (snipe flies), Therevidae (stiletto flies), Apioceridae (flower-loving flies) and Acroceridae (small-headed flies); and
- Cyclorrhapha - Conopidae (thick-headed flies) Tephritidae (fruit flies), Platystomatidae (platystomatid flies), Coelopidae (seaweed flies) and Tachinidae (tachinid flies).

Flies of the families Muscidae, Scatophagidae and Phoridae form the saprophytic, carrion and dung flies which are attracted, together with beetles, to the carrion flowers (Vogel 1954). These include trap-flowers (Ceropegia, Brachystelma) and the various Stapeliads (Stapelia, Huernia, Caralluma, Hoodia, etc - Asclepiadaceae). The lure for these species is a 'potential' food source on which they lay their eggs. The role of these flies as pollinators in southern African has never been studied.

The syrphid and bombyliid flies have evolved to occupy a niche more closely allied to the hymenopterans in pollination. They parallel these hymenopterans both morphologically and behaviourally, often showing a marked flower specificity (Barraclough and Londt 1985). Some species (eg the New World *Volucella*, Syrphidae) effectively mimic vibratile pollen harvesting by bees (Buchmann 1983). This group is well represented world-wide, where they play an important role in pollination. This is especially true in Namaqualand, where the large floral displays of Asteraceae following good rains are visited extensively by bombyliid flies (Vogel 1954).

Vogel (1954) summarized data for some proboscid lengths in the Tabanidae and Nemestrinidae (up to 47 mm and 70 mm long respectively), and hypothesized that these flies evolved to fill an ecological niche left vacant by butterflies. These flies are interesting since they appear to manifest preflight thermogenesis, in a manner similar to *Xylocopa* (Nicholson 1981) and nocturnal sphingid moths, and are active mainly in the late morning and very early afternoon (A G Rebelo, personal observation). Most species have forward orientated probocides and hover in front of a flower, insert their probicides by hovering forward and then hang onto the corolla lobes with their forelegs while feeding (Rebelo et al 1985). Other species, (eg *Megistorhynchus longirostris* which has a downwards pointing proboscis) seldom alight on the flowers they visit, but hover while feeding (Vogel 1954). Long proboscid flies also occur in Australia (Waterhouse 1980) and California (Grant and Grant 1965) and a study of the incidence of long-proboscid flies in mediterranean and semi-desert areas may yield interesting results.

It appears that the south-western Cape may be a subcentre for fly speciation (Bowden 1978). Flies appear to have evolved to fill niches left apparently vacant by the lack of suitable conditions for the favourable completion of entire life cycles in the Lepidoptera (Hennig 1983, 1984). This may be due to the lack of suitable larval food plants for Lepidoptera in nutrient-poor areas of the south-western Cape, and to dry summers in the Karoo and Namaqualand (Cottrell 1978). Similarly the lack of suitable nesting sites for the social Hymenoptera, because of the treeless nature of the nutrient-poor fynbos communities (Moll et al 1980), may have allowed the diversification of nonsocial Hymenoptera and bee flies.

Lepidoptera

To the north and east of the fynbos biome the Saturnidae, Noctuidae and Rhopalocerae (Papilionacae, Nymphalidae, Danaidae, Pieridae and Hesperidae) play an important role in diurnal pollination (Vogel 1954). However, the south-western Cape has a relatively depauperate butterfly fauna (Cottrell 1978). Porsch (1929) and Vogel (1954) attribute the paucity of butterfly taxa to the lack of water in the drier areas (Namaqualand and Karoo) during summer and the high velocities of summer winds in the south-western Cape. The major flower visitors recorded to date are: *Papilio demodocus*, *Danaus chrysippus*, *Catopsilia florella*, *Cynthia cardui*, *Meneris tulbaghia*, *Agrotis lineata*, *Lycaena orus* and *Colias electo* (Vogel 1954). Clearly, many species could be added to the list as casual visitors, but the populations are depauperate when compared to the tropics, or even Natal, where large swarms of butterflies occur on flowering bushes. Cottrell (1978) attributes the paucity of butterfly taxa in fynbos to the lack of suitable food plants. Most of the extant species use plants from the nutrient-rich renosterveld and karoo as larval food sources, rather than the sclerophyllous fynbos which is comparatively nutrient-poor (Cottrell 1978; Dickson and Kroon 1978). It is interesting to note that the best represented butterfly group in the south-western Cape, the Lycaenidae, sometimes utilizes ant larvae as a food source during their later larval stages (Clark and Dickson 1971; Claassens and Dickson 1974; Dickson and Koon 1978; Hennig 1983; Hennig 1984).

By contrast, the night-flying moths, excluding the Sphingoidea (which are poorly represented in the south-western Cape), are relatively speciose. Seitz, quoted by Vogel (1954), states that a 1:3 ratio of diurnal to nocturnal Lepidoptera is the norm, which parallels the ratio of day to night flowering Lepidoptera-pollinated plant species in the southern Cape (Vogel 1954). This discrepancy Vogel (loc cit) attributes to diurnal windy conditions in the south-western Cape, which largely abate at night. A more plausable explanation in this regard is that the moths, of such families as the Noctuidae, Pyralidae and the Geometridae, are less susceptible to windy conditions due to smaller wing size and stronger and more direct flight, compared to larger wings and more erratic flight of butterflies. Studies of the larval distribution and food habits of nocturnal lepidoptera may contribute to explaining why there appear to be so many species relative to diurnal species in the south-western Cape.

Hymenoptera

Wasps. Most adult wasps utilize flowers as nectar sources, and a syndrome for wasp pollination is considered distinguishable by some biologists (see below). Wasps, as a rule, are opportunistic foragers and have a low fidelity to specific flowers. While bees obtain their protein requirement from pollen, and are therefore important floral visitors, most wasps utilize animal protein, and consequently floral visitation is confined to nectar feeding and, occasionally, prey collection. Only the Vespidae are highly social and although they provision the larvae with animal protein, they are important nectar seekers, especially towards the end of the breeding season, when the energy demands of the colonies are high. By contrast, the Masaridae provision their progeny on pollen and nectar, and are probably important floral visitors in southern Africa (Eardley 1985).

The Philanthinae (Sphecidea), which may carry large quantities of pollen from their visits to flowers, prey extensively on Hymenoptera and Coleoptera (Eardley loc cit). Some higher wasps (eg Polistes) have tube-like mouthparts and can therefore forage on deeper flowers than most wasps, which are limited by their flat tongues to foraging on shallow exposed blossoms. Higher wasps also have good colour vision, an excellent time sense and readily cue to odours (Faegri and van der Pijl 1979).

No studies investigating the floral visitation of plants by wasps have been undertaken in the south-western Cape. However, the European wasp Vespula germanica, which arrived in the Cape Peninsula in the 1970's, has already become a prominent floral visitor at the Kirstenbosch National Botanical Gardens, and may prove to have an undesirable effect on local hymenopteran populations (Whitehead and Prins 1975).

In Europe and Australia some wasps are important participants in irregular floral associations (eg sexual deceit, prey deceit, etc) (Stoutemire 1974; Kullenberg and Bergstrom 1976), but no known incidence of similar relationships are known to occur in the south-western Cape.

By contrast, the coevolution between Ficus species (Moraceae) and the fig wasps (Chalcidoidea, Agaonidae) is very well documented (Galil 1977; Janzen 1979), with the wasps being specific visitors to Ficus synconia which do not develop into fruit without the wasps' attention.

Of the four species of Ficus which occur in the south-western Cape, only F sur has been investigated (Baijnath and Ramcharun 1983). Ficus sur has a species-specific agaonid pollinator, Ceratosolen capensis Grandi. The synconium developmental cycle is very similar to that of another Sycomore fig which has been well studied, viz F sycomorus. Apart from the primary sycophile (the legitimate pollinator, C capensis), seven other wasp species (one additional primary sycophile and six nonpollinating, secondary sycophiles) have been recovered from synconia of F sur grown in Durban. Ficus sur has, in addition to normal synconia, geocarpic synconia which may be buried in the subsurface layers of the soil, posing problems as to how agaonids gain entry to effect pollination.

Ants. Ants seldom pollinate plants: they usually only thieve nectar. Pierce's (1984) record of Mimetes cucculatus being pollinated by ants is obviously a transcription error (which should have appeared in the column under seed dispersal). There are several reasons why ants are poor pollinators: they seldom move from plant to plant; they tend to visit few flowers on the single plant and only move between flowers when the resources are depleted; they seldom make contact with both the anthers and stigma; they equally well visit nectaries and insect-secretions; and their secretions against fungal infection drastically reduce pollen viability (Beattie et al 1984). Plants pollinated by ants tend to be small intertwining ground creepers in hot dry desert areas, which have inconspicuous flowers (Faegri and van der Pijl 1979; Meeuse and Morris 1984). No attempt has been made to identify potential ant pollinated plant species in southern Africa, but the northern Cape and Namaqualand would seem to offer suitable habitats for such species.

The role of ants as nectar and flower protectors, primarily against nectar thieves and illegitimate visitors is reviewed in Faegri and van der Pijl (1979). Coetzee and Giliomee (1985) were unable to determine the role of argentinian ants (Iridomyrmex humilis) in Protea repens, but Paton (1986) showed that ants inhibited foraging by other insects in P eximia. This has not been adequately investigated in southern Africa, despite the abundance of extrafloral nectaries in some fynbos plants such as the Proteaceae. Ants are more prominent in fynbos as seed dispersers and possibly seed storers (Bond and Slingsby 1983).

Bees. The nine families of bees occurring in southern Africa are all important pollinators of the local flora, since they require pollen as a protein source for their progeny. The Anthophoridae, Apidae, Fideliidae and Megachilidae form the long-tongued bees, whereas the Andrenidae, Colletidae, Ctenoplectridae, Halictidae and Melittidae are short-tongues bees (Eardley 1985). The length of the mouthparts is important in determining the floral spectrum at which bees can forage for nectar, obviously bees with a longer tongue can forage at flowers from which the short-tongued bees may be excluded. Eardley (1985) regards the Andrenidae, Ctenoplectridae and Megachilidae as primarily pollen collectors, while the Fideliidae collect oil (Whitehead and Steiner 1985). Both groups of bees, however, require nectar for energy and may transfer pollen between nectar plants in addition to their main line plants. An extensive literature exists on the foraging behaviour, energetics and pollination efficiency of the social (mainly *Apis mellifera*) and the larger bees (*Bombus*, and other North American species) (Janzen 1971; Heinrich and Raven 1972; MacSwain et al 1973; Heinrich 1975, 1979, 1983; Frankie et al 1976; Pyke 1978; Strickler 1979).

Little is known about the foraging habits of the local subspecies of the honeybee *Apis mellifera capensis*, which is endemic to the south-western Cape, and is certainly one of the major insect pollinators of Mountain Fynbos plants (eg *Blaeria* and other minor genera of the Ericaceae (Rebelo et al 1984), *Protea repens* (Coetzee et al in preparation)), especially in areas in which apiaries are present (Rebelo this volume). *Apis m capensis* requires between 20 to 50 kg of pollen per hive per year (Anderson et al 1983).

In the *capensis* subspecies, like the *adansonii* subspecies, workers are able to produce female progeny. However, *capensis* is unique in that workers are wholly accepted as queens by other *Apis mellifera* subspecies. This has partly been the reason for the successful spread of the 'African honeybee' in South America (Editorial in South African Bee Journal 15: 2-4, 1987). Compared to other subspecies (eg *adansonii*, which occurs over much of the rest of sub-Saharan Africa) queens of *capensis* are not as prolific and produce smaller colonies (Anderson et al 1983). This is regarded as an adaptation to the Cape climate and flora. The cold and rainy conditions during winter, and the extremely windy conditions during summer would make it difficult for worker bees to maintain large colonies. The high winter humidity in the south-western Cape also affects colony size since condensation may hinder efficient thermoregulation (Anderson et al 1983). Similarly, the lack of dominant plant species with good nectar yields would favour small colonies geared to the numerous, but small nectar flows produced by the diverse flora (Anderson et al 1983). Colony size is probably also limited by the lack of suitable nesting sites in the form of tree-stems, due to the lack of trees in Mountain Fynbos (Moll et al 1980). Suitable nesting sites include caves, crevices (which are limited by waterlogging in winter) and trees in riverine forests. Distances of foraging have not been ascertained, but distances of 7,4 km and 13,7 km have been recorded for honeybees. Distances of 1,6 km are considered as bordering on economically viable (Anderson et al 1983) although distances of five kilometres have been recorded for ground nesting bees (Force 1981). Honeybees are also limited in the karoo vegetation by the lack of natural nectar sources in summer (Anderson et al 1983).

Also conspicuous in the south-western Cape are the carpenter bees (Xylocopa species) which forage extensively on large leguminous flowers (eg Aspalathus, Indigofera, Lebeckia, Podalyria, Psoralea and Virgilia), and which also appear confined to areas surrounding suitable tree-stem nesting sites.

The Cape flora is also characterized by a number of nontropical bee taxa, presumably of archaic Gondwanaland origin. The southern African bee species diversity peaks in the western Cape, parallelling the pattern observed in California, where species richness increases with increased aridity (Michener 1979). The bee fauna tends to increase inland, away from the cool, windy coastal region (Michener loc cit). This may in part be due to the lack of suitable nesting sites in Mountain Fynbos (a paucity of trees, Moll et al 1980), coupled with the lack of suitable dry nesting sites in the soil for over-wintering, which limits the diversity of bees in the tropics (Michener 1979). Moldenke (1976) concluded from studies in California that areas with larger bee faunas contained a greater proportion of oligolectic species (ie with specific floral associations) to polylectic species (visiting a wide variety of flower species of quite different morphologies). Michener (1979), based on sporadic collecting, feels that western Cape bee species are more oligolectic than bees from tropical Africa. Other factors which may limit the number of oligolectic species include the population sizes of polylectic (and oligolectic) bees, which may be determined by the lack of suitable nest sites or a marked seasonal resource availability. From this we predict that the number of oligolectic species will be lower in the fynbos region than in Namaqualand, and should show a marked decline with the introduction of bee hives into an area.

POLLINATION SYNDROMES OF INSECT POLLINATED PLANT SPECIES

Pollination syndromes are not distinct, exclusive categorizations, but overlap considerably. Categorization of pollination syndromes are further complicated by plants which are adapted for pollination by a variety of unrelated pollinating agents. These contrast considerably with other plants which have a species specific pollinator relationship, often of a sexual nature, with specific insects. Table 3.2 summarizes the salient features of the more common pollinator syndromes. In understanding pollination syndromes it is best to consider the various pollination functions of flowers:

- the production of a reward (or suitable fake);
- the selective advertisement of the reward;
- the exclusion of unwanted potential pollinators; and
- the protection of the reward from potential thieves.

In many cases the functions overlap with one another, or with other considerations, such as seed protection. Assuming that the quantity and quality of the nectar allow for energetically feasible exploitation by visitors, the abundance and distribution of the flowers on the plant, incidental visitors, and the environment, will determine the spectrum of pollinators and thieves which will visit the flowers. Environmental

TABLE 3.2 Features of the various pollination syndromes (a)

Syndrome	Reward type	Quantity of nectar	Nectar concentration	Sucrose/ Glucose + Fructose*	Amino acids	Histadine score	Positive lipids	Antioxi-dants
ants	nectar	very small	20 (5 - 50)	?	?	?	?	?
wasps	nectar sex	'post floral' exposed 0,6 1	24 (13 - 49)					
flies	nectar pollen shelter	small exposed	20 (16 - 23)		585	4,35	0,46	0,15
beetles	nectar pollen floral parts shelter	accessible variable	?		?	7,86	0,50	0,50
carrion flies	fake egg deposition site	usually none	-	-	-	-	-	-
carrion beetles	nesting							
butterflies	nectar	ample 0,9 1	22 (13 - 44)		820	6,40	0,11	0,91
long-proboscid fly	nectar	moderate hidden very deep	?	?	?	?	?	?
settling moths	nectar	ample 0,8 1	41 (39 - 42)		1150	5,75	0,25	0,020
hovering moths	nectar	copious 130 1	24 (17 - 40)		450	4,86	0,64	0,14
short-tongue bees	pollen nectar sex	moderate hidden	46 (25 - 75)		650	4,59	0,49	0,46
long-tongue bees	nectar pollen oil sex	moderate 9,7 1 hidden deep	31 (19 - 75)		397	5,64	0,48	0,45
bee flies	nectar pollen	moderate hidden	?	?	?	9,00	all	all
hummingbirds	nectar	copious 16,8 1	21 (12 - 34)		255	4,86	0,37	0,42
perching birds	nectar insects	copious 13,0 1	21 (5 - 30)		?	3,31	0,20	0,17
nonflying mammals	nectar	copious 8,8 1	36 (33 - 38)		?	?	?	?
bats	nectar	copious 1310 1	17 (11 - 26)		275	3,75	none	none
wind	none	none	-	-	-	-	-	-

* The four points will total 100%.

TABLE 3.2 (continued) Features of the various pollination syndromes (b)

SYNDROME	ATTRACTION						
	Primary attractant	Colour	Odour	Nectar guides	Outline	Mass effects	Size
ants	odour of nectar	cryptic green/brown	?	absent	simple no deep effect	none, few scattered	very small
wasps	visible nectar?	fleshy yellow/ brown	?	absent open necta	simple	variable	variable
flies	odour	light dull colours	faint of faetid,	present	simple no depth effect	flat surface or cylinder, horizontal or vertical	small flowers large inflorescence
beetles	odour	dull green/ cream	strong fruity or aminoid	absent	simple no depth effect	large flowers with many parts brush inflorescences	large
carrion flies carrion beetles	odour	dull, dark brown, purple	decaying protein	guides to traps	simple, with internal 'windows'	often inflorescences on large flat surfaces with mobile hairs	usually large traps
butterflies	visual	pink, red, white, yellow	weak fresh scent	simple or small orifice	simple	flat landing surface	variable
long-proboscid flies	visual?	pink, cream	none?	simple or dark spot	simple	variable	long thin
settling moths	odour	white, cream drab	strong nocturnal perfume	absent	deeply dissected lobes	large lax displays	
hovering moths	odour	white, cream drab	strong nocturnal perfume	absent	deeply dissected lobes or fringed petals hidden reward	large lax displays	
short-tongue bees	odour visual	bright yellow or blue	fresh honey-like	present	complex, hidden reward depth effects	variable	variable
long-tongue bees	odour visual	bright yellow or blue	fresh honey-like	present	complex, hidden reward depth effects	variable variable	variable variable
bee flies	odour visual	bright yellow or blue	fresh?	present	complex?, depth effect	variable	large
hummingbirds	visual	red, yellow, cream	none	absent	simple, hidden reward	variable	large
perching birds	visual	red, yellow, cream	none	absent	simple, hidden reward	variable, usually inflorescences	very large
nonflying mammals	odour	dull brown or green	yeasty, mousey	absent	simple	variable, usually inflorescences	very large
bats	odour	white, creamy	fermenting or batty	absent	simple	variable	very large
wind	-	brown, green	none	absent	simple	masses of flowers	very small

TABLE 3.2 (continued) Features of pollination syndromes (c)

SYNDROME	RESTRICTIONS ON UNWANTED VISITORS						
	Movements	Time of opening	Pollen-nectar distance	Flower shape	Flower orientation	Flower position	Pollinator support
ants	none	continuous	minute	regular, cup-life	variable	near ground	intertwin-scaffolding
wasps	none	continuous	small	regular, bell-shaped	horizonal approach	variable	variable
flies	none	continuous or nocturnal closing (shelter)	small	regular	flat surface, vertical or horizontal	variable	variable
beetles	none	continuous or nocturnal closing	small	regular, flat or large bowl-shaped landing area	horizontal landing area	variable	very robust large landing area
carrion flies	none	continuous	-	regular, but deep	variable	variable	one-way
carrion beetle				traps			entrances
butterflies	none	continuous	small to large	regular, flat rim, small - large tubes, funnel or trumpet	horizontal landing area, erect, flat	variable	flowers erect & flat
long-proboscid flies	none	continuous	large	regular, long thin tube, star-shaped lobes	vertical or horizontal	distal on shoots	none, or petals used
settling moths	nocturnal anthesis	nocturnally only	large deep spurs	zygomorphic, nectar hidden, funnel shape	horizontal	variable	flat & erect
hovering moths	nocturnal anthesis	nocturnally only	large deep spurs	zygomorphic, nectar hidden funnel or tube shape	horizontal or pendant	distal on shoots	none
short-tongue bees	none	continuous	moderate	zygomorphic, shallow, complex, semi-closed, landing platform	variable	variable	strong, good foothold
long-tongue bees	none	continuous	moderate	zygomorphic, deep complex, semi-closed, landing platform	variable	variable	strong, good foothold
bee flies	none	continuous	moderate	regular/zygomorphic, depth effect	variable	variable	strong?,
hummingbirds	none	continuous	large	regular, long tubular	horizontal or pendant	distal on shoots	none
perching birds	none	continuous	large	regular, long tubular or brush	horizontal or pendent	variable	stems for perching
nonflying mammals	none	continuous/ nocturnal	large 10mm	bowl or cylindrical regular	horizontal	near ground inside bush	near ground or robust
bats	nocturnal	nocturnal opening	large	regular, bowl-shape, cauliferous	vertical/ horizontal or pendant	pendant, outside canopy	large, robust
wind	none	continuous	-	simple-reduced	variable	distal on shoots	none, exposed

TABLE 3.2 (continued) Features of pollination syndromes (d)

SYNDROME	PROTECTION AND EXAMPLES			
	Protection	Sex organs	Pollen:ovule ratio	Preferred habitats
ants	none	hidden	low?	hot desert habitats
wasps	none	exposed	high?	tropics
flies	none	exposed	very high?	high altitudes, tropics, coastal
beetles	extremely robust	protected	high	tropics
carrion flies	robust, strong	exposed inside	low?	tropics
carrion beetles		trap		tropics
butterflies	none	anthers hidden	low?	tropics
long-proboscid fly	none	anthers hidden	low?	semi arid and high altitude
settling moths	none	anthers exposed versatile	low?	tropics
hovering moths	none	anthers exposed versatile	low?	tropics
short-tongue	robust	hidden or exposed	low (nectar) high (pollen)	semi-arid mediterranean regions, northern temperate regions and tropics
long-tongue bees	robust	hidden or exposed	low (nectar) high (pollen)	semi-arid mediterranean regions, northern temperate regions and tropics
bee flies	robust?	hidden or exposed	low?	xeric conditions?
hummingbirds	strong walled	hidden or exposed	low	new world tropics
perching birds	strong walled	hidden or exposed	low	old world tropics and mediterranean regions
nonflying mammals	very robust	exposed	low	meditteranean and tropical habitats
bats	very robust	exposed	low	tropics
wind	none	exposed to wind	extremely high	extreme cold areas high altitudes

factors such as wind speeds, temperature, rainfall and isolation also play a role in determining the activity levels and energy budgets of foraging pollinators.

In addition, the categorization of syndromes is an attempt to delimit types in what is actually a continuum of pollinator attraction strategies. Thus there are flies which mimic bees in their habits, nocturnal bees which respond to cues in a manner similar to settling moths, and diurnal hovering moths which are more correctly considered, with regard to pollination, as hummingbirds than moths (and which actively exclude hummingbirds from their territories).

Ant pollination: Myrmecophily

Ant pollination is probably the most recently discovered of the entomphilous syndromes (Meeuse and Morris 1984), having been properly described by Hickman (1974), although records of probable ant pollination are known from much earlier (Faegri and van der Pijl 1979). Ants are nonflying, efficient exploiters of nectar, and rarely move between flowers when nectar is present in large quantities. Consequently, any ant pollinated plant must ensure that ants move between flowers (this has independently been achieved in plants requiring protection from predators with the use of small quantities of nectar secreted by extra-floral nectaries). Ant-flowers are small and inconspicuous and produce minute quantities of nectar, both factors making flowers unattractive to other insects, thus disposing of any need for nectar protection or selective barriers to other pollinators. Consequently, the sessile flowers are borne in an exposed position close to the stems, along which ants walk in search of nectar. Outbreeding is achieved in two ways:

- each individual plant produces only a few blooms at a time; and
- plants tend to be prostrate and intertwined in mats near ground level and provide a scaffold along which ants move freely between plants, without having to leave the plants.

The small flowers produce minute quantities of sticky pollen, which must be protected from the powerful fungicides secreted by ants. These fungicides have been proposed as the reason for the scarcity of ant pollination (Beattie et al 1984). Because of the small size of the flowers the number of ovules per flower is low.

Ant pollination is thought to be most common in herbs which occur in hot, dry habitats where ants may be very active in moving between bushes over the hot sands (Faegri and van der Pijl 1979). Hagerup (1932) found ants to be very important pollinators of Saharan plants (mainly _Euphorbia_ species), where the heat apparently prevented other insects from foraging near the ground. The possible occurrence of ant pollination has not been investigated in southern Africa. Possible examples include various prostrate examples of the Aizoaceae (_Adenogramma_, _Limeum_), Euphorbiaceae (_Euphorbia_), Chenopodiaceae (_Chenolea_) and Crassulaceae (_Crassula_).

Wasp pollination: Vespidophily

Muller (1873) characterized figwort (Scrophularia nodosa) as a wasp flower, and several other flowers (Epipactis, Symphoricarpos) are now recognized wasp flowers. Wasp flowers also occur in the tropics, but, because of the nature of the wasp flower structure, biologists are reluctant to recognize a syndrome of wasp pollination. This is because wasps have flat tongues, only suitable for lapping nectar (Procter and Yeo 1973; Faegri and van der Pijl 1979), and wasp flowers are therefore characterized by having exposed nectar and by being allophilic (having no morphological adaptations for guiding or restricting visitors). This allows the exploitation of wasp flowers by a wide variety of insects apart from wasps, including flies and bees, making it difficult to delimit a distinct wasp flower syndrome. Nevertheless, some 'wasp flowers' (eg Hedera colchicha) are only visited by wasps, despite their apparent accessibility to flies and bees which visit related Hedera species (Faegri and van der Pijl 1979).

The typical wasp flower is a simple, radially symmetric flower, with exposed nectar, an allophilic character and has dull, brown colours. Nectar guides are not present since the nectar is visible, not hidden.

Wasp flowers have not been identified for the Cape flora, but this is probably due to their polyphilic nature, and the reluctance of pollination biologists to recognize the syndrome as a distinct class. Possible examples may include Crassula or Thesium.

Fly pollination: Myiophily

As envisaged herein, myiophily is restricted to what Faegri and van der Pijl (1979) call 'unspecialized flies restricted to more primitive blossoms'. This does not include the long-proboscid flies, bee flies and carrion flies, which are treated under separate headings below.

Because flies do not collect food for their progeny, they require low levels of energy and protein, relative to hymenopterans. Consequently, their activities on flowers are erratic, unreliable and their fidelity is low. Adult flies may be restricted to areas containing larval food sources (an aspect exploited by carrion flowers). Flies may be relatively important as pollinators under adverse conditions, when bees may be restricted.

Fly blossoms, like wasp blossoms, may be visited by a host of other insects, including small hymenopterans, coleopterans and lepidopterans. Nevertheless the syndrome is a fairly distinct one (Faegri and van der Pijl 1979). Fly blossoms are characterized by their small flowers, with a small pollen/stigma to nectar distance. Nectar production is typically minute, and can be relatively solid as many flies can moisten nectar before sucking it up. Flies are unable to carry large pollen loads, and fly blossoms typically occur in large numbers, each flower bearing a little pollen. This arrangement additionally serves to restrict pollen thieves. Individual flowers are regular, simple, with no depth effect, and are usually clustered in inflorescences showing the same features. Colours are generally light, but of a dull nature. Nectar is open, easily obtainable and generally visible, and thus there is no need for nectar guides. Since flies are not destructive foragers, plant sexual organs are often exposed. Odours vary from imperceptible to aminic or spermatic. Fly blossoms may be described as open-house blossoms, visited by flies not adapted as pollinators in any manner, but nevertheless essential to the reproductive success of the plants (Meeuse and Morris 1984).

Fly blossoms are common in the south-western Cape, and appear relatively common in karoo, renosterveld and strandveld vegetation types and in riverine thicket. No detailed studies on fly pollination have been undertaken in the region, and published examples of the syndrome are largely confined to commercially important Apiaceae. Possible examples include: *Rhus* (Anacardiaceae); *Hermas*, *Lichtensteinia* (Apiaceae); *Ilex* (Aquifoliaceae); *Cussonia* (Araliaceae); *Arctopus*, *Metalasia*, *Tarchonanthus* (Asteraceae); *Silene* (Caryophyllaceae); *Cassine*, *Maurocenia*, *Maytenus*, *Pterocelastrus* (Celastraceae); *Curtisia* (Cornaceae); *Crassula* (Crassulaceae); *Cunonia*, *Platylophus* (Cunoniaceae); *Euclea* (Ebenaceae); *Erica* (Ericaceae); *Nuxia* (Loganiaceae); *Myrica* (Myricaceae); *Chionanthus*, *Olea* (Oleaceae); *Brabejum* (Proteaceae); *Canthium* (Rubiaceae); *Colpoon* (Santalaceae); *Selago* (Scrophulariaceae); and *Lycium* (Solanaceae) (Rebelo 1987; A G Rebelo personal observation).

Beetle pollination: Cantharophily

Beetle blossoms are as characteristic of tropical areas as bee pollination is of semi-arid and temperate regions, but are overlooked because of their lack of specialization (Faegri and van der Pijl 1979).

Essentially, beetle blossoms are identical to fly blossoms, except for the need to protect the plant's sexual organs, especially the ovary, from the much stronger, and often larger, beetle visitors. Because beetles are relatively clumsy fliers, large landing surfaces are the rule with few visual attractions. Open, easily accessible nectar, pollen or fruit bodies serve as the food source. Flowers are generally of the dish and bowl type, with little depth effect, so that the nectar and pollen are typically close together. Typical anthophilous beetles are hairy or scaly and carry much larger pollen loads than smooth beetles. Pollen transfer is achieved by 'mess and soil', and beetles are capable of transporting large quantities of pollen. Beetles are attracted by strong fruity, spermatic and aminoid odours, and colours of beetle flowers vary from cream to greenish, generally of a dull nature.

In the Cape flora, Faegri (1965) regards *Leucadendron discolor* as converging to the *Magnolia*-type, classical beetle blossom. In addition, many *Protea* and *Leucospermum* species, considered by Faegri (1965) as bird blossoms, are visited by large numbers of beetles, and many species complete their entire life cycles within *Protea* inflorescences (Gess 1968; Coetzee and Latsky 1986; Rebelo and Seiler unpublished). Other examples include *Nebelia*, *Brunia* and *Berzelia* (Bruniaceae) and *Serruria* (Proteaceae) (A G Rebelo personal observation). Vogel (1954) considered beetle pollination to be allied to allophilic bee flowers, and characterized many of the Namaqualand Asteraceae as pollinated by beetles and bee flies.

Butterfly pollination: Psychophily

Pollination by diurnal, settling Lepidoptera carries many of the limitations of fly pollination. Butterflies (and diurnal moths) do not have to provision their young with food, but are often restricted in distribution to areas containing larval food plants. Butterflies, probably because of their long proboscis, have a preference for sucking nectar out of narrow tubes. Flowers generally have an erect orientation, and a tube surrounded by a flat rim used for support while probing. Flowers are usually grouped into flat inflorescences containing large numbers of flowers, each of which generally contain a little nectar. This arrangement hides the nectar in small parcels, thus preventing high-energy foragers from economically exploiting the resource, at the same providing a large platform with sufficient flowers to ensure an economical return to low energy foragers. The tube-shape of flowers, necessitates the provision of visual nectar guides and mechanical tongue grooves, which allow the anthers (usually fixed) to be inserted at the top of the tube, where they are able to contact visitors' mouthparts. This additionally minimizes pollen accessibility to pollen gatherers, and thus reduces the need for high pollen production.

Colours of butterfly flowers are generally vivid and may extend into the red end of the electromagnetic spectrum. Faegri and van der Pijl (1979) characterize the odour of butterfly flowers as being weak, fresh and agreeable. *Disa uniflora* and *Lantana* represent extremes in the butterfly syndrome, other examples including: *Cyrtanthus*, *Haemanthus* (Amaryllidaceae); *Geissorhiza*, *Gynandriris*, *Ixia*, *Lapeirousia*, *Moraea* (Iridaceae); *Satyrium* (Orchidaceae); *Blepharis* (Acanthaceae); *Pachypodium* (Apocynaceae); *Asclepias*, *Microloma* (Asclepiadaceae); *Impatiens* (Balsaminaceae); *Cyphia*, *Lobelia* (Campanulaceae); *Cadaba* (Capparaceae); *Dianthus*, *Silene* (Caryophyllaceae); *Cotyledon*, *Crassula*, *Kalanchoe* (Crassulaceae); *Erica* (Ericaceae); *Pelargonium* (Geraniaceae); various Lamiaceae; *Hibiscus* (Malvaceae); *Conophytum* (Mesembryanthemaceae); *Jasminium* (Oleaceae); *Oxalis* (Oxalidaceae); *Plumbago* (Plumbaginaceae); *Gardenia*, *Oldenlandia* (Rubiaceae); various Scrophulariaceae; *Hermannia* (Sterculariaceae); *Gnidia* and *Struthiola* (Thymeliaceae) (Vogel 1954).

Examples from Table Mountain are listed in Table 3.3.

Settling moth pollination: Phalaenophily

The major difference between pollination by butterflies and by moths is that the majority of moths are nocturnal. Consequently, settling moth blossoms tend to be pale in colour and have a sweet to sickly sweet odour. The majority of the features of settling moth pollination parallel those of hovering moth pollination, except that settling moths, because they do not hover while feeding, require a landing platform and do not require as large an energy source. Consequently the nectar and floral structure are similar in constitution to butterfly blossom nectar.

Examples include: *Dipcadi* (Hyacinthaceae); *Geissorhiza*, *Hesperantha*, *Ixia*, *Moraea* (Iridaceae); *Bartholina*, *Habenaria*, *Holothrix*, *Mystacidium* (Orchidaceae); *Asclepias* (Asclepiadaceae); *Impatiens* (Balsaminaceae); *Heliotropium* (Boraginaceae); *Erica* (Ericaceae); *Aridaria*, *Conophytum* (Mesembryanthemaceae); *Oldenlandia* (Rubiaceae); *Agathelpis*, *Buchnera*, *Manulea* (Scrophulariaceae); and *Gnidia* (Thymeleaceae) (Vogel 1954).

TABLE 3.3 Recorded nectar food plants of butterflies (Lepidoptera) on Table Mountain (comparable data do not exist for other regions of the Cape flora, nor can this list be considered comprehensive). Compiled from Claassens and Dickson (1974)

BUTTERFLY SPECIES	NECTAR FOOD PLANT	FAMILY	COLOUR
SATYRIDAE			
Meneris tulbaghia	Kniphofia uvaria	Asphodelaceae	Red
	Brunsvigia orientalis	Amaryllidaceae	Red
	Disa uniflora	Orchidaceae	Red
	Watsonia	Iridaceae	Red
	Aloe	Asphodelaceae	Red
LYCAENIDAE			
Capys alphaeus	Erica	Ericaceae	Pink
	Serruria	Proteaceae	Pink
	Selago serrata	Scrophulariaceae	Mauve-blue
	Penea mucronata	Peneaceae	Yellow
Argyrocupha malagrida	?	Mesembryanthemaceae	Pink
	Cuscuta	Convolvulaceae	White
Aloeiodes thyra	Lampranthus elegans	Ficoideae	Pink
	L falciformis	Ficoideae	Pink
	Lessera gnaphalodes	Asteraceae	Yellow
	Hermannia althaeofolia	Sterculiaceae	Orange/ Yellow
	H cuneifolia	Sterculiaceae	Orange/ Yellow
A pierus	?	Mesembryanthemaceae	Pink
	Lampranthus	Mesembryanthemaceae	Pink
Cacyreus lingeus	Salvia	Lamiaceae	Blue
	Coleus	Lamiaceae	?
Syntarucus pirithous	various, esp Medicago	Fabaceae	Blue
Lampides boeticus	Podalyria	Fabaceae	Pink
	Virgilia	Fabaceae	Pink
	Sutherlandia	Fabaceae	Scarlet
Lepidochrysops oreas	Selago	Scrophulariaceae	?
L variabilis	Selago	Scrophulariaceae	?
L methymna	Selago spuria	Scrophulariaceae	White/
PIERIDAE			
Colias electo	Trifolium africanum	Fabaceae	Purple
Pieris helice	Medicago	Fabaceae	Blue
PAPILIONIDAE			
Papilio demodocus	Watsonia	Iridaceae	Red
	Tritonia	Iridaceae	Red

Long-proboscid fly pollination: Rhinomyoiphily

The syndrome encompasses pollination by diurnal, hovering insects, mainly members of the Tabanidae and Nemestrinidae (Diptera). These flowers are characterized by their long, narrow (distally), straight tubes, with a small orifice at the top, which is surrounded by a simple nectar guide (usually a red dot). Anthers may be fixed and inserted just below the orifice, or may extend to just outside the orifice opening. Flowers generally have little perceptible odour. Orientation of flowers may be vertical or horizontal, and limit access to visitors with proboscides perpendicular or parallel to the long axis of their bodies. Flowers are generally light in colour, usually pink or white with a red nectar guide encircling the orifice. The nectar is hidden and more abundant than in butterfly blossoms. Nectar thieving by carpenter- and honeybees frequently occurs, and the bases of flowers may be protected by sticky substances, robust sepals, or by the base of the flower being inconspicuous and well away from the advertising petals. The advertising function is largely confined to the petal lobes, which are generally star shaped with a simple outline, although they may be orientated so as to act as a stabilizer on which hovering flies may rest their forelegs while hovering. Hovering flies require much energy while foraging and are often restricted to very few species in their habitats, making them efficient, eutropic visitors, and relatively few flowers are borne simultaneously on hovering fly plants.

Examples of hovering fly blossoms include Erica section Euryloma (Ericaceae), Pelargonium (Geraniaceae), Lapeirousia (Iridaceae) and Sonderothamnus (Peneaceae) (Vogel 1954; A G Rebelo personal observation).

Hovering moth pollination: Sphingophily

Like rhinomyiophily, sphingophily relies on a high energy utilizer as a pollinator, and hovering moth blossoms tend to have fairly large quantities of nectar. Sphingid moths, because of their rapid flight and hovering ability, tend to have a high metabolic rate and are therefore relatively important floral visitors. The absence of need for a landing pad has allowed the petals to form large visual surfaces, odour dispensers and guiding devices for the proboscides. Because moth blossoms flower at night, odour is the major attractant. Fragrances, with a strong sweet perfume are secreted at night, often in quantities too overwhelming for humans (eg Cestrum nocturnum - Faegri and van der Pijl 1979). Although moths can apparently see colours under dark conditions, moth blossoms are generally pale cream or white in colour, although red and drab blossom colours exist. Nectar guides have been shown to illicit the correct probing responses from moths, although guidance is probably more frequently determined by the shape of the blossom.

Visitation by diurnal insects is prevented by nocturnal anthesis and by long-lived blossoms closing during the day. As with flower opening, both nectar and odour secretion occur at night. Visitation by nonhovering insects is prevented by the absence of a landing pad and a long corolla tube. Because moths are not powerful, destructive visitors, moth blossoms are usually soft and fleshy, rather than robust and tough as in bird blossoms, and the versatile anthers are borne well away from the flower and deposit their pollen loads on the head and body of the moths where there is a greater surface area than the proboscis offers.

Moths have been shown to be nonspecific visitors, generally carrying mixed pollen loads, although some discrimination based on odour may exist.

Examples include *Crinum*, *Cyrtanthus*, *Gethyllis* (Amaryllidaceae); *Sansevieria* (Dracaenaceae); *Gladiolus*, *Hesperantha*, *Laperousia*, *Syringodea*, *Tritonia* (Iridaceae); *Habenaria*, *Mystacidium*, *Satyrium* (Orchidaceae); *Thunbergia* (Acanthaceae); *Acokanthera*, *Carissa*, *Pachypodium* (Apocynaceae); *Impatiens* (Balsaminaceae); *Dianthus*, *Silene* (Caryophyllaceae); *Ipomoea* (Convolvulaceae); *Crassula*, *Kalanchoe*, (Crassulaceae); *Erica* subsection *Euryloma* (Ericaceae); *Pelargonium* (Geraniaceae); *Hibiscus* (Malvaceae); *Jasminium* (Oleaceae); *Gardenia*, *Oldenlandia*, *Pavetta*, *Rothmannia* (Rubiaceae); *Cycnium*, *Harveya*, *Manulea*, *Sutera* and *Zaluzianskya* (Scrophulariaceae).

Small bee (Micro-mellitophily)
Short-tongue bee (Mellitophily)
Long-tongue bee (Mellitophily) —— pollination: Mellitophily
Bee fly (Myio-mellitophily)

Many of the 'lower' solitary bees feed on the blossoms of a few plant species, in contrast to social (eg *Apis* - old world and *Melipona* and *Trigona* - old and new world) and 'higher' solitary bees (eg *Bombus*, *Xylocopa* - both old and new world) which tend to visit a large variety of flowers.

Bees provision their progeny with nectar and pollen. They visit large numbers of flowers and, with their predilection towards constancy, are therefore very important pollinators for a large number of plant species.

Bees are powerful and intelligent visitors able to gain access to nectar generally hidden from other insects. They are capable of learning to exploit complex blossoms and can pierce corollas to steal nectar from blossoms otherwise inaccessible to them. Consequently bees tend to utilize all flowers with sufficient nectar or pollen to ensure an energetic profit. However, there is a class of blossoms which are exclusively visited by bees - these are perhaps best typified by the Labiatae, Scrophulariaceae, Papilionaceae and Orchidaceae among the nectar providers, and Rosaceae, Papaveraceae and Rutaceae among the pollen providers.

Bee blossoms tend to be zygomorphic, with hidden nectar in moderate quantities. Flowers have a large depth effect, with an ample landing pad, often with an intricate blocking mechanism preventing unhindered access to the nectar. Flowers are mechanically strong and provide a good foothold. The predominant colours are blue and yellow, usually with a prominent ultraviolet component. Nectar guides are generally present, especially in more complex blossoms. Odours, although not usually strong, are sweet and fresh, often honey-like. The anthers may be hidden, although they are exposed, numerous and prominent in blossoms in which pollen is the major attractant. Generally there are many ovules per ovary.

Vogel (1954) discusses the syndrome of micromellitophily or pollination by very small bees attracted to minute flowers which are attached to the stem on very thin stalks. These flowers may attract visitors by their vibration and movement. Other than their size and motility these resemble other mellitophilous blossoms closely in structure. Examples include: *Eriospermum* (Eriospermaceae); *Litanthus* (Hyacinthaceae); *Melasphaerula* (Iridaceae); *Mysticidium* (Orchidaceae); *Justicia* (Acanthaceae); *Cotula*, *Gymnodiscus*, *Ursinia* (Asteraceae); *Lightfootia*, *Lobelia*, *Wahlenbergia* (Campanulaceae); *Indigofera*, *Psoralea* (Fabaceae); *Pelargonium* (Geraniaceae); *Polygala* (Polygalaceae); *Oldenlandia* (Rubiaceae); *Diascia*, *Nemesia*, *Sutera*, *Utricularia* (Scrophulariaceae); and *Hermannia* (Sterculiaceae) (Vogel 1954).

Likewise, mellitophilous blossoms visited by larger bees (eg *Xylocopa*) tend to be larger, more robust and more complex than those pollinated by smaller bees. However, in other features they parallel mellitophilous blossoms. Examples include: *Aspalathus*, *Indigofera*, *Lebeckia*, *Podalyria*, *Psoralea* and *Virgilia* (Fabaceae).

Buzz pollination is a recently discovered phenomenon which may merit recognition as a syndrome, although as a subset of mellitophily. Buzz pollinated blossoms have anthers with pores, from which the pollen is released only when the entire structure is vibrated at very high frequency. Several bee species (excluding members of the leaf cutting bees, honeybees and Andreniidae) and a species of syrphid fly are capable of obtaining pollen by vibrating blossoms of the 400 plant genera currently known to contain buzz blossoms (Buchman 1983). Buzz pollination has not been recorded from plants in the Cape flora.

Fidelliid bees provision their progeny with oil (Whitehead and Steiner 1985). Oil secreting plant genera include *Diascia*, *Hemimeris* (Scrophulariaceae); *Anochilus*, *Ceratandra*, *Corycium*, *Disperis*, *Evota* and *Pterygodium* (Orchidaceae) (Steiner 1987).

Carrion flower pollination: Sapromyiophily

The Asclepiadaceae, Hydnoraceae and Araceae contain numerous members conforming to the classical sapromyiophilous syndrome. The pollinators of these blossoms include carrion and dung feeding members of both beetles and flies, which visit the flowers seeking both a meal and a site to lay their eggs.

Attraction is primarily by odour which may resemble one of any decaying substance, but generally of a proteinaceous nature. Odour production is often exothermic in nature and may involve marked increase in temperatures in the odour secreting floral parts, which serve to increase the production and volatilization of odours. No incidences of the increased temperature acting as an attractant are recorded in the Cape flora. Colours tend to be dark, dull generally red-mauve or greenish. Fine vibritile hairs, imitation flies (either warts or spotted patterns) and an appropriate texture act as additional lures.

The majority of sapromyiophilous blossoms are also trap blossoms to some degree. These generally involve slippery floral parts, hairs and appendages to prevent premature escape of visitors. Windows, areas of pale colour or transparent tissue, aid in ensuring that insects move into the traps.

Because the attraction of potential pollinators is by deceit and mimicry, no pollen or nectar are offered as rewards. Insects in the traps are released after pollination has occurred. In some blossoms several days may be required for male flowers to mature after female flowers are pollinated, and insects are generally detained till then.

Fungus gnats, Mycetophilidae, which breed in mushrooms, are attracted to flowers which have surfaces resembling mushroom lamellae. These flowers generally have a mushroom-like odour and may have the petals drawn out into long appendages. Like other sapromyiophilous blossoms they are dull red or mauve in colour, but the mushroom lamellae are generally white. Larvae hatch in blossoms, but generally perish due to lack of food (Meeuse and Morris 1984).

CONCLUSIONS

On the whole very little is known about the insect pollinators of the Cape flora. Although observations on insect pollinators have been made since the turn of the century, the majority of these are anecdotal and refer only to flower visitors, with little attempt to verify the presence of particular pollens or to analyse the effect of these visitors on the species or the community.

Since pollination is usually an essential process in the long term survival of plant species, and insects are the most numerous and probably the most important pollinating agents, this is a serious shortcoming in our attempt to understand the various plant/pollinator systems. To develop management strategies for conservation and regeneration of some or all the elements of a particular plant population, the complex relationship between pollinators and plants must be investigated and understood.

The plant/pollinator relationship has many facets, gene flow studies, seed production, identity, distribution and behaviour of pollinators, effect of competition, energetics of pollen production and collection, to name a few. Well planned investigations will be required to provide answers to many aspects of the relationship. This chapter has not only attempted to show how little detailed information is available but by referring to the major works on insect pollination has made guide lines available to future workers in the field.

REFERENCES

Anderson R H, Buys B and Johannsmeier M F 1983. Beekeeping in South Africa. Department of Agriculture Bulletin No 394.

Anonymous (editor) 1979. Reproduction in flowering plants. New Zealand Journal of Botany 17, 425-685.

Armstrong J A, Powell J M and Richards A J 1982. Pollination and evolution. Royal Botanic Gardens, Sydney.

Baijnath H and Ramcharun S 1983. Aspects of pollination and floral development in Ficus capensis Thunb. (moraceae). Bothalia 14, 883-888.

Baker H G 1985. Trends in pollination biology. Aliso 11, 213-228.

Baker H G and Hurd P D 1968. Intrafloral ecology. Annual Review of Entomology 13, 385-414.

Barraclough D A and Londt J G H 1985. Order Diptera. In: Scholtz C H and Holm E (editors) Insects of southern Africa. Butterworths, Durban.

Barth F G 1985. Insects and flowers: the biology of a partnership. George Allen and Urwin, London.

Beattie A J, Turnbull C, Knox R B and Williams E G 1984. Ant inhibition of pollen function: a possible reason why ant pollination is rare. American Journal of Ecology 71, 421-426.

Bentley B and Elias T 1983. The biology of nectaries. Columbia University Press, New York.

Bond W J and Slingsby P 1983. Seed dispersal by ants in shrublands of the Cape Province and its evolutionary implications. South African Journal of Science 79, 231-233.

Bowden R N 1978. Diptera. In: Werger M J A (editor) Biogeography and ecology of southern Africa. W Junk, The Hague.

Brantjes N B M 1978. Sensory responses to flowers in night-flying moths. In: Richards A J (editor) The pollination of flowers by insects. Academic Press, London. pp 13-20.

Brauns H 1926. A contribution to the knowledge of the genus Allodape. Annals of the South African Museum 23, 417-433.

Buchmann S L 1983. Buzz pollination in Angiosperms. In: Jones C E and Little R J (editors) Handbook of experimental pollination biology. Van Nostrand Reinhold, New York.

Claassens A J M and Dickson C G C 1974. The early stages of Aloeides thyra (L.)(Lep. Lycaenidae) with notes on ant associations, distribution and general ecology of the species. Entomologist's Rec. Journal Var. 86, 253-258.

Claassens A J M and Dickson C G C 1980. The butterflies of the Table Mountain range. Struik, Cape Town.

Clark G C and Dickson C G C 1971. Life histories of the South African Lycaenid butterflies. Purnell, Cape Town.

Coetzee J H and Giliomee J H 1985. Insects in association with the inflorescence of Protea repens (L.) Proteaceae and their role in pollination. Journal of the Entomological Society of South Africa 48, 303-314.

Coetzee J H and Latsky L M 1986. Faunal list of Protea repens (L.) L. Acta Horticulturae 185, 241-246.

Cottrell C B 1978. Aspects of the biogeography of southern African butterflies. Supplement to Zambezia, 1978.

Dickson C G C and Kroon D M (editors) 1978. Penningtons butterflies of southern Africa. Donker, Johannesburg.

Eardley C D 1985. Apoidea; Masaridae. In: Scholtz C H and Holm E (editors) Insects of southern Africa. Butterworths, Durban.

Faegri K 1965. Reflections on the development of pollination systems in African Proteaceae. Journal of South African Botany 31, 133-136.

Faegri K and van der Pijl L 1979. The principles of pollination biology. Pergammon Press, Oxford.

Force D C 1981. Post-fire insect succession in southern California chaparral. American Naturalist 117, 575-582.

Frankie G W, Opler P A and Bawa K S 1976. Foraging behaviour of solitary bees: implications for outcrossing of a neotropical forest species. Journal of Ecology 64, 1049-1057.

Galil J 1977. Fig biology. Endeavour 1, 52-56.

Gess F W 1968. Insects found on proteas. Journal of the Botanical Society of South Africa 54, 29-33.

Giliomee J H 1986. Hunting for insect pollinators on fynbos flowers. Veld and Flora 72, 6-7.

Grant V and Grant K A 1965. Flower pollination in the Phlox family. Columbia University Press, New York.

Hagerup O 1932. On pollination in the extremely hot air at Timbuctu. Dan Botaniser Ark 8.

Heinrich B 1975. The role of energetics in bumblebee-flower interrelationships. In: Gilbert L E and Raven P H (editors) Coevolution of animals and plants. University of Texas Press, Austin.

Heinrich B 1979. Resource heterogeneity and patterns of movement in foraging bumblebees. Oecologia 140, 235-245.

Heinrich B 1983. Insect foraging energetics. In: Jones C E and Little R J (editors) Handbook of experimental pollination biology. Van Nostrand Reinhold, New York.

Heinrich B and Raven P H 1972. Energetics and pollination ecology. Science 176, 597-602.

Henning S F 1983. Biological groups within the Lycaenidae (Lepidoptera). Journal of the Entomological Society of southern Africa 46, 65-86.

Henning S F 1984. Life history and behaviour of the rare myrmecophilus lycaenid Erikssonia acraenia Trimen (Lepidoptera: Lycaenidae). Journal of the Entomological Society of southern Africa 47, 337-342.

Hermann J M 1985. Insect pollination of some Erica species in the south western Cape. Veld and Flora 71, 57-59.

Hickman J C 1974. Pollination by ants - a low-energy system. Science 184, 1290-1292.

Janzen D H 1979. How to be a fig. Annual Review of Ecology and Systematics 10, 13-51.

Jones C E and Little R J (editors) 1983. Handbook of experimental pollination biology. Van Nostrand Reinhold, New York.

Kevan P G and Baker H G 1983. Insects as flower visitors and pollinators. Annual Review of Entomology 28, 407-453.

Kullenberg B and Bergstrom G 1976. The pollination of Ophrys orchids. Botaniser Notiser 129, 11-20.

Macswaine J W, Raven P H and Thorp R W 1973. Comparative behaviour of bees and Onagraceae IV. Clarkia bees of the Western United States. University of California Publications in Entomology 70, 1-80.

Marloth R 1896. The fertilization of Disa uniflora Berg by insects. Transactions of the South African Philosophical Society 8, 93-95.

Marloth R 1903. Some recent advances on the biology of Roridula. Annals of Botany 17, 151-157.

Marloth R 1907. Notes on the morphology and biology of Hydnora africana. Thunb. Transactions of the Philosophical Society of South Africa 16, 465-468.

Marloth R 1913-1925. The flora of South Africa (2 Volumes). Darters and Company, Cape Town.

Meeuse B and Morris S 1984. The sex life of flowers. Faber and Faber, London.

Michener C D 1970. Nest sites of stem and twig inhabiting African bees (Hymenoptera: Apoidea). Journal of the Entomological Society of Southern Africa 33, 1-22.

Michener C D 1979. Biogeography of the bees. Annals of the Missouri Botanical Gardens 66, 277-347.

Moldenke A R 1976. Evolutionary history and diversity of bee faunas of Chile and Pacific North America. Wassmann Journal of Biology 34, 147-178.

Moll E J, Mckenzie B and Mclachlan D 1980. A possible explanation for the lack of trees in the fynbos. Cape Province, South Africa. Biological Conservation 17, 221-228.

Moor F D de 1985. Meloidae. In: Scholtz C H and Holm E (editors) Insects of southern Africa. Butterworths, Durban.

Mostert D P, Siegfried W R and Louw G N 1980. Protea nectar and satellite fauna in relation to thefood requirements and pollination role of the Cape Sugarbird. South African Journal of Science 76, 409-412.

Muller H 1873. Die Befruchtung der Blumen durch Insecten. Engelman, Leipzig.

Nicholson S 1981. The flight of the Carpenter Bee. South African Journal of Science 77, 152.

Paton J 1986. The role that insects play in the pollination of Protea neriifolia and Protea eximia. Unpublished Zoology Honours Project, University of Cape Town, Cape Town.

Pearson H H W 1907. Notes on South African cycads I. Transactions of the South African Philosophical Society 16, 341-352.

Phillips J 1926. Virgilia capensis: a contribution to its ecology and silviculture. South African Journal of Science 23, 435-454.

Pierce S M 1984. A synthesis of plant phenology in the fynbos biome. South African National Scientific Programmes Report No 88. CSIR, Pretoria. pp 57.

Porsch O 1929. Die Bedrohung der Lebensgemeinschaft Blume und Vogel. Buletinul Facultatii de Stiinte din Cernauti 3, 193-207.

Proctor M L and Yeo P 1973. The pollination of flowers. Collins, London.

Pyke G H 1978. Optimal foraging movement patterns of bumblebees between inflorescences. Theoretical Population Biology 13, 72-98.

Rattray G 1913. Notes on the pollination of some South African cycads. Transactions of the Royal Society of South Africa 3, 259-270.

Real L (editor) 1983. Pollination Biology. Academic Press, London.

Rebelo A G 1987. Mass emigration of the kelp flies (Coelopidae). Journal of the Entomological Society of southern Africa 50,257-258.

Rebelo A G, Siegfried W R and Crowe A A 1984. Avian pollinators and the pollination syndromes of selected Mountain fynbos plants. South African Journal of Botany 3, 285-296.

Rebelo A G, Siegfried W R and Oliver E G H 1985. Pollination syndromes of Erica species in the south western Cape. South African Journal of Botany 51(4), 270-280.

Richards A J (editor) 1978. The pollination of flowers by insects. Academic Press, London.

Robertson H G 1980. Pollination of selected Erica species in the Cape Fynbos. Unpublished Zoology Honours Project, University of Cape Town.

Scholtz C H and Holm E (editors) 1985. Insects of southern Africa. Butterworths, Durban.

Steiner K E 1987. Oil-producing orchids and oil-collecting bees in southern Africa. Paper read to the South African Association of Botanists 1987 Annual Congress (Durban).

Steiner K E and Whitehead V B 1985. The association between oil-flowers and oil-collecting bees in the Drakensberg of southern Africa. (Paper read at the Association pour le étude taxonomique de la Flora de l'Afrique Tropical Synposium, St Louis, Missouri).

Stoutemire W P 1974. Australian terrestrial orchids, thynnid wasps and pseudocopulation. American Orchid Society Bulletin 1974, 13-18.

Strickler K 1979. Specialization and foraging efficiency of solitary bees. Ecology 60, 998-1009.

Trimen R 1864. On the fertilization of Disa grandiflora. Journal of the Linnean Society of Botany 7, 144-147.

Van Wyk S 1983. 'n Monographiese studie van die genus Virgilia Poir. Unpublished MSc Thesis. University of Stellenbosch, Stellenbosch. 177 pp.

Vogel S 1954. Blütenbiologische Typen als Elementeder Sippengliederung dargestellt anhand der Flora Südafrikas. Fischer. Verlag, Jena.

Vogel S 1974. Ölblumen und Ölsammelende Bienen. Tropische Subtropische Pflanzenwelt 7, 285-547.

Vogel S 1984. The Diascia flower and its bee - an oil-based symbiosis in southern Africa. Acta Botanica Neerlandica 33, 509-518.

Waterhouse D F (editor) 1980. The insects of Australia. Melbourne University Press, Carlton.

Watmough R H 1974. Biology and behaviour of Carpenter Bees in southern Africa. Journal of the Entomological Society of southern Africa 37(2), 261-281.

Whitehead V B 1984. Distribution, biology and flower relationships of fideliid bees of Southern Africa (Hymenoptera, Apoidea, Fideliidae). South African Journal of Zoology 19, 87-90.

Whitehead V B and Prins A J 1975. The European Wasp Vespula germanica (F.) in the Cape Peninsula. Journal of the Entomological Society of southern Africa 38, 39-42.

Whitehead V B, Schelpe E A C L E and Anthony N C 1984. The bee, Rediviva longimanus Michener (Apoidea: Melittidae), collecting pollen and oil from Diascia longicornis (Thumb.) Druce (Scrophulariaceae). South African Journal of Science 80, 286.

Whitehead V B and Steiner K E 1985. Oil-collecting bees of South Africa. African Wildlife 39, 144-147.

CHAPTER 4 BIRD POLLINATION IN THE CAPE FLORA

A G Rebelo

Bird pollination is the best studied of the pollination syndromes in the Cape flora, probably because there are only nine avian pollinator species in the Cape floral region. In addition, avian foraging behaviour at flowers is easily observed and ornithophilous flowers tend to be conspicuous. Nevertheless, many putatively ornithophilous plant species have never been assessed for bird pollination in southern Africa, primarily because of the high plant species richness and their restricted, and often remote, distribution ranges.

INTRODUCTION

Although the genera Nectarinia (Nectariniidae) and Promerops (Promeropidae) contain all the southern African avian species which utilize nectar as a major food source, 73 additional species (eight per cent of a total avifauna of about 890 species) have been recorded as opportunistically utilizing nectar as a food source (Oatley 1964; Oatley and Skead 1972). Starlings (Sturnidae), weavers (Ploceidae) and bulbuls (Pycnonotidae) comprise the major groups of opportunistic nectar feeding birds (Oatley and Skead 1972). Members of these families, together with blackheaded orioles Orioles larvatus, forktailed drongos Dicrurus adsimilis, and Cape white-eyes Zosterops pallidus, opportunistically visit a wide variety of nectariferous plants, mainly of the genera Aloe (Asphodelaceae), Erythrina and Schotia (Fabaceae). While these birds probably play a role in the pollination of the plant species they visit, their contribution is possibly overshadowed by the much higher incidence of sunbird visits.

THE ORNITHOPHILOUS SYNDROME

The features of the ornithophilous syndrome (Grant and Grant 1967; Faegri and van der Pijl 1979; Ford et al 1979) are diffuse and centre around making the flowers inconspicuous and energetically uneconomical for insects to visit. This is achieved by relying almost exclusively on the keen vision of avian nectarivores for advertising flowers. Consequently display colours are vivid, often strongly contrasting, and dominated by red, yellow and green, colours which are not visible to most insects or which contrast little with a leafy background. Flower morphology generally has a low figural intensity (proportion of contour length or edge to volume) and a small frontal display area, which decreases its visibility to insects. Landing platforms and nectar guides are absent (although exserted anthers may provide a platform for agile insects such as bees) and flowers are often horizontal or pendant. The tube is often curved, preventing exploitation by visitors with straight mouthparts. Odours are absent, thus providing no olfactory cues to insects. Nectar is dilute (eight to 25 per cent sucrose equivalents), and thus falls below the optimum for most insect visitors.

Features which are primarily adaptations to bird visits also exist. Perches to support the relatively heavy avian visitors are required. Floral parts are robust, especially where these may form part of the perch, but also to prevent nectar thieving, both by insects and by other bird species. Nectar production and floral anthesis peak in the early morning when birds tend to be most active. Selected features are discussed below.

Blossom classes

Two major classes of bird blossoms, viz the brush and the tube type (Faegri and van der Pijl 1979) comprise the majority of the ±320 ornithophilous species in the Cape flora (Table 4.1).

The tube type is defined as having a narrow tube which excludes most nectar feeding visitors with mouthparts shorter than the effective tube length (Faegri and van der Pijl 1979). The tube type is the dominant type in bird pollinated plants, but since insects may be predominant visitors to those species with protruding anthers (eg Aloe), tube blossoms must further be divided into those with internal anthers (tube) and those with anthers exserted (brush-tube). Brush-tube blossoms are thus intermediate between tube and brush blossoms (defined below) in that their pollen, but not their nectar, is accessible to nonavian visitors. Examples of tube blossoms include Anapalina, Erica (sections Pleurocallis, Evanthe, Dasyanthus) and Leonotis. Brush-tube blossoms include Aloe, Erica (section Gigandra) and Kniphofia. Tubes generally vary in length from about 10 mm to 55 mm (Aloe = 40,1 ± 6,7 mm (N = 24 species in Cape Floral Kingdom); Erica = 19,3 ± 6,0 mm (N = 63, all south-western Cape ornithophilous species)) in length. While the average tube length of Erica closely matches the bill length of its principal pollinator, the orangebreasted sunbird (Rebelo and Siegfried 1985; Rebelo et al 1985), the longer tube of Aloe species are formed by unfused corolla lobes which accommodate the entire heads of sunbirds (Reynolds 1982).

The brush type of blossom is defined as having an external surface of the pollination unit formed by the sexual organs, with the perianth reduced or split into segments interspersed between the sexual organs (Faegri and van der Pijl 1979). Generally the style and the anthers protrude to the same level, about one beak's length (10 to 36 mm) above the nectar source. Flowers are usually grouped into inflorescences in which the individual flowers are difficult to discern since they form a continuous display unit. Examples include the inflorescences of the Proteaceous genera Protea and Leucospermum, and the introduced genus Eucalyptus (Myrtaceae). Brush type flowers are seldom visited exclusively by birds, but may represent a generalized adaptation to pollination by a large array of visitors, biased to visits by large pollinators in relation to flower size (Stiles 1981). Large numbers of bees, and often beetles, visit brush flowers, even when birds appear to be legitimate pollinators of these plants (Gess 1968; Coetzee and Giliomee 1985). Certainly, the concentration of nectar exposed to the environment will increase due to evaporation, especially on hot, dry days (Corbet et al 1979) when insects are most active. Sunbirds and sugarbirds appear to stop foraging on Virgilia oroboides, Brunia albiflora, Oldenbergia grandis and Protea species earlier on warmer days, but whether this is due to competition with insects or a greater energy intake requirement under cooler conditions, is not known. In addition, bees may collect pollen, not removed by earlier bird activity, from flowers. Thus, while insects may pollinate flowers sufficiently to allow seed set in Protea repens from which birds have been excluded (Coetzee and Giliomee 1985), this does not rule out the possibility that birds, by foraging earlier in the morning when the flowers open, may account for the majority of pollen transfer under natural conditions. The same may be true for those Aloe species with exserted anthers, and which are heavily visited by bees during the middle of the day (Anderson et al 1983). Increased bee activity due to the introduction of apiaries may drastically reduce sunbird visits to some plant species (eg Leucospermum oleifolium at the Kirstenbosch National Botanic Gardens; Erica perspicua at Betty's Bay (A G Rebelo personal observation)).

However, certain members of the genus Protea (viz sections Speciosae and Ligulatae (in part)) have awns on the perianth segments, which overtop the sexual organs to form a landing platform for avian pollinators, and which protect the pollen from bee removal. These 'bearded proteas' are additionally visited by a large number of beetle species, and appear to be preferred by Protea mites Proctolaelaps species (Ryke 1964) which are phoresic on both the bird and insect visitors. The importance of these arthropods as pollinators of bearded Protea species or as a protein source for breeding sugarbirds and sunbirds is unknown.

The tube is the dominant blossom shape for hummingbird flowers in the New World, whereas in Australia brush-blossoms dominate the honeyeater pollinated flora, occurring prominently in the Fabaceae, Myrtaceae and Proteaceae (Keighery 1982). In southern Africa seven genera possess brush blossoms versus 29 with tube blossoms (Table 4.1). Eight genera with tubular blossoms have exposed anthers and are regularly visited, and probably pollinated, by bees in addition to birds.

Perch provision

Since neither the Nectariniidae or the Promeropidae readily hover, but prefer to forage from a perch, a perch capable of supporting a six to 40 gram visitor is required in ornithophilous plants in the Cape flora. Few flowers are structurally capable of achieving this, and various forms of perches exist.

The majority of tube-blossom plant species have inflorescence peduncles which serve as perches (Aloe), while others have the flowers associated with older wood (Erica, Erythrina) or thick stems (Halleria). Other species have special perches:

- Strelitzia has a modified spathe and tepals;
- Antholyza has a downy leafless 'stem';
- Saltera has four to five robust flowers grouped into a tube reinforced by robust bracts; and
- Retzia has the flowers supported in a dense cluster of leaves.

Ornithophilous Erica species have significantly thicker stems than either entomophilous or anemophilous species, presumably to support the weight of their large perching avian pollinators (Siegfried et al 1985).

Brush inflorescences provide perches by massing large numbers of robust flowers. In ornithophilous species of Protea, Leucospermum and Aloe longistyla the landing platform is provided by a central mass of unopened flowers. However, sections Ligulatae and Speciosae of Protea have awns on

TABLE 4.1 Plant genera considered by Scott-Elliot (1890) = S; Porsch (1924, 1929) = P; Marloth (1931) = M; Vogel (1954) = V; Skead (1967) = K; Oatley and Skead (1972) = 0; and A G Rebelo personal observation = A to contain ornithophilous species (ie plants apparently morphologically adapted to bird pollination).

GENUS (family)	NO OF SPECIES[1]		BLOSSOM TYPE[2]	OBSERVED VISITORS	SOURCE
	In Cape flora	Bird visited			
Brunsvigia (Amaryllidaceae)	10	4 (4)	gullet	N chalybea	A
Cyrtanthus (Amaryllidaceae)	19	6 (6)	tube	-	M, V
Haemanthus (Amarylldaceae)	9	6 (6)	brush	N chalybea	P, V, A
Aloe (Asphodelaceae)	26	85 (24)	br/tb	various (see 0)	M, V, 0
Gasteria (Asphodelaceae)	29	? (?)	tube	-	V
Kniphofia (Asphodelaceae)	6	6 (6)	br-tb	-	V
Albuca (Hyacinthaceae)	11	1 (1)	tube	N chalybea	A
Daubenya (Hyacinthaceae)	0	1 (0)	tube	-	V
Lachenalia (Hyacinthaceae)	60	4 (4)	tube	-	P, V
Massonia (Hyacinthaceae)	8	1 (1)	gullet	-	P, V
Polyxena (Hyacinthaceae)	2	1 (1)	brush	-	V
Veltheimia (Hyacinthaceae)	1	1 (1)	tube	-	-
Anapalina (Iridaceae)	7	7 (7)	tube	-	V
Anomalesia (Iridaceae)	2	3 (2)	tube	-	V
Antholyza (Iridaceae)	2	2 (2)	br-tb	-	V
Babiana (Iridaceae)	36	1 (1)	br-tb	-	S, M, V
Chasmanthe (Iridaceae)	3	3 (3)	tube	N violacea	S, P, V
Crocosmia (Iridaceae)	0	3 (0)	gullet	-	V
Gladiolus (Iridaceae)	69	5 (5)	gullet	N afer	V
Homoglossum (Iridaceae)	10	10 (10)	gullet	-	V
Klattia (Iridaceae)	2	2 (2)	brush	N violacea	A
Witsenia (Iridaceae)	1	1 (1)	brush	-	V
Watsonia (Iridaceae)	39	5 (5)	gullet	N chalybea, famosa, violacea	M, V, A
Disa (Orchidaceae)	54	2 (2)	tube	-	V
Satyrium (Orchidaceae)	27	1 (1)	gullet	N chalybea	(V), A
Strelitzia (Strelitziaceae)	3	5 (1)	flag	N spp	K
Oldenburgia (Asteraceae)	4	1 (1)	brush	P cafer	A
Mystropetalon (Balanophorac)	2	2 (2)	br-tu	N violacea	A
Tecomaria Bignoniaceae)	1	1 (1)	tube	N spp	S, V, K
Lobostemon (Boraginaceae	28	1 (1)	gullet	various	V, A
Brunia (Bruniaceae)	7	2 (2)	brush	N famosa, violacea, P cafer	A
Lonchostoma (Bruniaceae)	5	1 (1)	tube	-	A
Schotia (Caesalpiniaceae)	0	9 (0)	br-tb	N spp	S, V
Cadaba (Capparaceae)	1	1 (1)	tube	N fusca	M, V, K
Combretum (Combretaceae)	0	1 (0)	brush	-	V
Cotyledon (Crassulaceae)	10	1 (1)	tube	N spp	M, V
Crassula (Crassulaceae)	97	1 (1)	tube	N violacea	M, A
Kalanchoe (Crassulaceae)	1	2 (2)	tube	-	V
Tylecodon (Crassulaceae)	7	1 (1)	tube	-	V

TABLE 4.1 (continued)

GENUS (family)	NO OF SPECIES[1]		BLOSSOM TYPE[2]	OBSERVED VISITORS	SOURCE
	In Cape flora	Bird visited			
Erica (Ericaceae)	540	96 (96)	br-tb/tb	N famosa, violacea	V, R
Pelargonium (Geraniaceae)	125	1 (1)	tube	-	V
Streptocarpus (Gesneriaceae)	2	1 (1)	tube	-	V
Greyia (Greyiaceae)	0	3 (0)	brush	-	M, V
Leonotis (Lamiaceae)	2	9 (2)	tube	N spp	S, M, V
Salvia (Lamiaceae)	16	1 (1)	tube	N spp	S, V
Moquinella (Loranthaceae)	1	1 (1)	tube	N fusca	V, K
Septulina (Loranthaceae)	2	2 (2)	tube	N fusca	V, K
Tapinanthus (Loranthaceae)	0	7 (0)	tube	N famosa, fusca	V, K
Hibiscus (Malvaceae)	6	1 (1)	funnel	-	M,V
Nymania (Meliaceae)	1	1 (1)	funnel	-	M, V
Melianthus (Melianthaceae)	3	2 (2)	funnel	-	S, V
Crotalaria (Papilionaceae)	3	1 (1)	flag	N afra	V
Erythrina (Papilionaceae)	1	3 (1)	flag	various	S, V, K, O
Liparia (Papilionaceae)	2	2 (2)	flag	N violacea	M, V
Sutherlandia (Papilionaceae)	2	1 (1)	flag	N spp	S, V
Salteria (Peneaceae)	1	1 (1)	tube	N famosa	S, M, V, A
Faurea (Proteaceae)	1	1 (1)	brush	-	M
Leucospermum (Proteaceae)	44	34 (34)	brush	N famosa, violacea, P cafer	K
Mimetes (Proteaceae)	12	12 (12)	br-tb	N famosa, violacea, P cafer	K
Protea (Proteaceae)	69	33 (33)	brush	various	K
Retzia (Retziaceae)	1	1 (1)	tube	N violacea, P cafer	M, V, A
Burchellia (Rubisceae)	1	1 (1)	tube	N afra	V
Alberta (Rubiaceae)	0	1 (0)	tube	-	V
Dermatobothrys (Scrophul.)	0	1 (0)	tube	-	V
Halleria (Scrophulariaceae)	3	4 (3)	tube	N spp	M, V
Harveya (Scrophulariaceae)	12	3 (3)	tube	-	V
Hyobanche (Scrophulariaceae)	4	7 (4)	tube	-	V
Phygelius (Scrophulariaceae)	0	2 (0)	tube	-	V
Lycium (Solanaceae)	5	? (2)	br-tb	-	K
Nicotiana (Solanaceae)	0	1 (0)	tube	N famosa, fusca	M, V, K
TOTAL	424 (318 IN THE CAPE FLORAL KINGDOM)				

[1] Data for bird pollinated plant species are not available for Cape flora specifically, but for southern Africa. Estimates of the number of species in the Cape Floral Kingdom (sensu Bond and Goldblatt 1984) are in parenthesis.

[2] Br-tb refers to the brush-tube blossom category; br/tb refers to genera with either tube or br-tb type species.

the perianth segments which overtop the stigma and pollen presenter and form a permanent landing platform for avian pollinators. An exception to both these categories is Protea aurea in which the florets bend outwards to form a flattened wheel on which sugarbirds perch. Brunia has many small, shallow, delicate flowers, supported by hard woody bracts and conglomerated into dense ball-like inflorescences, which, in turn, are aggregated into flat-topped conflorescences, which function as feeding platforms. In Mimetes the brush-tube inflorescences are aggregated into columnar brush conflorescences, which occur immediately below the flattened feeding platform formed by leaves at the branch tip.

In certain plant species, avian visitors must perch on the ground adjacent to the flower in order to forage (eg Liparia, Mystropetalon, Protea acaulos, Protea scabra). By contrast, flowers of 73 species (in 21 genera) in Western Australia, which are regularly visited by birds, require birds to perch on the ground to forage, although many of these species may be visited by mammals as well (Keighery 1982).

The role of perches requires further investigation, since nectar thieving is often achieved by birds utilizing novel perching positions. Thus sunbirds often cling to the outer involucral bracts of Protea inflorescences and probe between the bracts in order to obtain otherwise inaccessable nectar (Skead 1967). In doing so they do not contact the plant's sex organs and therefore do not effect pollination. However, in P lepidocarpodendron gaps (windows) exist between the inflorescence bracts, at the level of the pollen presenters and stigmatic surfaces. It is not known if sugarbirds and sunbirds probing inflorescences through these windows may transfer pollen.

Colour

Birds are able to perceive colour over the entire spectrum between red through to far ultraviolet (Goldsmith 1980), and although spectral sensitivity and finest hue discrimination occur in the longer wavelengths (red), the situation is complicated, relative to mammal vision, by the complex interplay of cone pigments and coloured oil droplets (Stiles 1981). The tendency of ornithophilous floral colours to range over the red end of the electromagnetic spectrum is attributable to the inability of many insects, especially social bees, to detect light of long-wavelength (Raven 1973). Other floral colours cryptic to insects include yellow and green, since these have a low contrast with foliage (assuming they do not reflect ultra-violet light differently from foliage), but can readily be discerned by the keen eyesight of birds.

The majority (49%) of bird pollinated Erica species monomorphic for flower colour are red, with yellow being second in importance (18%). White (including cream) and green each contribute a further 12% and pink and purple together comprise only nine per cent of ornithophilous Erica species. In comparison, 45% of insect pollinated Erica species are pink or purple and 36% are white (Rebelo and Siegfried 1985). Similarly 65% of monomorphic Aloe species are red, with only five per cent of species pink (data from Reynolds (1982) from species list in Bond and Goldblatt (1984)). Only one out of 80 species of a related, smaller-flowered, insect pollinated genus Haworthia is red, the majority of species (80%) being white (data from Scott 1985). Among the Proteaceae (Rebelo and Rourke unpublished) 83% of the species in Mimetes are either red, orange or yellow. In the genus *Leucospermum* the majority of species (57%) are yellow, with orange and red flower colours confined to bird pollinated species (30% of bird pollinated species). In *Protea* pink and white are the predominant colours, irrespective of the putative pollination syndrome.

Red (49%), white (26%) and yellow (24%) predominate among the bird pollinated species in the south-western Australian flora (Keighery 1982). In addition, dull, hidden flowers also occur in the Australian flora and are extensively visited by birds (Keighery 1982). In the Cape flora *Protea* species of the section *Pinifolia* and *Crateriflora* have hidden flowers which are often visited by birds, but which appear to be predominantly rodent pollinated (Breytenbach and Rebelo this volume). However, the incidence of plant species which appear to share both bird and mammal pollinators appears to be far greater in Australia than in southern Africa.

Colour polymorphism

Significantly more bird pollinated *Erica* species are polymorphic for colour (ie have populations of plants with different floral colours on separate plants) than are insect pollinated species. Colour combinations with red occur in 80% of polymorphic bird pollinated species, while 93% of insect pollinated species have pink morphs. Only four *Aloe* species are colour polymorphic for colour (Reynolds 1982), but none of the insect pollinated *Haworthia* species are recorded as being colour polymorphic (Scott 1985). All seven colour polymorphic *Leucospermum* species are bird pollinated, and of the 29 colour polymorphic *Protea* species 79% are bird pollinated, the remainder being rodent pollinated. With the exception of *Mimetes cucullatus* (bird pollinated), only three other Proteaceae (all insect pollinated) are polymorphic for flower colour (Rebelo and Rourke unpublished). Pink, white and red are the predominant colour combinations in colour polymorphic *Protea*.

The significance of these patterns of colour polymorphism are not known. It is possible that bird pollinated species experience greater gene flow between populations and less discriminatory selection against rarer colour morphs than do insect pollinated species. Thus, while insect pollinated species may tend to speciate or reduce the frequency of rare morphs, bird pollinated species may tend to hybridize or form variable populations. The most extreme polymorphic species in the Proteaceae (*Protea cynaroides*, *P longifolia* and *P magnifica*) and the Ericaceae (*Erica coccinea*, *E longifolia*, *E macowanii* and *E plukenetti*) are all bird pollinated (Baker and Oliver 1967; Rourke 1980; Rourke and Rebelo unpublished). It may be incorrect to infer that colour polymorphism reflects genetic polymorphism in plant populations, as flower colour may be a highly variable feature which may have evolved as a means of optimally achieving gene flow. Elucidation of the dynamics of colour polymorphism requires a detailed knowledge of the breeding systems of plant species, for which data are not available. However, two of the most colour polymorphic species (ie *Protea longifolia* and *Erica longifolia*) in the Cape flora rank as the most promiscuous species in their genera with regard to hybridization with other species (Rourke 1980; A G Rebelo personal observation).

Polychromatic blossoms

An additional feature of bird pollinated species, not adequately investigated in the Cape flora, is the presence of polychromatic blossoms, in which flowers or inflorescences possess strikingly different 'parrot' colours (Faegri and van der Pijl 1979). These may be produced in a variety of ways:

- by possessing contrasting colours on a single blossom part (eg *Erica macowanii*, *Witsenia morea*, both on the corolla; *Protea lepidocarpodendron* on the involucral bracts);
- by having different colours on different floral parts (eg *Mimetes* species, *Protea magnifica*, bracts and flowers; *Aloe* species and *Erica coccinea*, corolla and anthers); and
- due to age-related colour changes in blossoms on inflorescences (eg *Aloe microstigma*, *Leucospermum oleifolium*), or inflorescences on conflorescences (*Mimetes hirtus*).

Polychromatism is related to visual attraction and in inflorescences, aids the orientation of visitors to recently opened flowers, but does not function as do nectar guides in insect pollinated blossoms.

Colour in bird pollinated plants thus plays the major role in selective advertisement of flowers. While many features appear to hinder visibility to insects, colour polymorphism hints that selective pressures on flower colour vary between potential pollen vectors, with birds being less discriminating in their choice of flower colour.

DISTRIBUTION PATTERNS OF ORNITHOPHILOUS PLANTS WITHIN THE CAPE FLORA

The four per cent incidence of ornithophilous plant species (318) (as determined by floral morphology) relative to the total Cape flora (8 504 species) is double that of the two per cent incidence of ornithophily (424 out of 21 350) for southern Africa (Table 4.1). Thus, 75% of the ornithophilous plant species in southern Africa occur in the Cape flora.

However, the proportional representation of ornithophily within the vegetation types of the Cape flora is largely unknown. The major families contributing to the high levels of ornithophily in the Cape flora are the Ericaceae (ie *Erica*) and Proteaceae, which contribute 30% and 25% of the ornithophilous species respectively (Table 4.1). Both these families are largely confined to the sandstone-derived 'nutrient-poor soils' (depauperate in nitrogen, phosphorus and potassium) of the region, as are several related plant families and genera in which ornithophily has arisen independently: Asteraceae (*Oldenburgia*), Bruniaceae (*Brunia*, *Lonchostoma*), Peneaceae (*Saltera*) and Retziaceae (*Retzia*). Similarly, many ornithophilous geophyte and monocot species (eg *Anapalina*, *Chasmanthe*, *Homoglossum*, *Watsonia*, and *Witsenia*) occur on the relatively nutrient-poor soils of the Cape flora.

The incidence of ornithophilous species at Hangklip is greatest in the Coastal (Sand Plain Lowland) Fynbos and Mountain Fynbos vegetation assemblages, which occur on the relatively nutrient-poor soils (unpublished). By contrast, few plant species are bird pollinated in the calcium rich soils of Strandveld plant assemblages at Hangklip. The majority of ornithophilous Strandveld plants flower in the early seral stages following fire or disturbance (eg Anomalesia, Brunsvigia, Haemanthus, Leonotis, Salvia and Satyrium), although Lobostemon (Boraginaceae) occurs in mature Strandveld assemblages (A G Rebelo personal observation). Likewise in forests at Hangklip (including riverine, scree and kloof forest sensu Boucher (1978)) only Halleria lucida and Protea mundii (an early seral colonizer) are ornithophilous. Bird pollinated species are absent in littoral dune and marsh assemblages at Hangklip.

The incidence of ornithophilous plant species is also low in Renosterveld and Karoo plant assemblages, both of which typically occur on relatively nutrient-rich soils, derived from shales. Examples of ornithophilous species in these vegetation types include Aloe, Gasteria, Kalanchoe and Tylecodon, all of which are either leaf or stem succulents. In these assemblages nonsucculent ornithophilous plant species typically occur only in water courses: Nicotiana and various hemiparasites (Septulina and Tapinanthus).

This pattern of high ornithophilous plant species richness on nutrient-poor soils (either derived from Table Mountain Sandstone - Mountain Fynbos plant assemblages; or aeolian sands - Sand Plain Fynbos) might perhaps be explicable in terms of plant-nutrient resources and water relationships: plants growing on nutrient-poor soils, are capable of producing a surfeit of carbon (including energy) relative to other nutrients, which may be utilized in the production of phenols, tannins, lignins, sclerophyllous tissues, nectar and wood (Bloom et al 1985). It follows, therefore, that these plants should produce relatively few seeds compared to plants under more nutrient-rich conditions, since seeds require nutrient reserves to establish themselves, especially under nutrient-poor conditions. If fewer seeds are produced, each provisioned with nutrients, these will be ideal food sources, and may need protection, for example, by serotiny or myrmechochory. Similarly, the production of energy- and carbon-rich floral stuctures, to support potentially heavy avian pollinators, may be possible. Furthermore, except during the summer drought period, water is adequately available. Consequently, the production of large quantities of nectar, which is energy and water expensive, may not affect the growth and reproduction of plants, and may allow large populations of nectarivorous birds (and mammals) to be sustained. In addition, large numbers of flowers may be produced relative to the potential production of nutrient-rich seed (Rebelo and Rourke 1986), so increasing the total nectar production.

By contrast, in the vegetation assemblages growing on relatively 'nutrient-rich' soils (Renosterveld and Karoo), energy and water may be limiting factors relative to the supply of other nutrients. Consequently, it may be possible for plants to produce many seeds, perhaps limited mainly by the relative amount of carbon available. The lower carbon to nitrogen ratio and the higher plant productivity should support a greater herbivore biomass, some of which could potentially be pollinators (Diptera, Lepidoptera and Hymenoptera (Apoidae)). Similarly, if pollen production is not limited by nutrients which may be needed for pollen-tube growth, more pollen may be produced, allowing a high bee population to be maintained. These insect pollen vectors require cheaper floral structures and rewards (nectar and pollen), in terms of the carbon balance of plants, than do birds. If water and carbon are relatively limiting then production of the copious nectar required for bird pollination might not be sustainable. This may help to explain why Renosterveld, Karoo and Strandveld plant species appear to produce flowers which are smaller than those produced by Mountain Fynbos species. It might also explain the lack of ornithophily and therophily in plant assemblages on nutrient-rich soils.

The most notable exception to the low incidence of ornithophily on nutrient-rich soils occurs in some Aloe-dominated Renosterveld and Karoo plant assemblages. Most aloes in the Cape flora flower during winter, when water is abundant.

A similar pattern in the distribution of ornithophily occurs in Australia, where bird pollination is concentrated in the southern heathlands of the Stirling/Eyre Provinces of Western Australia (Keighery 1982). The percentage of ornithophilous species relative to the total flora of Western Australia is 7,4% for tropical flora, 5,6% for desert flora, and 15% for temperate flora. Keighery (1982) cites the continuous cold and wet weather on the southern coast (which may be unsuitable for insect activity), which allows a year-round growth season and protracted flowering seasons, together with adequate soil water levels (which may allow the production of large amounts of nectar) as factors contributing to this preponderence of high species richness of ornithophilous plants. As in the Cape flora, ornithophily in the temperate region of Western Australia is insignificant in foreshore regions, swamps and salt lakes, and is most prominent in woodland and heathland assemblages, which tend to occur on nutrient-poor lateritic and sand substrata (Keighery 1982).

Patterns of variation in the proportion of ornithophilous plant species to the total flora of other mediterranean regions or the tropics are not readily available, but we predict that ornithophily will be relatively uncommon in those mediterranean regions which lack nutrient-poor soils (cf Ford (1985) for Europe; Grant and Grant (1967) for California; Johow (1898) for Chile). Based on these assumptions we predict that ornithophily within the tropics should occur on predominantly nutrient-poor substrata, and should occur in parallel with trends towards sclerophylly.

Unfortunately, a paucity of studies of pollination syndromes at the community-scale prevents the ready testing of correlations, such as the one described above, in any detail. A fundamental question regarding ornithophily in the Cape flora, is whether unrelated plant species in a particular vegetation assemblage are more similar in the floral attributes which constitute ornithophily (eg pigmentation, corolla morphology, robustness, nectar constitution and quantity, pollen-ovule ratios etc) than are the ornithophilous species in other vegetation assemblages.

PATTERNS OF AVIAN NECTARIVORE DISTRIBUTION AND COMMUNITY ORGANIZATION

Eight species of sunbird occur in the Cape flora (Skead 1967) of which six occur in the Cape Floral Region (sensu Bond and Goldblatt 1984). In addition, a single species of Promerops, the Cape sugarbird P cafer, occurs in the southern and south-western Cape. Six species of nectarivorous birds occur in Cape Fynbos Shrublands (fynbos, renosterveld and strandveld), five in Karroid Shrublands, seven in Subtropical Transitional Thicket, and two in Afromontane Forest (Table 4.2; vegetation assemblages sensu Moll et al 1984)). Only two nectarivore species, the Cape sugarbird and the orangebreasted sunbird N violacea, are endemic to the southern and south-western Cape. Both endemic species are confined to fynbos, where they may comprise the dominant avian component, both numerically and in terms of biomass (Siegfried 1983), and frequently occur on distant, isolated fynbos outliers (Skead 1967).

The low number of putatively avian pollinator species contrasts strongly with the large number of ornithophilous plant species in Mountain Fynbos (Rebelo et al 1984). Compared with other plant assemblages and geographical zones (Table 4.3), the ratio of ornithophilous plant species to avian pollinators is particularly high. The high ratio for the south-western Cape is due partly to a decline in species richness of avian nectarivores (Nectariniidae) with latitude in southern Africa, and partly to the high plant species richness of the Cape flora. In other areas, high values tend to occur on smaller islands further from the mainland (Feinsinger et al 1982); with increasing altitude (Grant and Grant 1967) and with smaller size of study area, especially where plant species have restricted local distributions (Table 4.3).

The significance of the ratio between pollinators and their flowers is that it reflects the relative specialization of interactions between the plants and their avian pollinators. Thus assemblages with a low ratio of birds to plants tend to have more generalist plant and bird species, while high ratios may indicate specialist, tightly coevolved relationships. This relationship is also dependent on the geographical seasonal phenology of the plant species. Interactions tend to be more specific in hummingbird associations and less specific in honeyeater associations in the tropics, and tend to be less specific where plant productivity is lower (eg increased altitude, increased latitude) and where bird populations may be restricted for other reasons (eg smaller island sizes). Whether these generalizations can be extended to decreased productivity under nutrient-poor conditions or restrictions in avian population size by patchy environments remain to be tested.

Recorded foodplant preferences of the eight southern Cape avian nectarivores reflect their habitat preferences (Tables 4.2 and 4.4), in addition to displaying a catholic foraging behaviour. It appears that avian nectarivores utilize all nectariferous plant species to which they have access. For example, when all three avian nectarivore species are present in Mountain Fynbos, sugarbirds tend to forage preferentially on Proteaceae, orangebreasted sunbirds on Erica species, and malachite sunbirds N famosa on geophytes (Siegfried 1983; Rebelo et al 1984). However, these patterns break down when one or more species are absent.

TABLE 4.2 Habitat distribution (Skead 1967; Maclean 1985) and mensural data (Maclean 1985; Safring unpublished; Fraser and Seiler unpublished), for the nine species of avian nectarivore occurring in the south and south-western Cape. Vegetation assemblages are delimited as in Moll et al (1984)

SPECIES	MASS (g) (female, male)	CULMEN LENGTH (mm)	WING LENGTH (mm) (female, male)	HABITAT[1]					
				Fynbos	Renosterveld	Strandveld	Karroid shrubland	Subtropical thicket	Afromontane forest
Anthreptes collaris	6- 9, 6- 9	13-15	48-50, 49-54					+	+
Nectarina afra	8-11, 11-13	24-29	58-64, 61-70	+			++	+++	
N amethystina	8-17, 10-17	25-30	65-69, 71-76	+			+	+	
N chalybea	6-10, 6-10	18-23	47-53, 52-58	+	++	++	++	+	++
N famosa	12-16, 15-21	29-34	66-72, 76-86	++	++	++	++	++	
N fusca	8 - 10	18-22	48-52, 54-59				++	+	
N veroxi	9-12, 9-12	24-27	56-62, 59-67					++	
N violacea	8-10, 9-11	20-23	52-57, 50-52	+++					
Promerops cafer	29-39, 34-40	30-36	80-84, 90-98	+++					

[1] Present + ; common ++ ; abundant +++

TABLE 4.3 Relationships between the number of putative avian pollinator species and associated ornithophilous plant species. Except where indicated data are as in Rebelo et al (1984)

Number of bird species[1] (A)	Number of ornithophilous plant species[2] (B)	Ratio (B:A)	Locality	Region	Reference
SITE SPECIFIC STUDIES					
Hummingbird-sapsucker Associations					
7	1-2	0,1-0,3	Lowlands	California	Grant and Grant 1967
7	5-6	0,7-0,9	Highlands	California	Grant and Grant 1967
14	10	1,4	Monteverde	Costa Rica	Feinsinger 1978
11	15	1,4	Fonte, Andes	Colombia	Snow and Snow 1980
8	11	1,4	Toqui, Andes	Colombia	Snow and Snow 1980
+20	+31	1,6	Andes	Venezuela	Stiles 1981
11	19	1,7	Las Tuxtlas	Mexico	Stiles 1981
9	17	1,9	Las Canas	Costa Rica	Wolf 1970
12	24	2,0	Andes	Colombia	Snow and Snow 1980
7	14	2,0	San Blas	Mexico	Montgomerie and Gass 1981
1	2	2,0	Grizzly Lake	California	Montgomerie and Gass 1981
6	12	2,0	Sta Monica	California	Stiles 1981
1	2	2,0	Andes	Chile	Arroyo et al 1982
22	50	2,2	Finca La Salvia	Costa Rica	Stiles 1981
4	9	2,3	White Mountains	Arizona	Brown and Kodric-Brown 1979
8	18	2,3	Santa Rosa	Costa Rica	Stiles 1981
21	+55	+2,6	La Mort	Costa Rica	Stiles 1981
6	17	2,8	Cloud forest, Chirripo	Costa Rica	Wolf et al 1976
12	33	2,8	Arima valley, Trinidad	West Indies	Stiles 1981
12	(58)	(6,4)	Arima valley, Trinidad	West Indies	Snow and Snow 1972
6	18	3,0	Villa Mills	Costa Rica	Stiles 1981
5	19	3,8	Cerro	Costa Rica	Wolf et al 1976
3	12	4,0	Middle forest, Chirripo	Costa Rica	Wolf et al 1976
5	20	4,0	High oak forest, Chirripo	Costa Rica	Wolf et al 1976
1	8	8,0	Paramo, Chirripo	Costa Rica	Wolf et al 1976
Honeycreeper Associations					
3	2	0,7		Hawaii	Pimm and Pimm 1982
Honeyeater Associations					
30	+21	+0,7	Mount Lofty Ranges	Australia	Paton and Ford 1977
3	2	0,7	Little Barrier Island	New Zealand	Gaze 1982
7	11	1,6	Wongamine, Adelaide	Western Australia	Collins 1980
Sunbird Associations					
7	5.(19)	0,7	Zaria	Nigeria	Pettet 1977
3	6	2,0		Macronesia	Oleson 1985
3	(12)	4,0		Macronesia	Vogel 1984
3	8	2,7	Proteaceous/Ericaceous moorland	Kenya	Cheke 1971
6	18	3,0	Secondary forest	Kenya	Cheke 1971
4	14	3,5	Ericaceous moorland	Kenya	Cheke 1971
3	24	8,0	Jonkershoek	South-western Cape	Rebelo et al 1984
3	29	9,7	Mountain Fynbos, Kleinmond	South-western Cape	Rebelo unpublished data
4	45	11,3	Kleinmond	South-western Cape	Rebelo unpublished data
REGIONAL SUMMARIES					
16	17.(34)	1,1	Trinidad	West Indies	Feinsinger et al 1982
25	47	1,9	Eastern Andes	Colombia	Snow and Snow 1980
5	13.(30)	2,6	Tobago	West Indies	Feinsinger et al 1982
7	19	2,7		California	Grant and Grant 1967
+55	+150	2,7		Costa Rica	Stiles 1981
(75)	(300)	4,0		Costa Rica	Stiles 1981
10	34	3,4	High altitudes	Kenya	Cheke 1971
6	25	4,2	Chirripo	Costa Rica	Wolf et al 1976
20	+240	+12,0	non temperate	Southern Africa	herein
+72	1000	13,9		Australia	Ford et al 1979
7	129	18,4	western	USA	Austin 1975
22	+560	+24,5		southern Africa	herein
+22	608	27,6	south-western	Australia	Keighery 1982
1	31	31,0	Eastern	USA	Austin 1975
6	+200	+33,3	south-western Cape	South Africa	Rebelo et al 1984
9	320	35,6		Cape flora	herein

[1] Figures in parenthesis include opportunistic nectar feeders.
[2] Figures in parenthesis include nonornithophilous plant species occasionally visited by birds.

TABLE 4.4 Primary food plants visited by avian nectarivores in the southern and south-western Cape (Skead 1967; Maclean 1985). Important exotic species are included in parentheses.

NECTARIVORE	PRIMARY FOODPLANTS
Anthreptes collaris	primarily insects, Burchellia, Halleria, Schotia, Erythrina, Xeromphis, also seeds and berries
Nectarinia afra	Erica, Aloe, Protea, Schotia, Erythrina, Salvia, Cotyledon, Gasteria, Tecomaria, Strelitzia, Plumbago, Hibiscus, (Canna), spiders, insects
N amethystina	Strelitzia, Schotia, Moquinella, Bauhinia, Watsonia, Crotalaria, Aloe, Salvia, Hibiscus, Tecomaria, Protea, Kniphofia, Royena, Erythrina, Cassia, (Tithonia, Eucalyptus, Cestrum, Pointsettia, Canna), spiders, insects
N chalybea	Cotyledon, Erythrina, Schotia, Cadaba, Lycium, Protea, Aloe, Salvia, Tecomaria, Bauhinia, Moquinella, Septulina, Lachenalia, Phygelius, Virgilia, Erica, Lobostemon, Carissa, Cissus, (Albuca, Nicotiana, Eucalyptus), spiders, insects
N famosa	Protea, Mimetes, Chenolea, Lycium, Strelitzia, Tecomaria, Erica, Erythrina, Leonotis, Halleria, Aloe, Leucospermum, Cotyledon, Kniphofia, Watsonia, Melianthus, Buddleja, Greyia, Chasmanthe, (Nicotiana, Opuntia, Gladiolus), insects, spiders
N fusca	Aloe, Moquinella, Septulina, Lycium, Cadaba, (Nicotiana, Canna, Hibiscus, Lantana, Oleander), insects
N veroxi	Moquinella, Septulina, Leonotis, Strelitzia, Schotia, Erythrina, Scadoxus, Aloe, spiders, insects
N violacea	Erica, Protea, Leucospermum, Mimetes, Lobostemon, Lobelia, Leonotis, Liparia, (Eucalyptus), insects, spiders
Promerops cafer	Protea, Leucospermum, Mimetes, Aloe, Tecomaria, Erica, Watsonia, Kniphofia, (Agave, Eucalyptus), insects, spiders

For example, in the absence of Cape sugarbirds, large groups of malachite sunbirds may forage from *Leucospermum conocarpodendron* at Cape Point, although they are scarce in these plant assemblages when sugarbirds are present (A G Rebelo personal observation).

This lack of apparent specific pollinator-plant association is also observable in foraging choices of birds at mixed food sources. Skead (1967) states that 'sunbirds take nectars as they come' and 'do not seem to have any particular preference'. Orangebreasted sunbirds appear to forage without preference in habitats containing several ornithophilous *Erica* species, often transferring pollen between species (unpublished data). Nor is foraging restricted to classically ornithophilous plants. Orangebreasted sunbirds and lesser doublecollared sunbirds *Nectarinia chalybea* frequently visit (and transport pollen of) typically bee and carpenter bee plant species (eg *Aspalathus*, *Podalyria*, *Psorales*, *Virgilia* (Fabaceae, flag-blossoms) and *Polygala* (Polygalaceae, flag-blossom), especially in the early mornings and during inclement weather, when these insects are less active (Collins and Rebelo in press; A G Rebelo personal observation).

The factors which limit distributions of avian nectarivores in southern Africa are incompletely known. Sugarbirds are limited in their distribution range to the occurrence of *Protea* species. Whereas the Cape sugarbird is confined to Mountain and Sand Plain Fynbos assemblages (sensu Moll et al 1984), *Promerops gurneyi*, a congeneric species, occupies *Protea*-dominated assemblages in Natal and Transvaal (Skead 1967). Similarly, while orangebreasted sunbirds are largely confined to areas containing *Erica* species, it is not obvious why they do not occur in other vegetation assemblages which contain species with morphologically similar flowers. The impression that orangebreasted sunbirds occur in dense patches of nectar-producing flowers from which they exclude lesser doublecollared sunbirds, is extremely difficult to test, since population manipulation experiments are limited by the large sizes of the highly mobile bird populations. Nevertheless, many Mountain Fynbos assemblages appear to be underutilized by avian nectarivores during winter, perhaps due to a summer dearth in nectar availability which may limit population sizes (unpublished data).

Distribution ranges of avian nectarivores may be influenced by the abundance of different insect food sources. Avian nectarivores require protein for growth, moult and breeding, and may be considered as insectivorous birds which utilize nectar as an energy source to enable the exploitation of otherwise uneconomical insect prey as a food source. Thus the gut contents of sunbirds may contain very small insects, similar to those exploited by specialist aerial feeders, such as swallows (J S Taylor, quoted by Skead 1967). Avian nectarivores obtain insects both by probing crevices, and by hawking flying insects. Species differ in the extent of their hawking activity, which may relate to the importance of insects in their diet. The lesser doublecollared sunbird appears to depend most on insects, followed by the malachite, orangebreasted sunbird and Cape sugarbird (A G Rebelo personal observation). However, breeding Cape sugarbirds forage from *Protea* species, utilizing both nectar and insects found in the inflorescences (Mostert et al 1980), and the above sequence may merely reflect the proportion of insects gleaned by the species while feeding in *Protea* inflorescences. However, hawking activity in Cape sugarbirds varies between localities, and while common at Kirstenbosch National

Botanic Gardens during June 1985, was seldom observed at Cape Point during the same period (W Seiler personal communication). In addition, breeding activity of Cape sugarbirds is linked to the flowering of certain Protea species (Winterbottom 1962), rather than to periods of maximum insect abundance (insect data from Schlettwein 1984).

Culmen length, mass and wing-loading do not assist in predicting which species of avian necativore may co-occur in different assemblages, since many coexisting species overlap in these characters (Table 4.3). Culmen lengths and bill curvature determine the foraging efficiencies of sunbirds at flowers, not only by restricting access to nectar, but also by influencing the rate of nectar uptake per probe (Gill and Wolf 1978). In addition, bill width and depth determines the range of flowers for which birds have legitimate access to nectar.

Body mass plays an important role in determining foraging efficiency: Yellowbellied sunbirds Nectarinia venusta, feeding at Aloe graminicola, take longer to extract nectar per flower than malachite sunbirds. But, because of their smaller size, their foraging efficiency is nearly equivalent to that of malachite sunbirds, despite their shorter beak which limits foraging to flowers with high nectar volumes (Wolf and Wolf 1976). Body size also plays a role in determining the costs of moving between flowers, which varies inversely with flower density and increases with larger body size (Wolf and Gill 1980). In addition, larger avian nectarivores tend to dominate smaller species during aggressive interactions (Skead 1967; Wolf 1978). However, the level of aggression varies with resource availability, so that Cape sugarbirds territorial on Protea lepidocarpodendron exclude malachite sunbirds while tolerating the smaller orangebreasted sunbirds (unpublished data), but exclude both species when territorial on Mimetes hirtus (Collins 1983a,b,c).

The species spectrum of nectarivorous birds within plant assemblages may be determined by the degree of monopolization by larger, more aggressive species (Wolf 1978). In addition, the number of avian species in pollinator communities is limited by the diversity and patterns of phenology of the plant species. Thus, single flower systems (large, localized, monospecific stands of a single species, which flower for a short period) of East Africa limit the number of sunbird-pollinator species, because each bird species must be able to visit a wide spectrum of morphologically diverse plant species through the year (Wolf 1978). By contrast, the Neotropical hummingbird communities, with their more diverse flower systems, support a much larger array of more specialized pollinator species.

Cape Fynbos Shrublands appear to be intermediate between the Neotropical and East African systems, with various ornithophilous Erica species forming a 'single year' round resource, with which the orangebreasted sunbird has evolved a close relationship (Table 4.3). Similarly, the Proteaceae and Cape sugarbirds appear to form a similar coevolved system. No such associations appear to exist for the lesser doublecollared sunbird or the malachite sunbird, both of which are highly itinerate (Siegfried 1983). Consequently, the malachite sunbird appears to be a generalist, exploiting ephemeral resources, such as geophytes in early seral succession stages, and dense patches of short blooming species, such as Leonotis which occurs in disturbed Strandveld assemblages. Even rich nectar sources which consistently bloom every season, such as many Aloe species, may not be visited by malachite sunbirds in some years, and yet team with them in others (Skead 1967). Apparently, greater doublecollared Nectarinia afra and black sunbirds N amethystina, while also itinerate, tend to be more faithful in returning to Aloe stands in the Karroid Shrublands (Skead 1967).

Avian nectarivores comprise up to 50% of the avian biomass in Mountain Fynbos assemblages, but less than five per cent of the total avian biomass in Sand Plain Fynbos, Renosterveld and Strandveld assemblages (Table 4.5; Siegfried 1983). However, Renosterveld and Strandveld have two-to-six times the avian biomass of Mountain and Sand Plain Fynbos. The difference in proportional avian nectarivore biomass between these assemblages reflects both a greater incidence of nectarivores and a greater proportion of birds using the nectar-arthropod resource base in Mountain Fynbos (Siegfried 1983).

PLANT PHENOLOGY AND POLLINATOR MIGRATION

General phenological patterns of plants in the fynbos biome have been reviewed by Pierce (1984), but species were not considered with regard to pollination biology. Data analysed by Pierce (1984) which revealed that a single species of Proteaceae in any pollinator category blooms in any month, do not always conform to observed community patterns at Hangklip, as the data were collected in well defined assemblages. Normally assemblages intergrade or occur in close association, such that three Protea species (coronata, lepidocarpodendron and mundii) and Mimetes cucullatus may bloom simultaneously within 20 m of one another during June (A G Rebelo personal observation). Phenological data are often site specific, with adjacent populations flowering at different times. This is most noticable in the highly variable Erica (coccinea, macowanii, and plukeneti) and Protea (cynaroides, nitida and repens) species, whose flowering phenology appears to vary considerably with altitude, relief and geographic location (A G Rebelo personal observation).

Seasonal flowering patterns in the dominant ornithophilous genera in the Cape flora display a variety of patterns (Table 4.6). Leucospermum displays a spring peak in flowering abundance, which closely matches that of other Proteaceae genera with myrmechochorous seeds, suggesting that flowering in these genera is regulated by seed dispersal requirements (Lamont et al 1985; Collins and Rebelo in press). Aloe and Protea exhibit winter-spring peaks in flowering, while Mimetes displays a distinct winter peak. Interpretation of these patterns is complicated by the large distribution ranges of these genera within the Cape flora. Data for ornithophilous Erica species in the south-western Cape display bimodal autumn and spring peaks in flowering. Continuous year round availability of nectar is thus provided by Erica, Mimetes and Protea (Table 4.6), although seldom in the same plant assemblages. By contrast, related insect-pollinated species tend not to present flowers during winter months, and bloom for shorter periods than bird (or mammal) pollinated species (Table 4.6).

Few pollination-orientated phenological studies have been undertaken in assemblages of the Cape flora. In Mountain Fynbos at Jonkershoek bird

TABLE 4.5 Relative species richness and percentage standing crop biomass of nectarivorous, granivorous, frugivorous and insectivorous birds in Mountain Fynbos, Sand Plain Fynbos, Renosterveld and Strandveld assemblages. Data from Siegfried (1983) and Siegfried and Crowe (1983)

Avian guild	Proport per guild			
(N)	Mountain Fynbos 8	Sand Plain Fynbos 2	Renosterveld 1	Strandveld 2
SPECIES RICHNESS				
Nectarivore	12-27	4-6	9	6-8
Insectivore	30-55	48-51	38	46-57
Frugivore	0-10	3-11	12	7-8
Granivore	20-44	37-40	41	29-38
Total species	8-23	27-35	34	35-39
BIOMASS				
Nectarivore	50,5	2,9	1,4	2,9
Insectivore	30,3	39,7	21,6	22,4
Frugivore	0,0	1,4	3,6	20,2
Granivore	11,5	59,9	70,0	51,9
Total biomass (kg 100 ha^{-1})	9,4-4,1	8,1-0,3	45,9	44,1-2,1

TABLE 4.6 Proportional flowering phenology of species and distinct subspecies in major ornithophilous and related insect and wind pollinated plant genera (with more than 10 ornithophilous species) in the Cape Floral Region (*sensu* Bond and Goldblatt 1984)

Genus (Family)	No of species	Proportion of species flowering per month												Average flowering period (months)	References
		J	F	M	A	M	J	J	A	S	O	N	D		
BIRD POLLINATED															
Aloe (Asphodelaceae)	24	25	13	8	4	25	29	42	38	50	29	21	21	3,1 + 1,9	Reynolds 1982
Erica (Ericaceae)	66[1]	55	50	48	57	53	47	47	47	58	57	53	48	7,9 + 3,3	Rebelo unpublished
Leucospermum (Proteaceae)	34	35	9	6	6	9	9	41	77	100	97	88	77	5,5 + 2,1	Rebelo and Rourke unpublished
Mimetes (Proteaceae)	12	25	33	42	42	58	67	67	67	58	58	50	42	6,1 + 3,8	Rebelo and Rourke unpublished
Protea (Proteaceae)	33	36	30	27	52	58	67	67	67	73	55	42	36	5,4 + 2,8	Rebelo and Rourke unpublished
INSECT POLLINATED															
Haworthia (Asphodelaceae)	100	19	21	16	8	0	0	4	11	26	43	40	20	2,1 + 0,3	Scott 1985
Erica	314[1]	63	51	46	44	31	29	36	43	67	73	74	71	6,2 + 2,9	Rebelo unpublished
Leucospermum	14	29	0	0	0	0	0	29	79	93	100	100	79	5,1 + 0,9	Rebelo and Rourke unpublished
Protea	4	0	25	25	25	0	0	50	50	50	75	50	25	3,8 + 1,0	Rebelo and Rourke unpublished
MAMMAL POLLINATED															
Leucospermum	1	0	0	0	0	0	0	100	100	100	100	100	0	5	Rebelo and Rourke unpublished
Protea	33	21	15	18	12	30	42	55	64	67	48	33	18	4,1 + 1,3	Rebelo and Rourke unpublished
WIND POLLINATED															
Erica	17[1]	24	24	29	41	47	65	82	76	94	88	59	53	6,7 + 3,0	Rebelo unpublished

[1] South-western Cape only

pollinated Protea species tend to flower during autumn and winter while other Proteaceae tend to flower in summer (Rebelo et al 1984). Within the genus Protea, high altitude species tend to flower for shorter periods in summer (one to three months) compared to the longer blooming species which peak in winter (six to nine months). Likewise bird pollinated Erica species at Jonkershoek show the same pattern (three to four versus one to 12 months for summer and winter peaking species respectively), although the trend is complicated by winter-blooming species having a much greater altitudinal range than summer blooming species. Summer blooming Erica species at Jonkershoek, however, are confined to high altitude seeps and marshes (Rebelo et al 1984). Only two bird pollinated Erica species flowered during spring, while a similar nectar dearth in Protea occurred in early summer.

These patterns suggest that water availability may have been an ultimate influence on flowering phenology of bird pollinated plant species: during winter, species at low altitudes bloom when rainfall is high, but at high altitudes low temperatures may freeze nectar or prevent its secretion in large quantities. During summer, water availability may limit copious nectar secretion by bird pollinated plant species at low altitudes, but the frequent mist precipitation at high altitudes (Nagel 1961) provides sufficient water for copius nectar production. The pattern of a long, continuous blooming season at lower altitudes in winter versus a short boom in flower production at high altitudes in summer, may be due to a shorter effective growth period at higher altitudes because of cold winter conditions (Rebelo et al 1984). The above hypothesis would also account for the winter spring blooming peak in Aloe species in karroid assemblages.

Work undertaken at Hangklip confirm these above trends for Mountain Fynbos assemblages (unpublished data). However, coastal flats assemblages (Sand Plain Fynbos) behave differently because flowering in bird pollinated species tends to occur in spring and autumn. This is consistent with the above hypothesis if waterlogging, due to water draining from the mountains, restricts root metabolism during winter. In this regard it is important that phenological studies include altitudinal and geographical variation so that such hypotheses may be tested.

Seasonal and altitudinal patterns of bird movement

Skead (1967) recorded malachite and lesser doublecollared sunbirds as predominantly summer visitors to the Strandveld communities on the Cape Flats. This is not borne out by the preliminary Bird Atlas data (supplied by courtesy of the Cape Bird Club; Rebelo and Prys-Jones unpublished), which show a winter peak (April to August) in observations on the Cape Flats (largely Strandveld and gardens) and, even more markedly, in the Swartveld (Renosterveld and wheatland). Squares containing predominantly Sand Plain Fynbos display a winter peak in abundance of malachite and lesser doublecollared sunbirds. In south coast Strandveld, lesser doublecollared and malachite numbers appear to remain constantly high throughout the year. In Mountain Fynbos malachite sunbird abundance peaks in winter in the north (Clanwilliam), but remains constantly high all year in the south. The greater doublecollared sunbird occurs largely in the east of the Cape flora and shows a summer peak in abundance, apparently being absent from the area in winter. However, interpretation of these trends is complicated by the large areas surveyed, which include many vegetation types, surveys which are largely confined to roads, and which may be biased by seasonal differences in bird visibility, due either to moulting or altitudinal migration of bird species.

Atlas data for sugarbirds and orangebreasted sunbirds are easier to interpret. Orangebreasted sunbirds are largely confined to Mountain Fynbos, being far more common in the south (south of Bainskloof) than in the north, where they are recorded only sporadically, suggesting that they are less common in the drier Mesic Mountain Fynbos. While they are invariably absent from Sand Plain Fynbos, they do occur in Limestone Fynbos in lower numbers (A G Rebelo personal observation). Seasonal abundance of orangebreasted sunbirds in Mountain Fynbos is either constant throughout the year, or shows a slight decline in summer, perhaps attributable to an upward altitudinal migration to areas where summer blooming _Erica_ species occur (Rebelo et al 1984). The Cape sugarbird follows a similar pattern to orangebreasted sunbirds in Mountain Fynbos, but additionally occurs in Sand Plain Fynbos during winter. Rebelo et al (1984) found that Cape sugarbirds disappeared from the _Protea_ stands in Jonkershoek State Forest during summer. Some birds were seen at higher altitudes probing off the summer-blooming Proteaceae, but too few were seen to account for the entire winter populations. Large numbers of birds enter gardens during summer (Skead 1967), which is reflected in the Bird Atlas data for squares with large urban and peri-urban coverage (eg Bellville, Stellenbosch, Somerset West).

No studies have been undertaken specifically to ascertain the movements of nectarivores in the southern and south-western Cape. At Hangklip, Cape sugarbird populations are confined to _Leucospermum conocarpodendron_ and _Mimetes hirtus_ populations during summer (unpublished data). Both plant species occur in dense stands in lowland areas, which are rapidly being urbanized. The effect of large-scale decline in these resources due to urbanization is unknown. Further evidence that there is a summer dearth of nectar in Mountain Fynbos is the summer influx of Cape sugarbirds into suburban gardens (Skead 1967). The effect of early colonist activity in removing summer flowering _Protea_ species from the Cape Flats are unknown. Certainly, long-term conservation of Mountain Fynbos assemblages is linked to continued existence of lowland food sources as far as avian pollinators are concerned. Various introduced _Eucalyptus_ species, both in plantations and gardens, appear to provide nectar for sugarbirds during this period.

ORIGINS AND EVOLUTION OF ORNITHOPHILY

The incidence of bird pollination is most marked in the tropics with the Neotropical (±320 species regular visitors; 450 species total suspected visitors), Australasian (±200; 308), Oriental (±70; 187), and Afrotropical (±55; 154) regions containing far more nectarivorous species than the Neartic (±10; 33) or Palaeartic (±5; 5) regions (Stiles 1981). Of these pollination systems the major research has been undertaken in the Australian and Neotropical regions.

Bird pollination in Australia is characterized by extremely locally abundant sources of nectar, particularly in nutrient-poor vegetation assemblages (cf Keighery 1982), such that birds do not appear to exhaust supplies. Between nectar flushes are long periods of low nectar availability, and many species of honeyeaters and lories are social and highly nomadic (Stiles 1981). Consequently, birds appear adapted to the flora as a whole, whereas the plants are generalist species, with a high preponderance of brush blossoms (Paton and Ford 1977). Tube-blossoms often have lateral slits, allowing access to a wide range of bill lengths (Ford et al 1979).

By contrast, the Neotropical communities show a much greater degree of specialization (Stiles 1981), with many plant species normally visited by a few species of hummingbirds. Hummingbirds comprise the hermits, which trapline, and the nonhermits, which partition floral resources by flower morphology, patch size and flower density. Hummingbird associations appear to be structured around dominance and interspecific territorial interactions. Nonhermit hummingbirds tend to be most prominent in the canopies of wet lowland forest, dry forest, montane and subalpine habitats, reaching their greatest diversity in the tropical highlands. Hermits dominate understorey wet tropical forest and riverine habitats with scattered flowers, and are usually associated with the large monocot herbs of the Scitamineae. The few perching nectarivores (Icteridae) in the Neotropics tend to occur in the dry tropical lowlands, and in the drier areas of Mexico. The vast majority of Neotropical ornithophilous plants are herbs, shrubs, small trees and epiphytes, with few canopy trees, while in Australia canopy trees may dominate ornithophilous plant communities (Stiles 1981).

Bird pollination in the Neartic (Stiles 1981) is characterized by highly migratory hummingbird species, which segregate geographically or by habitat during the breeding season. Birds are morphologically rather uniform and do not discriminate between various ornithophilous flower species. Likewise, ornithophilous flowers tend to be uniform, and seem to have converged in morphology and attraction, with brush-blossoms featuring prominently.

Of the mediterranean regions, only the Cape flora and south-western Australian flora compare with the tropical pollination systems in terms of the numbers of bird, and especially, plant species. These are associated with the nutrient poor soils, in these biomes, and the lack of similar communities in Chile, California and the Mediterranean may be attributable to their not possessing any similar substrata.

Since fossils of flower-visiting bird taxa do not appear before the Pleistocene, and because the different continental blocks are dominated by different, unrelated families, ornithophily must have evolved independently in the different continents, probably only originating in the early- to mid-Tertiary (Stiles 1981). However, among the plants the southern families Proteaceae, Myrtaceae, Ericaceae-Epacridaceae appear exceptionally predisposed to ornithophily. That this may have evolved independently in response to environmental constraints is the most plausible hypothesis, especially since ornithophilous genera belong to different subfamilies, which are largely isolated on different continents. However, certain anomalies (eg ornithophilous primitive Asteraceae (section Mutisieae) in South America and Africa; and Erythrina species) may suggest that ornithophily may be considerably older than the Tertiary, and may have had a Gondwanaland precursor.

CONCLUSION

The syndrome of bird pollination is largely confined to the nutrient-poor soils of Mountain Fynbos and Lowland Fynbos plant communities, and is relatively depauperate in renosterveld, strandveld and karoo vegetation types. This relationship to soil nutrient status, paralleled and more marked in Australia, suggests that ornithophily may have evolved in communities where carbon is relatively freely available and large inflorescences and prodigous nectar quantities are easily produced. This hypothesis deserves further investigation.

The provision of perches for nectarivores by plants may also bear further investigation, especially in relation to the purported thieving of nectar by sunbirds, probing Protea inflorescences from between the involucral bracts, and thus, supposedly, circumventing access to the pollen presenters and stigmatic surfaces. The 'windows' in some Protea involucral bracts suggest that such feeding may result in effective pollination.

Colour polymorphism is far more frequent in ornithophilous plant species than in any other syndrome in the Cape flora. It is proposed that this is due to birds ignoring colour differences in flowers, under conditions in which insects would not visit rare colour morphs, resulting in pollen flows between populations, which would have speciated if insect pollinated. In addition, the proposed longer gene flow distances and interspecific pollen transfer experienced in bird mediated pollen transfer may contribute to colour polymorphism in species. However, while colour polymorphism may reflect greater polymorphism in bird pollinated species, it may equally well merely be a signal evolved primarily to achieve optimal gene flow by birds. The significance of colour polymorphism in terms of genetic heterogeneity of ornithophilous species, and its relation to pollen transfer distances needs to be assessed.

While it would be of interest to ascertain why the Cape sugarbird and orangebreasted sunbird are relatively confined to fynbos, and why lesser doublecollared sunbirds are usually absent from fynbos, a more pertinent question is where these birds forage during periods of nectar dearth (summer). The highly itenerant Malachite sunbird is also interesting in this regard. These data are essential, especially in light of the apparent importance of Lowland Fynbos as a summer nectar source and the impending threat of urbanization of much of these areas. If these summer resources are essential in maintaining avian nectarivore numbers, the loss of these habitats may result in a collapse of the winter-bird pollination system. The conservation of the lowlands deserves top priority as the interrelationships between the different vegetation types in the Cape flora are completely unknown.

REFERENCES

Anderson R H, Buys B and Johannsmeier M F 1983. Beekeeping in South Africa. Department of Agricultural Technical Services Bulletin Number 394.

Arroyo M T K, Primackn R and Armesto J 1982. Community studies in pollination ecology in the high temperate Andes of central Chile. I. Pollination mechanisms and altitudinal variation. American Journal of Botany 69, 82-97.

Austin D F 1975. Bird flowers in the eastern United States. Florida Science 38, 1-12.

Baker H A and Oliver E G H 1967. Ericas in southern Africa. Purnell, Cape Town.

Bloom A J, Chapin F S and Mooney H A 1985. Resource limitation in plants - an economic analogy. Annual Review of Ecology and Systematics 16, 363-392.

Bond P and Goldblatt P 1984. Plants of the Cape flora: a descriptive catalogue. Journal of South African Botany, Supplement 13.

Boucher C 1978. Cape Hangklip area. II. The vegetation. Bothalia 12, 455-497.

Brown J H and Kodric-Brown A 1979. Convergence, competition, and mimicry in a temperate community of hummingbird pollinated flowers. Ecology 60, 1022-1035.

Cheke R A 1971. Feeding ecology and significance of interspecific territoriality of African montane sunbirds (Nectariniidae). Rev. Zool. Bot. Afr. 84, 50-64.

Coetzee J H and Giliomee J H 1985. Insects in association with the inflorescences of Protea repens (L.) L. (Proteaceae) and their role in pollination. Journal of the Entomological Society of southern Africa 48, 303-314.

Collins B G 1980. Seasonal variations in the abundance and food preferences of honeyeaters (Meliphagidae) at Wongamine, Western Australia. Western Australia Naturalist 14, 207-212.

Collins B G 1983a. Seasonal variation in the energetics of territorial Cape sugarbirds. Ostrich 54, 1-13.

Collins B G 1983b. Pollination of Mimetes hirtus (Proteaceae) by Cape sugarbirds and orange-breasted sunbirds. Journal of South African Botany 49, 125-142.

Collins B G 1983c. A first approximation of the energetics of Cape sugarbirds (Promerops cafer) and the orange-breasted sunbird (Nectarinia violacea). South African Journal of Zoology 18, 363-369.

Collins B G and Rebelo A G (in press). The breeding biology and pollination of Proteaceae in Australia and south western Africa.

Corbet S A, Willmer P G, Beament J W L, Unwin D M and Prys-Jones O E 1979. Post-secretory determinants of sugar concentration in nectar. Plant Cell Environment 2, 293-308.

Faegri K and v d Pijl L 1979. The principles of pollination ecology. Pergamon, Oxford.

Feinsinger P 1978. Ecological interactions between plants and hummingbirds in a successional community. Ecological Monographs 48, 269-287.

Feinsinger P, Wolfe J A and Swarm L A 1982. Island ecology: reduced hummingbird diversity and the pollination biology of plants, Trinidad and Tabago, West Indies. Ecology 63, 494-506.

Ford H A 1985. Nectarivory and pollination by birds in southern Australia and Europe. Oikos 44, 127-131.

Ford H A, Paton D C and Forde N 1979. Birds as pollinators of Australian Plants. New Zealand Journal of Botany 17, 509-519.

Gess F W 1968. Insects found on proteas. Journal of the Botanical Society of South Africa 28, 29-33.

Gill F B and Wolf L L 1978. Comparative foraging efficiencies of some montane sunbirds in Kenya. Condor 80, 391-400.

Goldsmith T H 1980. Hummingbirds see new ultraviolet light. Science 207, 786-788.

Grant K A and Grant V 1967. Effects of hummingbird migration on plant speciation in the Californian flora. Evolution 21, 457-465.

Johow F 1898. Uber ornithophilie in der Chilenischen Flora. Sitzb. Konigl. Press. Akad. Wissen. Berlin 1, 332-341.

Keighery G J 1982. Bird pollinated plants in Western Australia and their breeding systems. In: Armstrong J A, Powell J M and Richards A J (editors) Pollination and evolution. Royal Botanic Gardens, Sydney.

Lamont B, Collins B G and Cowling R M 1985. Reproductive biology of the Proteaceae in Australia and South Africa. Proceedings of the Ecological Society of Australia 14, 213-224.

MacLean G L 1985. Roberts' birds of southern Africa. John Voelcker Bird Book Fund, Cape Town.

Marloth R 1931. The flora of South Africa. 3 Volumes. Darter Brothers, Cape Town.

Moll E J, Campbell B M, Cowling R M, Bossi L, Jarman M L and Boucher C 1984. A description of major vegetation categories in and adjacent to the fynbos biome. South African National Scientific Programmes Report No 83. CSIR, Pretoria. 29 pp.

Montgomerie R D and Gass C L 1981. Energy limitation of hummingbird populations in tropical and temperate communities. Oecologia 50, 162-165.

Mostert D P, Siegfried W R and Louw G N 1980. Protea nectar and satellite fauna in relation to the food requirements and pollinating role of the Cape sugarbird. South African Journal of Science 76, 409-412.

Nagel J F 1961. Fog precipitation in the Table Mountain area with special reference to orographic effects. Notos 10, 59-73.

Oatley T B 1964. The probing of Aloe flowers by birds. Lammergeyer 3, 2-8.

Oatley T B and Skead D M 1972. Nectar feeding by South African birds. Lammergeyer 15, 65-74.

Oleson J M 1985. The Macronesian bird-flower element and its relation to bird and bee opportunists. Botanical Journal of the Linnean Society 91, 395-414.

Paton D C and Ford H A 1977. Pollination by birds of native plants in Australia. Emu 77, 73-85.

Pettet A 1977. Seasonal changes in nectar feeding by birds at Zaria Nigeria. Ibis 119, 291-308.

Pierce S M 1984. A synthesis of plant phenology in the fynbos biome. South African National Scientific Programmes Report No 88. CSIR, Pretoria. 57 pp.

Pimm S L and Pimm J W 1982. Resource use, competition, and resource availability in Hawaiian honeycreepers. Ecology 63, 1468-1480.

Porsh O 1924. Vogelblumenstudien. I. Jarb. Wiss. Bot. 63, 553-706.

Porsh O 1929. Vogelblumenstudien. IV. Biol. Gen. 5, 157-210.

Raven P H 1973. Why are bird-visited flowers predominantly red. Evolution 26, 674.

Rebelo A G and Rourke J P 1986. Seed germination and seed set in the Proteaceae: ecological determinants and horticultural problems. Acta Horticulturae 185, 75-88.

Rebelo A G and Siegfried W R 1985. Colour and size of flowers in relation to pollination of Erica species. Oecologia 65, 584-590.

Rebelo A G, Siegfried W R and Crowe A A 1984. Avian pollinators and the pollination syndromes of selected Mountain Fynbos plants. South African Journal of Botany 3, 285-296.

Rebelo A G, Siegfried W R and Oliver E G H 1985. Pollination syndromes of Erica species in the south western Cape. South African Journal of Botany 51, 270-280.

Reynolds G W 1982. The aloes of South Africa. Balkema, Cape Town.

Rourke J P 1980. The proteas of southern Africa. Purnell, Cape Town.

Ryke P A J 1964. Acarina associated with Protea flowers in the Cape Province. Journal of the Entomological Society of southern Africa 26, 337-354.

Schlettwein C H G 1984. Comparison of insect biomass and community structure between fynbos sites of different ages after fire with particular reference to ants, leafhoppers and grasshoppers. MSc Thesis, University of Stellenbosch, Stellenbosch.

Scott C L 1985. The genus Haworthia (Liliaceae): a taxonomic revision. Aloe Books, Johannesburg.

Scott-Elliot G F 1890. Ornithophilous flowers in South Africa. Annals of Botany 4, 265-290.

Siegfried W R 1983. Trophic structure of some communities of fynbos birds. Journal of South African Botany 49, 1-43.

Siegfried W R and Crowe T M 1983. Distribution and species diversity of birds and plants in fynbos vegetation of Mediterranean-climate zone, South Africa. In: Kruger F J, Mitchell D T and Jarvis J U M (editors) Mediterranean type ecosystems. The role of nutrients. Springer-Verlag, Berlin. pp 403-416.

Siegfried W R, Rebelo A G and Prys-Jones R P 1985. Stem thickness of Erica plants in relation to avian pollination. Oikos 45, 153-155.

Skead C J 1967. Sunbirds of southern Africa. Balkema, Cape Town.

Snow B K and Snow D W 1972. Feeding niches of hummingbirds in a Trinidad valley. Journal of Animal Ecology 41, 471-485.

Snow B K and Snow D W 1980. Relationships between hummingbirds and flowers in the Andes of Colombia. Bulletin of the British Museum of Natural History 38, 105-139.

Stiles F G 1981. Geographic aspects of bird-flower coevolution with particular reference to central America. Annals of the Missouri Botanical Gardens 68, 323-351.

Vogel S 1954. Blutenbiologische typen als elemente der sippengliederung: dargestellt annhard der flora Südafrikas. Gustav Fischer: Jena.

Vogel S 1984. The Diascia flower and its bee - and oil based symbiosis in southern Africa. Acta Botanica Neerlandica 33, 509-518.

Winterbottom J M 1962. Breeding season of the long-tailed sugarbird Promerops cafer (L.). Ostrich 33, 77.

Wolf L L 1970. The impact of seasonal flowering on the biology of some tropical hummingbirds. Condor 72, 1-14.

Wolf L L 1978. Aggressive social organization in nectarivorous birds. American Zoologist 18, 765-778.

Wolf L L and Gill F B 1980. Resource gradients and community organization of nectarivorous birds. Acta 17 Congress International 2. Ornithology 1106-1113.

Wolf L L, Stiles F G and Hainsworth F R 1976. Ecological organization of a tropical highland hummingbird community. Journal of Animal Ecology 45, 349-379.

Wolf L L and Wolf J S 1976. Mating system and reproductive biology of malachite sunbirds. Condor 78, 27-39.

CHAPTER 5 MAMMAL POLLINATION IN THE CAPE FLORA

A G Rebelo and G J Breytenbach

As recently as 1979 (cf Faegri and van der Pijl 1979) mammal pollination was considered an infrequent occurrence, with the exception of the relatively well investigated syndrome of chiropterophily (bat pollination). Although pollination by nonflying mammals was mentioned by Kerner (1985), Porsch (1936) was probably the first biologist to describe flowers as being adapted for pollination by nonflying mammals. Most nonflying mammals seen visiting flowers (squirrels, tree-shrews and lower primates) are destructive to the extent of consuming the flowers (Faegri and van der Pijl 1979). Wiens et al (1983) summarize the historical discoveries of mammal pollination.

INTRODUCTION

Nonflying mammal pollination (NMP), or potential pollination by mammal pollen and nectar feeders, is currently recorded for a variety of taxa:

- **In Australia:**
  Antechinus (Dasyuridae), *Cercartetus* (Burramyidae), *Petaurus* (Petauridae), *Rattus* (Muridae) and *Tarsipes* (Tarsipedidae) on *Banksia* (Proteaceae) (Sleumer 1955; Glauert 1958; Morcombe 1968; Carpenter 1978; Wiens et al 1979; Hopper 1980; Smith 1980).
  Acrobates (Burramyidae) and *Pseudocheirus* (Petauridae) on *Eucalyptus* (Myrtaceae) (Smith 1980).
  Armstrong (1979) and Turner (1982) review the literature on marsupial pollination (20 to 25 species, most diverse in foraging habits being *Tarsipes rostratus*) in Australia, which occurs primarily in the plant families Myrtaceae (nine genera, primarily *Eucalyptus*) and Proteaceae (six genera, primarily *Banksia*).

- **In Africa:**
  Genetta (Viverridae) on *Maranthes* (Chrysobalanaceae) (Lack 1977). *Galago* (Lorisidae) on *Adansonia* (Bombacaceae) (Coe and Isaac 1965). *Galago* and *Cercophithecus* (Cercopihtecidae) on *Strelitzia* (Frost and Frost 1981).
  Acomys, *Aethomys*, *Praomys*, *Rhabdomys* (all Muridae) and *Elephantulus* (Macroscelididae), on *Protea* (Proteaceae) (Wiens et al 1983).

- **In Madagascar:**
  Cheirogaleus (Lemuridae) on *Delonix* (Fabaceae).
  Lemur (Lemuridae) on *Fernandoa* (Bignoniaceae), *Kigelia* (Bignoniaceae), *Combretum* (Combretaceae), *Ceiba* (Bombacaceae - introduced) and *Hura* (Euphorbiaceae).
  Microcebus (Lemuridae) on *Ceiba*.
  Phaner (Lemuridae) on *Crateva* and *Adansonia* (Sussman and Raven 1978).

- **In the Neotropics:**
  Cebus (Cebidae) on *Combretum* (Combretaceae) and *Ochroma* (Bombacaceae) (Prance 1980; Sussman and Raven 1978).
  Cryzomys and *Peromyscus* (Cricetidae) on *Blakea* (Melastomataceae) (Lumer 1980).

Didelphis (Didelphidae) on Ceiba (Toledo 1977);
Caluromys (Didelphidae) on Mabea (Euphorbiaceae), Ochroma and Trichanthera (Acanthaceae) (Steiner 1981, 1983).
Monkeys, opossums and procyonids on Combretum, Ceiba, Quararibea (Bombacaceae) and Lecythis (Lecythidaceae) (Mori et al 1978; Janson et al 1981).

The majority of plant and animal taxa associated with NMP occur in Australia and the Neotropics, with Madagascar having more representatives than tropical Africa. More than half the African mammals that visit proteas are generalist rodents. By contrast in Australia the marsupial Tarsipes rostratus is the most highly adapted mammalian nectar feeder known.

There has been a tendency in the recent literature to include NMP as a distinct pollination syndrome (Turner 1982; Baker and Baker 1983; Wiens et al 1983; Meeuse and Morris 1984). However, as with other pollination syndromes, NMP flowers are not exclusively visited by nonflying mammals. This is especially true in the tropics, where NMP flowers are also extensively visited by bats, sphingid moths and other insects at night (see references above). In contrast, many Western Australian and south-western Cape (South Africa) NMP flowers are also visited by bees and birds during the day.

Bat pollination in Africa has been recorded for a wide variety of tropical trees and climbers (eg Adansonia, Bombax (Bombacaceae), Ceiba, Dumoria (Sapotaceae), Ipomoea, Kigelia (Bignoniaceae) and Parkia (Fabacea) (Faegri and van der Pijl loc cit). Most of the African bat pollinators belong to the Pteropodidae. Only eight members of the Pteropdidae occur in southern Africa (Smithers 1983), of which only three species, the Gambian Epauletted fruitbat Epomophorus gambianus, the Straw-coloured fruitbat Eidolon helvum and the Egyptian fruitbat Rousettus aegyptiacus, are recorded as feeding off nectar (Rosevear 1965).

Pollination by bats is largely confined to the tropics, some exceptions being migratory bats visiting the southern United States (mainly pollinating Agave and Cactaceae) during the summer (Faegri and van der Pijl 1979). Ipomoea albivena (Convolvulaceae) is apparently the only African bat pollinated species to occur outside the tropics (Faegri and van der Pijl 1979), but the Zoutpansberg (23°00'S) can essentially be considered tropical. There is an extensive literature on bat pollination, which has been reviewed by Faegri and vd Pijl (1979).

STUDIES IN THE CAPE FLORA

Since the Cape Floral Kingdom lies totally outside the tropics, it is consistent with the current knowledge on bat pollination that no plant species in the south-western Cape shows the classical chiropterophilous syndrome. Only one species of bat recorded as being a pollinator Rousettus aegyptiacus, which is largely a fruit feeder, occurs in the region. Only one plant species, the Marsh Rose Orothamnus zeyheri (Proteaceae) is a remotely possible candidate for bat pollination (AGR). This has large inverted inflorescences, surrounded by large fleshy-looking pink hairy bracts, borne near the tops of the one to three meter tall stems. The entire plant secretes an odour reminiscent of freshly ironed washing. It occurs in colonies in seepage areas at high altitudes, and bears flowers throughout the year (with a marked peak in spring, especially in younger plants) (Boucher 1981). However, it has been reported that seed set in Orothamnus zeyheri was increased when bee hives were placed in the vicinity of the plants (van der Merwe 1978). This species warrants further investigation. No evidence of bird or insect visitation under natural conditions has been observed, despite many hours of diurnal observation when both birds and insects have been visiting surrounding plants (van der Merwe 1978; A G Rebelo personal observation). No nocturnal observations have been undertaken, nor have any clawmarks of bird, rodent or bat visitors been recorded.

Only four papers have been written on the subject of mammal pollination in the south-western Cape, all concerning Protea pollination by rodents (Rourke and Wiens 1977; Wiens and Rourke 1978; Wiens et al 1983; Wiens 1985). Rodent pollination was not recognized by Vogel (1954) in his monograph on pollination on the subcontinent.

Table 5.1 summarizes the species of putatively rodent pollinated plants in the fynbos biome. The syndrome is confined to the genera Protea and Leucospermum in the Proteaceae. Several other Leucospermum species have flowers which approximate the rodent pollination syndrome, in that they occur on ground level, often slightly hidden below other plants, except that they are not robust and emit a fragrant odour which occasionally attracts solitary bees. It therefore seems likely that rodent pollination evolved from insect pollinated species in Leucospermum, in contrast to having probably evolved from bird/insect pollinated species in Protea (Rourke and Wiens 1977). The closest resemblance to the NMP syndrome outside the Proteaceae, occurs in Liparia (Leguminosae), which is, however, visited by sunbirds (Nectariniidae) (Marloth 1932). In addition, Aloe claviflora Burchell (Asphodelaceae) bears pendant flowers on a horizontal raceme, with flowers usually situated less than 100 mm above the ground (Reynolds 1982). From the orientation of the flowers, pollination is probably achieved by the pollen vector feeding from the ground. However, nothing is known about the floral ecology and visitors to this Namaqualand species.

THE NMP (NONFLYING MAMMAL POLLINATION) SYNDROME - THEROPHILY

Various authors (Porsch 1934; Carpenter 1978; Holm 1978; Turner 1982; Wiens et al 1983) have attempted to define the traits characterizing the therophilous syndrome. These include (Turner 1982):

- flowers in tight inflorescences;
- inflorescences strongly attached to stems;
- presence of stiff (incurved) styles;
- nocturnal anthesis and nectar production;
- channelling of nectar from inflorescence to the ground;
- inflorescences close to the ground;
- dull flower colour;
- inflorescences hidden in foliage;
- musky odour, predominantly produced at night;
- copious production of nectar and pollen;
- concentrated, sucrose-rich nectar.

TABLE 5.1 Potentially rodent pollinated Proteaceae in the Cape Floral Kingdom*

Species (grouped by subgenus)	Inflorescence shape	Outside brack colour	Inside bract colour	Floret colour	Awn colour	Style shape 1	Inflores -cence position 2	Odour	Bush shape
Paracyneroides									
P cryophila	crateriform	white	carmine	pink	white	arcuate	term-geo	yeasty	sprawling
P scabriuscula	campanulate	white	carmine	carmine	white	straight	term-geo	yeasty	cushion plant
P scolopendrifolia	crateriform	carmine	carmine	carmine	white	straight	term-geo	yeasty	procumbent
P prUinosa	cyathiform	white	scarlet	white	white	-arcuate	term-geo	yeasty	prostrate
Ligulatae									
P pudens	campanulate	rusty	rusty	white	black	straight	term-geo	none	procumbent
Obvallatae									
P caespitosa	ovoid	pink	pink	white	brown	straight	int-geo	?	compact
Subacaules									
P scorzonerifolia	obconic	yellow	n v	yellow	white	straight	term-geo	?	rhizomatous
P lorea	obconic	yellow	yellow	yellow	white	straight	term-geo	none	rhizomatous
P aspera	ovoid-oblong	rusty	rusty	cream	cream	-arcuate	term-geo	none	prostrate
P scabra	turbinate	rusty	yellow	cream	brown	+arcuate	term-geo	none	tufted shrublet
P denticulata	ovoid	brown	red	carmine	brown	-arcuate	terminal	none	low dense
P piscina	obconic	yellow	yellow	yellow	yellow	-arcuate	term-geo	nonr	rhizomatous
P restionifolia	ovoid	brown	yellow	yellow	brown	-arcuate	term-geo	?	low shrublet
Exertae									
P venusta	campanulate	pink	silver	silver	white	straight	term-geo	sweet	sprawling
Crinitae									
P foliosa	cyathiform	green	green	cream	white	straight	ext-term	?	tall rounded
P tenax	crateriform	green	yellow	cream	cream	straight	term-geo	yeasty	decumbent
P vogtsiae	cyathiform	carmine	yellow	cream	white	curved	term-geo	yeasty?	caespitose
P intonsa	cyathiform	carmine	n v	cream	white	arcuate	int-geo	yeasty?	dense tufted
P montana	cyathiform	green	n v	cream	white	straight	term-geo	yeasty?	procumbent
Microgeantae									
P acaulos	crateriform	red	yellow	yellow	black	+arcuate	term-geo	musty?	prostrate
P angustata	crateriform	yellow	yellow	yellow	brown	+curved	terminal	yeasty	rhizomatous
P laevis	cratiform	yellow	yellow	yellow	silver	+curved	term-geo	?	decumbent
P convexa	crateriform	green	green	carmine	silver	+arcuate	term-geo	?	prostrate
P revoluta	crateriform	yellow	yellow	yellow	white	arcuate	term-geo	?	prostrate
Crateriflora									
P recondita	crateriform	green	green	yellow	carmine	+arcuate	ext-term	yeasty	sprawling
P effusa	crateriform	red	red	yellow	red	+arcuate	int-pend	yeasty	sprawling
P sulphurea	crateriform	crimson	yellow	yellow	rusty	+curved	int-pend	musty	sprawling
P pendula	crateriform	silver	rusty	silver	brown	+arcuate	int-pend	yeasty	compact dense
Hypocephalus									
P amplexicaulos	crateriform	brown	silver	yellow	red	+arcuate	int-caul	yeasty	sprawling
P cordata	crateriform	rusty	rusty	white	red	+curved	int-geo	yeasty	low upright
P decurrens	crateriform	brown	brown	white	rusty	+curved	int-geo	yeasty	small erect
P subulifolia	crateriform	brown	brown	white	red	+curved	int-geo	yeasty	low upright
P humiflora	crateriform	brown	white	yellow	red	+curved	int-caul	yeasty	sprawling
Pinifolia									
P witzenbergiana	crateriform	rusty	rusty	white	brown	+arcuate	int-pend	yeasty	prostrate
P pityphylla	crateriform	red	red	yellow	red	+arcuate	int-pend	yeasty	sprawling
L hamatum	turbinate	crimson	n a	yellow	crimson	cygneou	term-geos	?	sprawling

Key to Table 5.1

1. Well developed feature indicated by (+); weak feature by (-)
2. int-caul = interior caulifery, int-geo = interior geoflory, int-pend = interior penduly, term-geo = terminal geoflory: see text for definitions n a = not applicable; n v = not visible, ? = not known.

* Candidacy was based primarily on geoflorous and cryptic or concealed infloresceknown yeasty/musty odours. The probable degree of therophily verse ornithophily is discussed in text. Of the species presented below, the following were not contherophilous by Rourke and Wiens (1977) or Wiens et al (1983): P pityphylla, P pudens, P witzenbergiana the following species were included in the first account, but excluded in Wiens et al (loc cit): P lorea and P scorzonerifolia.

Several of these features overlap with both bat and bird pollination syndromes. Consequently, many Protea species (and Banksia and Eucalyptus species in Australia) are also frequently visited by birds. However, it is probably true that the more of the above mentioned features the plant possesses, the greater the role of NMP in the pollination of the species. Thus, noncryptic therophilous Protea species (P acaulos, P angustata) are also visited by sunbirds (Rebelo unpublished), while Australian Banksia and Eucalyptus species are also visited by birds and insects. Many small mammals are not nocturnal, and diurnal nectar and odour production, while allowing exploitation by birds and bees, may specifically cater for these potential pollinators (eg Rhabdomys, Otomys, Elephantulus in south-western Cape (Nel et al 1980; Breytenbach 1982) and Tarsipes in Australia (Turner 1982)).

A summary of the features of possibly therophilous species in the south-western Cape is presented in Table 5.1. The NMP syndrome in the fynbos biome (sensu Wiens et al 1983) appears to be characterized by the following subset of Turner's (1982) therophilous syndrome:

- bowl shaped heads born on short (less than 5 mm), stout peduncles;
- outside bracts of inflorescence dark-coloured;
- copious, sucrose-rich nectar with a high total carbohydrate
- composition (36%);
- robust, inflexed, wiry styles;
- cryptic, geoflorous, axillary positioning of heads;
- distinctive yeasty or musty odour;
- 10 mm distance between pollen-presenter/style and mouth of nectar tube;
- a nectar reservoir with a troughlike structure.

The discrepancies between Turner's and Wiens's characterizations of the therophilous syndrome probably stem from Wiens concentrating on the most exclusive members of the syndrome in characterizing therophily. In contrast, the Australian version of the syndrome includes many largely ornithophilous plant species, while the majority of tropical plants appear to be primarily chiropterophilous, and only secondarily therophilous. Had Wiens et al (1983) attempted to incorporate Protea repens (an ornithophilous species, the inflorescences of which may contain many rodent faeces (Rebelo and Zeiler unpublished)) - listed by Wiens et al (1983) as strongly supporting frequent visitation of the heads by rodents) his syndrome would very much approximate that of Turner (1982).

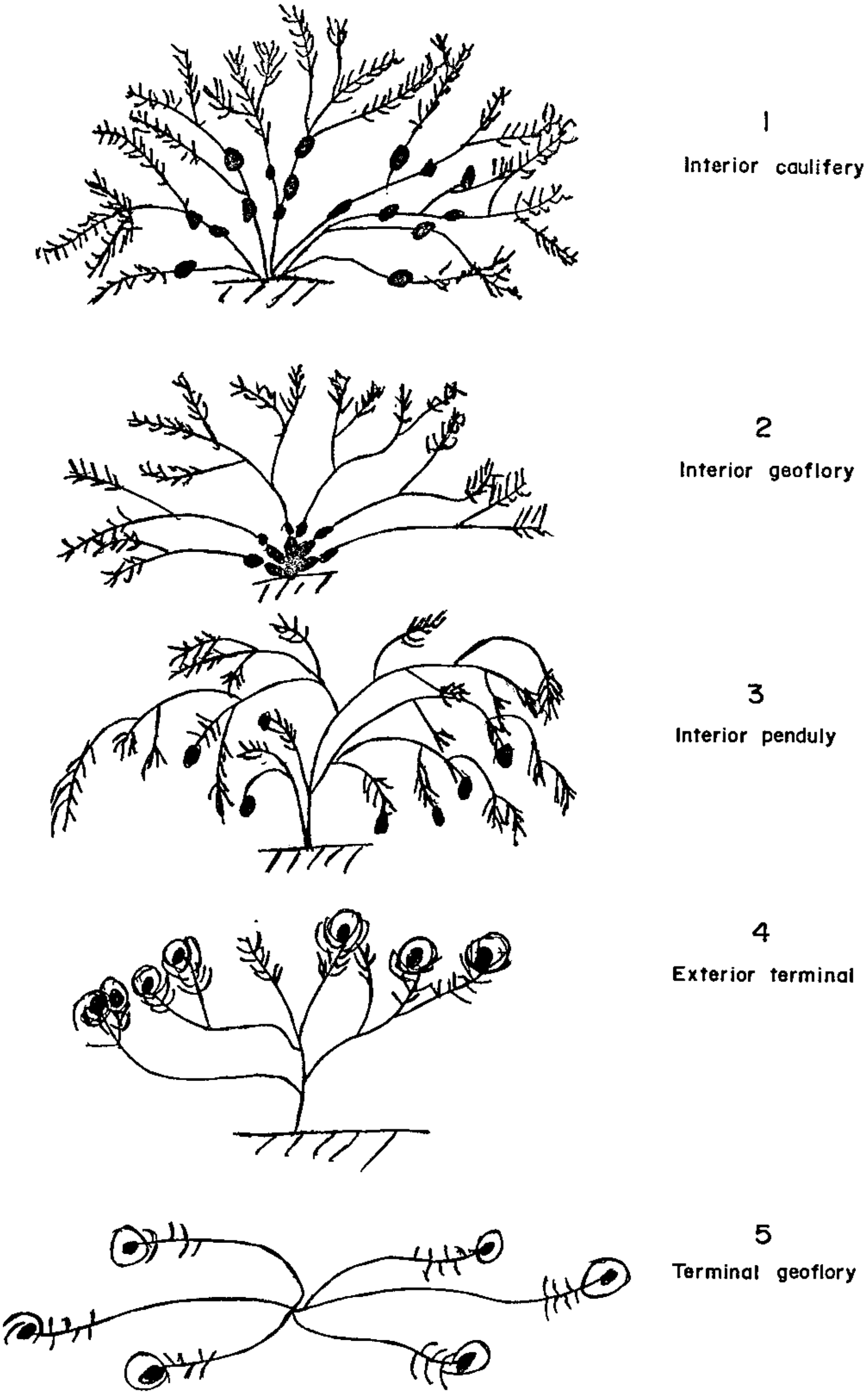


FIGURE 5.1 Strategies for minimizing visual detection of therophilous Proteaceae by nonpollinators (Wiens et al 1983).

Several features of NMP syndrome in the south-western Cape require elaboration:

Crypsis

Regarding crypsis, Wiens et al (1983) recognize several strategies for minimizing visual detection of therophilous Proteaceae (Figure 5.1): (1) Interior caulifery - inflorescences borne near the centre of the bush on old stems and hidden by the foliage of overgrowing stems; (2) Interior geoflory - inflorescences borne at ground level and hidden by the foliage of overgrowing stems; (3) Interior penduly - inflorescences born at the ends of pendulous branches, hidden by the foliage of overgrowing branches, with heads often drooping to near ground level; and (4) Exterior terminal - inflorescences borne near the exterior of the bush but totally enveloped in leaves basal to the inflorescence. In addition, a fifth category (5) Terminal geoflory can be recognized in which inflorescences are borne at ground level on the tips of rhizomatous branches, and are concealed only by the leaves. Often terminal geoflorous inflorescences are borne at the outer perimeter of the plants, but terminal geoflory tends to grade imperceptibly with age to interior geoflory in some species of rhizomatous Protea species. Each of the five strategies represent simultaneous solutions by different subgenera, which have independently converged towards therophily (Wiens et al 1983), to the need for crypsis.

Wiens et al (1983) attempt to explain the crypsis in terms of rodent protection from avian predators. However, small mammals (mainly Praomys verraeuxii and Rhabdomys pumilio) are frequently observed feeding on seeds from the terminally borne, exposed serotinous inflorescences of several Protea species in the southern Cape (Breytenbach 1982). In addition owls and diurnal aerial predators occur at low densities in fynbos plant communities, and it is unlikely that this explanation can account for the lack of crypsis in some rodent pollinated Australian Banksia species.

We disagree with Wiens et al (1983) in their statement that ornithophilous Protea species have brightly coloured bracts - several species (nine out of 33 taxa) have green or yellow inflorescences, and seem to rely on the keen vision of birds for detection, simultaneously remaining cryptic to visitors utilizing colour cues. The sugarbird visited P coronata, for instance, has green inflorescence bracts and is hidden in the foliage. We propose that crypsis is required if the nectar resource is to be protected from nectar thieves. This is because the high concentrations and large volumes of nectar make therophilous inflorescences energetically greatly sought after by insects (especially bees) and by birds. Wiens et al (loc cit) found P humiflora to be virtually stripped of nectar and pollen on warm days by honey bees (Apis mellifera). The cryptic position of the inflorescences is thus essential in insuring that unwanted visitors do not readily exploit the resources.

That birds do exploit noncryptic therophilous Protea species is easy to observe, and orangebreasted sunbirds (Nectarinia violacea) may defend breeding territories while feeding exclusively off the nectar of P angustata (Rebelo unpublished). Protea angustata has inconspicuous yellow-coloured inflorescence bracts, and inflorescences, which are borne near ground level, produce a strong yeasty odour (Table 5.1) and show signs of being visited by rodents as well. The orangebreasted sunbird has occasionally also been observed to feed on P acaulos and P scabra, both cryptic species which require that the bird perch on the ground in front of the inflorescence to feed (A G Rebelo personal observation). The orangebreasted sunbird is also recorded as regularly visiting the incurved pendulous inflorescences of P pendula, which are hidden amongst the foliage and produce a yeasty odour (Rourke 1980a). Wiens et al (1983) record 'inconsequential' visitation by birds to strictly therophilous Protea species: orangebreasted sunbirds to P cryophila, malachite sunbirds Nectarinia famosa to P humiflora and P humiflora pollen on the heads of Cape buntings Emberiza capensis.

What advantage the plant accrues by secreting so large a quantity of sugar rich, energy expensive nectar, which must therefore be concealed, rather than secreting a more dilute nectar and advertising the reward to a greater potential pollinator spectrum, is unknown. Casual observations, however, suggest that rodent pollinated Protea species are visited by very few insects species (other than honeybees), at least in comparison with the bird pollinated Protea species. It may prove fruitful to investigate the role of crypsis in reducing insect visitation, especially in the light of the high insect damage (mainly by beetles and lepidoptera larvae) reported in ornithophilous serotinous Protea species (Coetzee 1984).

Inflorescence colour

The role of colour in contributing to the inconspicuousness of therophilous Protea species has been discussed above. Inconspicuous colours have long been recognized as an ornithophilous feature and, together with a shift to the red end of the spectrum (Raven 1973), has been interpreted as making bird flowers less conspicuous to insects. Odour appears to play the major role in attracting rodents to therophilous Proteaceae (Wiens et al 1983).

Colours of therophilous fynbos flowers are presented in Table 5.1. While the colour of the inflorescence bracts is usually similar on the outside and inside, the colour is usually inconspicuous. However, the white outer bracts and awns in the Paracyaroides group, contrast strongly with the darker foliage. In contrast, the floret and awn colours, generally hidden within the involucral bracts in the more therophilous species, are generally more conspicuous, usually consisting of a contrasting light (white, silver or yellow) and dark (red, brown) colour. The significance of this target is clearly visible to the naked eye even in the dark, but their perception by rodents is unknown (Wiens et al 1983).

Putatively rodent pollinated Proteaceae species (producing yeasty odours) with terminal geoflorous inflorescences tend to have more brightly coloured involucral bracts, suggesting that birds (and insects) may play a role in their pollination. Both Protea lorea and P scorzonerifolia appear to be primarily ornithophilous, and the importance of rodents in their pollination has been queried by Wiens et al (1983).

Hooked styles

Carpenter (1978) suggests that hook-styles constituted part of the therophilous syndrome, at least in Banksia species. Subsequent research has shown pollen transfer to be greater in hook-styled than straight- styled Banksia species for both mammal and bird pollen vectors (Hopper 1980; Whelan and Burbridge 1980). However, the relationship between hook- styles and therophily are no longer tenable, as many straight-styled Banksia species are visited by mammals as well (Wiens et al 1979; Turner 1982).

In the fynbos Proteaceae curved and straight styles occur among all pollination syndromes. In *Protea* the majority of putatively rodent pollinated species have curved styles (Table 5.1), while the majority of bird and insect pollinated species have straight styles. This is, however, closely correlated with the shape of the inflorescences, with all deep inflorescences having straight styles, while shallow and bowl-shaped inflorescences tend to have styles curved to position the stigma towards the centre of the inflorescences.

There is a tendency for styles to be straight in insect pollinated *Leucospermum* species. Bird pollinated species usually have curved styles (especially in globose inflorescences where birds sit on top of the inflorescences while nectar-feeding), while the only rodent pollinated species has strongly curved (cygneous) styles, despite having a 'flat' inflorescence.

From Table 5.1 it can be seen that the most exclusively therophilous species (ie those with interior caulifery, interior geoflory and exterior terminal inflorescences which are most inaccessible to birds) do tend to have strongly curved, strongly arcuate or falcate (curved to nearly right angles) styles. The relationship between style shape in determining successful pollen transfer, by any vector, remains uninvestigated in fynbos Proteaceae.

The ten millimetre rule

Irrespective of the inflorescence morphology, the style shape or the length of the stigma or perianth, therophilous Proteaceae have an effective 10 mm stigma-nectar distance. This distance is thus the distance between the reward and the pollen and stigmatic groove, and correlates closely with the rostrum length of the major rodent pollinators (Wiens et al 1983). This is apparent even in the very large-flowered therophilous *Protea* species, such as *P cryophila*, which has a style length of 80 to 90 mm, and is achieved by elevating the nectar pool in the perianth tube. Unfortunately, data does not appear to have been collected for all the therophilous *Protea* species, nor has the range in rostrum length for putative rodent pollinators been ascertained.

Flowering phenology

In contrast to ornithophilous Proteaceae which tend to bloom in winter, therophilous Proteaceae tend to bloom in spring (Table 5.2) (Wiens et al 1983). This is apparently the peak of the breeding season for local murid rodents (Wiens et al 1983), and nectar supplied may play a role in female gestation, lactation and juvenile survival, although no research has been undertaken on the topic. Wiens et al (1983) consider that nectar may largely comprise a "dessert" (sweet treat or junk-food trip) rather than an important component of the annual rodent energy budget. This contrasts strongly with the opinion among ornithologists (Recher and Abbott 1970) that nectar may be utilized as an energy source which allows the exploitation of otherwise energetically unavailable resources, such as may occur in areas where insects are at a very low abundance, or when size classes or habits (of insects) prevent their exploitation for energetic reasons. Their suggestion warrants closer investigation since insect densities are low in fynbos, and fynbos insectivores (eg *Elephantulus edwardii*, *Myosorex varius*) are some of the only known insectivores in the world to feed extensively on seed (Nel et al 1980; Breytenbach 1982).

We note, in this regard, that most therophilous and ornithophilous Proteaceae tend to occur on nutrient-poor soils, and that the breeding phenology of the major pollen vectors occurs during the period in which the respective Proteaceae reach their peak in flowering (cf Rebelo et al 1983; Wiens et al 1983), irrespective of the incidence of insects and seeds in the environment.

TABLE 5.2 Patterns of flowering phenology in *Protea* in the fynbos biome grouped by putative pollinating-agent. Data are from Bond and Goldblatt (1984), with *P nana* as insect pollinated, and *P lorea* and *P scorzonerifolia* as bird pollinated. The total number of species per pollination syndrome are: bird = 33, mammal = 33 and insect = 4 species

Pollinating agent	Month											
	J	F	M	A	M	J	J	A	S	O	N	D
Numbers of species												
Bird	12	10	9	17	19	22	22	22	24	18	14	12
Mammal	7	5	6	4	10	14	18	21	22	16	11	6
Insect	0	1	1	1	1	1	2	2	2	3	3	1
Percentage of total species per syndrome												
Bird	36	30	27	52	58	67	67	67	73	55	42	36
Mammal	21	15	18	12	30	42	55	64	67	48	33	18
Insect	0	25	25	25	25	25	50	50	50	75	75	25

Importance of nontherophilous pollen vectors

While a strong case has been made above for the extensive visitation of seemingly therophilous Proteaceae by birds and insects, little data are available on the actual effectiveness of these visitors (or the mammals) as effective pollen vectors. In *Protea amplexicaulos* and *P humiflora* (both strictly therophilous) seed set was reduced, by 95% and 50% respectively, when rodents were prevented from visiting the inflorescences (Wiens et al 1983). *Protea humiflora* is apparently partially self-fertile, although very few seeds are normally set when selfed. However, attempted cross-pollinations did not yield as many seeds as did rodent pollination, and inflorescences from which mammals were excluded, but which were exposed to insects, yielded a much greater seed set (25%) than manually cross-pollinated inflorescences (Wiens et al 1983). Obviously much is still to be learned about Proteaceae stigmatic receptivity and pollen deposition.

NONFLYING MAMMALS AS POLLINATORS

What advantages mammals pose over birds or insects as pollinators are unknown. However, most mammal pollinated Proteaceae flower simultaneously with the majority of ornithophilous Leucospermum species, ie in spring (Rourke 1972), and thus birds may not be predictably available as pollinators during the season. Skead (1967) records the unpredictability of sunbirds as seasonal visitors to some areas in the eastern Cape and Karoo, but virtually nothing is known about bird movements, or the factors influencing them, in the fynbos biome.

Breytenbach (1982) and Wiens et al (1983) recorded home range sizes of 25 to 58 m radius for nectar-feeding rodent species. This is similar to the 35 m radius recorded for breeding male Sugarbirds (Seiler and Rebelo unpublished) and larger than that of nonbreeding sugarbirds (Collins 1983). Wiens et al (1983) recorded the movement of fluorescent dyes to a distance of 15 m from the labelled inflorescence. There is thus apparently little difference between pollen movement by birds and mammals, although the number and distance of movement by 'floaters' (nonterritorial opportunistic rovers) in both pollinating groups are unknown, but is probably greater with regard to pollination in birds.

The species of rodent utilizing the Proteaceae as a nectar source are ubiquitous in the southern Cape, and frequent many habitats, including the nutrient-poor sites where therophilous Proteaceae may occur. In contrast to the distinctive therophilous syndrome in plants, the nectar-feeding rodents have no apparent adaptations for nectarivory, suggesting that the evolution of the therophilous syndrome occurred exclusively in the plants. This parallels the ornithophilous syndrome, where the endemic avian pollinator of Protea species, the sugarbird, has apparently evolved with Protea as a genus, but shows no variation or preferences among Protea species, other than may be explained by nectar resources (Rebelo et al 1983). Thus, Wiens et al (1983) described the rodent - Protea relationship as a noncoevolved system.

A variety of mammals, apart from the mammals which pollinate the therophilous Protea species, utilize Protea as a food source. Most of these are rodents which utilize the seeds as a food source (Nel et al 1980; Breytenbach 1982). In addition, the Chacma Baboon Papio ursinus is probably a major predator on both ornithophilous and therophilous Protea species. Baboons feed off nectar by breaking off the flower heads and sucking out the nectar, and are thus probably never pollinators. Large numbers of inflorescences may be destroyed in this manner (Wiens et al 1983).

THE DISTRIBUTION, ECOLOGY AND EVOLUTION OF MAMMAL POLLINATION

To date, the occurrence of therophily has only been reported in the tropics and in the mediterranean and adjacent regions of Australia and southern Africa. No reports of therophily exist for any other mediterranean region, nor for any of the relatively well studied temperate regions. In fact, therophily is closely linked with chiropterophily in the tropics and with ornithophily in the mediterranean regions. Sussman and Raven (1978) propose, based mainly on Madagascar's lemurids where therophily is not obviously linked to chiropterophily, that therophily represents an ancient syndrome. They suggest that, since the late Cretaceous the early mammals, mainly marsupials, have had pollinatory-relationships with angiosperm flowers. These were outcompeted by placental mammals, and persist only in Australia and South America. The early primates replaced marsupials as flower visitors, and were in turn replaced by bats in both the New and Old World tropics. Survivors of the early primate pollinators include the Lemuridae of Madagascar and some other primates in tropical regions 'where fruit-eating and flower-visiting bats are and presumably always have been rare'. In contrast, rodent pollination syndromes, found in more temperate regions where bats are largely absent, evolved relatively recently. They thus view the tropical therophilous syndrome as a 'living fossil'.

This theory has its attractions, and perhaps the Proteaceae may offer a test of this theory. While insufficient fossil evidence, both plant and pollinator, exists to clarify the issue at present, several points can be made. The evolution of therophily in the genus _Protea_ appears to have evolved independently at least five times (Wiens et al 1983), with a _Leucospermum_ evolving the same relationship. Likewise, therophily evolved several times in Australia (Keighery 1982). Of the related families shared by Australia and southern Africa, only the Proteaceae are therophilous, in contrast to ornithophily which has evolved in several related families. The majority of the extant therophilous southern African Proteaceae have apomorphic (derived) characters (eg _Protea cordata_, _P amplexicaulis_, _P caespitosa_; Rourke 1980b). Unlike Australia, there are no mammals adapted primarily for nectar feeding in southern Africa.

Assuming that therophily was a feature of the early Proteaceae at the time Gondwanaland broke up is difficult, because of the similarities in gross morphology (utilizing the basic Proteaceae floral and inflorescence structure) between therophily, ornithophily and cantharophily (beetle pollination). Either of the three could easily be derived from any other. However, distributional, phyletic and ecological factors point to ornithophily-cantharophily as the ancestral syndrome, with therophily being the derived syndrome in each case, and having evolved independently from other syndromes on both continents. The situation is complicated, however, by the observation that therophilous Proteaceae in southern Africa tend to have small distribution ranges and comprise small localized populations (Wiens et al 1983), compared to the large distributional ranges and often continuous populations in many of the ornithophilous species. This may have favoured both a higher extinction and a higher speciation rate, with a consequent apomorphic characterization of extant therophilous taxa.

Why therophilous species tend to occur in small localized populations is unknown. This is apparently both a feature of the southern African therophilous genera and the Australian genera (_Dryandra_ and _Banksia_ (Wiens et al 1983), but no records of population sizes in therophilous _Eucalyptus_ species are available. The reasons for small population sizes in therophilous Proteaceae (or alternatively the advantage of evolving therophily in localized Proteaceae) as discussed by Wiens et al is unsatisfactory. The environmental factors they mention (continuing dissection of the Table Mountain Sandstone; highly specialized ecological conditions, eg soil types) and the interrelationships between plants and pollinators (more reliable service; temporal partitioning within sympatric species; readily attracted to ephemeral and highly restricted resource) apply equally well to bird and rodent pollinated plant species, if not more so to bird pollinated species. The 'restricted population hypothesis' is an observation, not a hypothesis. A more parsimonious line of investigation is to propose that because rodents are unable to move as far as birds, the distance of pollen transfer is probably less. Consequently, gene flow is reduced in therophilous Proteaceae under conditions in which birds may fly several hundred meters to complete a foraging bout. Therophilous species may therefore be more prone to speciation, genetic drift and extinction than ornithophilous species. This may account for several therophilous Protea species occurring sympatrically with staggered flowering seasons (Wiens et al 1983), in contrast to the large, relatively monospecific stands of ornithophilous species. While labile gene pools may influence extinction rates of small populations, this theory does not satisfactorily explain the small population sizes in therophilous species.

In addition to staggered flowering seasons in therophilous species, there are also two marked strategies concerning succession. While many species (eg P amplexicaulis, P cordata, P humiflora) regenerate exclusively from seed and take at least four years to produce their first flowers, the rhizomatous Protea species (eg P acaulos, P angustata, P scabra) flower almost exclusively in the first few years following fire. The rhizomatous species therefore bloom largely during the seral stages when plant cover is low, and rodent predation therefore potentially high. All three species mentioned above are visited by orangebreasted sunbirds, in addition to rodents (as evidenced by faecal droppings in flowers and runs between flowering Protea bushes), in the early seral communities. No data are available on the relative importance of birds and mammals in these early seral flowering species. Orangebreasted sunbirds defend territories on P angustata, in four year old fynbos, when the overall vegetation height is less than a meter, and before seed-regenerating ornithophilous Protea and Erica species have begun to flower. The importance of seral stage relative to the flowering of putatively therophilous rodent species and rodent colonizing ability in relatively open veld need to be elucidated.

Given that bats have taken over 'therophilous' flowers in the tropics and rodents in the fynbos, is there any indication of what may have happened to the theoretical therophilous taxa in the Karoo and other neighbouring vegetation communities?

Frost and Frost (1981), in discussing pollination of Strelitzia nicolai suggest that the original pollinator with which the plant evolved its distinctive shape, is an unknown extinct mammal, not necessarily a bat as suggested by Faegri and van der Pijl (1979). Certainly the absence of recorded mammal visitation to plants outside the tropics and the fynbos biome should not be interpreted as an absence of the syndrome in these communities in South Africa.

As an example, nothing is known about nectar secretion rates, times of anthesis or visitors to most of the Aloe species which bear tall, robust inflorescences, and which have classically been considered bird pollinated

(Vogel 1954; Oatley 1964, but see Pooley 1968). However, the ornithophilous exclusivity of Aloe species has never been investigated other than to note the incidence of bee visitation. Reynolds (1982) mentions that Aloe castanea produces copious quantities of exceptionally sweet and sticky nectar, has a reddish-brown perianth, and robust, near-sessile flowers with anthers and stigma exserted 12 to 15 mm. Many of the species in the section Anguialoe (A sessiliflora, A vryheidensis, A dolomitica, A castanea) share many of these features and are characterized by the densely flowered sessile, campanulate (open-mouthed), yellow-brown flowers, with a copious supply of dark nectar (Reynolds 1982). Another potential candidate for rodent pollination is A alooides. Although Aloe castarea, A dolomitica and A sessiliflora produce an abundant exposed nectar, readily accessible to bees, bees ignore the nectar and only utilize these species for their pollen (Anderson et al 1983). Since nectar in exposed flowers probably becomes concentrated due to evaporation, the reason for bees ignoring these species is unknown. None of these species occur in the Cape Floral Kingdom, however, where most Aloe species have pedunculate flowers, which do not appear robust enough to support rodents moving over the flowers and are extensively visited by bees and birds.

In addition, the possibility of other plant species being visited by mammals in, for example, the eastern Cape and Natal vegetation communities exists. Several tropical and subtropical mammals extend into the subtropical and temperate regions of the subcontinent, especially the east coast. These include arboreal dassies, monkeys and squirrels, many of which have not been adequately studied with respect to their possible interrelationships with floras.

CONCLUSIONS

Based on current evidence mammal pollination appears confined to the tropics, where it is dominated by bat pollination, and mediterranean regions with west Gondwanaland affinities, where the syndrome is more distinct from bat pollination, but appears more affiliated to bird pollination. The distribution pattern of therophily and chiropterophily is interpreted as an ancient nonflying mammal syndrome, which has been usurped by bats in the tropics with relict areas (refugia) still possessing the ancestral syndromes (Sussman and Raven 1978).

It appears that, in the refugia at least, a distinct syndrome for therophily, as distinct from chiropterophily, is discernible. This syndrome is characterized by the production of yeasty and musty odours, cryptic flowerheads, robust flowers with nocturnal anthesis, and a copious production of energy-rich, sucrose-dominated nectar. In the Cape flora, therophily appears to be a more distinctive syndrome than in Australia where plants are often visited by birds as well. Thus in Australia, the therophilous syndrome shares many features of the bird pollination syndrome.

The syndrome appears to have evolved independently several times in southern African Proteaceae, probably from bird pollinated species, and is currently found in two genera - Protea and Leucospermum. A currently inexplicable relationship between small plant population size and therophily appears to exist, and requires investigation.

REFERENCES

Anderson R H, Buys B and Johannsmeier M F 1983. Beekeeping in South Africa. Department of Agricultural Technical Services Bulletin 394.

Armstrong J A 1979. Biotic pollination mechanismsin the Australian flora - a review. New Zealand Journal of Botany 17, 467-508.

Baker H G and Baker I 1983. Floral nectar sugar constituents in relation to pollinator type. In: Jones C E and Little R J (editors) Handbook of experimental pollination biology. Nostrand Reinhold, New York.

Bond P and Goldblatt P 1984. Plants of the Cape flora: a descriptive catalogue. Journal of South African Botany Supplementary Volume 13.

Boucher C 1981. Autecological and population studies of *Orothamnus zeyheri* in the Cape, South Africa. In: Synge H (editor) Biological aspects of rare plant conservation. John Wiley and Sons, New York.

Breytenbach G J 1982. Small mammal responses to environmental gradients in the Groot Swartberg of the southern Cape. Unpublished MSc Thesis, University of Pretoria, Pretoria.

Carpenter F L 1978. Hooks for mammal pollination? Oecologia 35, 123-132.

Coe H G and Isaac F M 1965. Pollination of the baobab (*Adansonia digitata* L.) by the lesser bush baby (*Galago crassicaudatus* E. Geoffroy). East African Wildlife Journal 3, 123-124.

Coetzee J H 1984. Insekte in assosiasie met *Protea repens* (L.) L. Unpublished MSc Thesis, University of Stellenbosch, Stellenbosch.

Collins B G 1983. Seasonal variation in the energetics of territorial Cape Sugarbirds. Ostrich 54, 121-125.

Faegri K and van der Pijl R 1979. The principles of pollination ecology. Pergammon, Oxford.

Frost S K and Frost P G H 1981. Sunbird pollination of *Strelitzia nicolai*. Oecologia 49, 379-384.

Glauert L 1958. The honey maize? Australian Museum Magazine 12, 284-285.

Holm E 1978. Flowers adapted to mammal pollination. The Western Australian Naturalist 14, 71-74.

Hopper S D 1980. Bird and mammal pollen vectors in *Banksia* communities at Cheyne Beach, Western Australia. Australian Journal of Botany 28, 61-75.

Jansen C H, Terbourgh J and Emmons L H 1981. Non-flying mammals as pollinating agents in the Amazonian forest. Biotropica 13, 1-6.

Keighery G J 1982. Bird pollinated plants in Western Australia and their breeding systems. In: Armstrong J A, Powell P M and Richards A J (editors) Polination and evolution. Royal Botanic Gardens, Sydney.

Kerner A 1895. The natural history of plants, Volume II. Blackie and Son, London.

Lack A 1977. Genets feeding on nectar from *Maranthes polyandra* in northern Ghana. East African Wildlife Journal 15, 233-234.

Lumer C 1980. Rodent pollination of *Blakea* (Melastomataceae) in a Costa Rican cloud forest. Brittonia 32, 512-517.

Morcombe M K 1968. Australia's western wildflowers. Landfall Press, Perth.

Marloth R 1932. The flora of South Africa. Darter Brothers, Cape Town.

Meeuse B and Morris S 1984. The sex life of flowers. Faber and Faber, London.

Merwe P van der 1978. Die morfologie en voortplanting van *Orothamnus zeyheri* (Proteaceae). Research report 1977, Department of Nature and Environmental Conservation, Cape Town.

Mori S A, Prance G T and Bolten A B 1978. Additional notes on the floral biology of Lecythidaceae. Brittania 30, 113-130.

Nel J A J, Rautenbach I L and Breytenbach G J 1980. Mammals of the Kammanassie mountains, southern Cape Province. South African Journal of Zoology 15, 255-261.

Oatley T B 1964. The probing of *Aloe* flowers by birds. Lammergeyer 3, 2-8.

Pooley A C 1968. A short note on the diet of the Vervet Monkey *Cercopithecus aethiops* in Zululand. Lammergeyer 9, 29-31.

Porsch O 1934. Säugtiere als Blumenausbeuter und die Frage der Säugetierblume. I. Biol. Gen. 10, 657-685.

Porsch O 1936. Säugetiere als Blumenausbeuter und die Frage der Säugetierblume. III. Biol. Gen. 12, 1-21.

Prance G T 1980. A note on the probable pollination of *Combretum* by *Cebus* monkeys. Biotropica 13, 260-270.

Raven P H 1973. Why are bird flowers predominantly red. Evolution 26, 674.

Rebelo A G, Siegfried W R and Crowe A A 1983. Avian pollinators and the pollination syndromes of selected Mountain Fynbos plants. South African Journal of Botany 3, 285-296.

Recher H F and Abott I J 1970. The possible ecological significance of hawking by honeyeaters and its relation to nectar feeding. Emu 70, 90.

Reynolds G W 1982. The aloes of South Africa. Balkema, Cape Town.

Rosevear D R 1965. The bats of west Africa. Trustees British Museum of Natural History, London.

Rourke J P 1972. Taxonomic studies on *Leucospermum*. Journal of South African Botany 8.

Rourke J P 1980a. Rodents as pollinators of dwarf proteas. Veld and Flora 66, 54-56.

Rourke J P 1980b. The proteas of southern Africa. Purnell, Cape Town.

Rourke J P and Wiens D 1977. Convergent floral evolution in South African and Australian Proteaceae and its possible bearing on pollination by non-flying mammals. Annals Missouri Botanical Gardens 64, 1-17.

Skead C J 1967. Sunbirds of southern Africa. Balkema, Cape Town.

Sleumer H 1955. Proteaceae. In: Steenis C G G J van (editor) Flora Malesiana. Series 1. Volume 5: 147-206.

Smith M J 1980. The marsupials of Australia. Volume I. Landsdowne Editions, Melbourne.

Smithers R H N 1983. The mammals of the southern African subregion. University of Pretoria, Pretoria.

Steiner K 1981. Nectarivory and potential pollination by a Neotropical marsupial. Annals of the Missouri Botanical Gardens 68, 505-513.

Steiner K 1983. Pollination of *Mabea occidentalis* (Euphorbiaceae) in Panama. Systematic Botany 8, 105-117.

Sussman R W and Raven P H 1978. Pollination by lemurs and marsupials: an archaic coevolutionary system. Science 200, 731-736.

Toledo V M 1977. Pollination of some rain forest plants by non-hovering birds in Veracruz, Mexico. Biotropica 9, 262-267.

Turner V 1982. Marsupials as pollinators in Australia. In: Armstrong J A, Powell J M and Richards A J (editors) Pollination and evolution. Royal Botanical Gardens, Sydney.

Vogel S 1954. Blutenbiologische Typen als elemente der sippengliederung: dargestellt aanhard der flora Südafrikas. Gustav Fischer: Jena.

Whelan R J and Burbridge A H 1980. Flowering phenology, seed set and bird pollination of five Western Australian Banksia species. Australian Journal of Ecology 5, 1-7.

Wiens D 1985. Secrets of a cryptic flower. Natural History 5, 71-76.

Wiens D, Renfree M and Wooller R O 1979. Pollen loads of honey possums (Tarsipes spenserae) and non-flying mammal pollination in south western Australia. Annals of the Missouri Botanic Gardens 66, 830-838.

Wiens D and Rourke J P 1978. Rodent pollination in southern African Protea species. Nature 276, 71-73.

Wiens D, Rourke J P, Casper B B, Rickart E A, Lapine T R, Peterson C J and Channing A 1983. Non-flying mammal pollination of southern African Proteas: a non-coevolved system. Annals of the Missouri Botanic Gardens 70, 1-31.

CHAPTER 6 WIND POLLINATION IN THE CAPE FLORA

D Koutnik

Anemophily is the pollination of seed plants by wind. This is a passive mechanism requiring no external biotic vector for successful transfer of pollen to a receptive stigma. It does, however, require specialized floral adaptations for efficient pollen transfer. These adaptations are generally thought to have evolved from insect pollinated ancestors in the angiosperms (Whitehead 1969; Faegri and van der Pijl 1979), but are accepted as the primitive conditions in the gymnosperms.

STUDIES OF THE CAPE FLORA

The study of anemophily has not attracted many researchers possibly as a result of the inherent difficulties in tracing pollen movement in the atmosphere. It is not surprising that there is only one published account of the study of wind pollination for South African taxa. Phillips (1926) confirmed wind pollination for the gymnosperms Podocarpus (two species) and Widdringtonia, and observes that Trichocladus (two species), Trimeria, Brachylaena, Tarchonanthus and Lachnostylis are at least partially pollinated by wind.

Most reports of anemophily are attributed to north temperate forests, especially the low diversity coniferous forests of high latitudes (Regal 1982). Reproductive dynamics of anemophilous species have been examined by Lemen (1980) for the genus Amaranthus. The only well-documented example of wind pollination in the tropics is that of Bawa and Crisp (1980) for a species in the Moraceae. The ecological considerations of wind pollination have recently been reviewed by Whitehead (1983). The aerodynamic characteristics of adaptations to wind pollination are receiving attention by Niklas (1982, 1983, 1985).

THE ANEMOPHILOUS SYNDROME

The present discussion of the adaptations of plants to an abiotic mode of pollination will be restricted to the angiosperms. Although much will be equally applicable to the gymnosperms, the latter are primitively anemophilous and have slightly different morphological considerations. There are no documented cases of insect pollination (entomophily) for the gymnosperms (Dorga 1964) although Rattray (1913) has reported the visits of curculionid beetles to the cones of Encephalartos species. The study of Taxus cuspidata by Niklas (1985) might be extrapolated to provide an indication of the pollination mechanism of Podocarpus.

As noted above, the angiosperms are considered to be primitively entomophilous and secondarily anemophilous. Yet the success of the angiosperms is largely attributed to the adoption of a biotic mode of pollination. The reduced floral axis, with a perianth enveloping the sexual organs and a protected ovule, are all features of animal pollination which hinder efficient abiotic pollination.

It is therefore assumed that anemophily has arisen independently many times within the angiosperms in both dicots and monocots. Despite this independence, the many wind pollinated species exhibit a number of adaptive similarities. These include the structure and location of the flowers; the number, size and sculptural characteristics of pollen grains and the timing of flowering and of pollen release.

There are several structural characteristics of the flower shared by most anemophilous species that optimize the efficiency of wind pollination. The perianth is often reduced or absent, thus permitting air circulation around the unobstructed anthers and stigmas. Anthers and stigmas are also exerted beyond the perianth, enabling more efficient pollen dispersal and capture. The stigmas may be highly elaborate to increase the receptive surface area, while retaining a small volume and diameter (structures with a large volume have a thick boundary layer and a reduced capacity for pollen collection, although the boundary layer thins at high wind velocities).

The location of the flower on a plant is another factor influencing the efficiency of pollen transfer and interception. Flowers are optimally situated on exposed parts of plants, frequently high up on the plant. Additionally, in species with unisexual flowers, male components are situated higher in the plant or more distally on the branch than the female components.

Plants which produce large quantities of pollen grains will obviously increase their ability to effect pollination. It is not surprising that most anemophilous species are characterized by a large production of pollen. Aerodynamic considerations also play a role in the evolution towards anemophily. Pollen grains are best dispersed when small and light. The average size of pollen for wind pollinated plants is 20 to 40 microns, compared to the five to 250 microns for pollen in general (Whitehead 1969).

Many conifers have large pollen grains but these are mostly accompanied by the development of air sacs which increase buoyancy and dispersability. Pollen sculpture is plain, usually psilate or scabrate, with little or no ornamentation. The pollen is also not sticky (nonadherent) because the pollenkitt is dry and powdery (Hesse 1978). Wind pollinated members of families that are predominantly animal pollinated often have distinctive pollen morphologies with reduced sculpture (eg Artemisia in the Asteraceae).

To be effective, the release of pollen by a plant must occur at the time of day and season of year that is most favourable to the dispersal of the pollen. High relative humidity tends to increase the density of a pollen grain and consequently will reduce its dispersal capacity. Wind velocity must be appreciable to transport pollen, although high wind velocity may increase pollen filtration by physical barriers (eg leaves, branches). High air turbulence increases dispersion that maximizes pollen concentrations away from the source. Rain has a tremendous capacity to capture pollen and a single rain shower can effectively eliminate pollen from the atmosphere.

The ideal characteristics of the anemophilous syndrome can be summarized as follows:

- large scale production of pollen adapted for atmospheric dispersability;
- flower and inflorescence structure appropriately placed within the plant to maximize pollen release and capture;
- stigmatic surface with large interception area, and temporal and seasonal pollen release for maximum efficiency (ie low humidity, low rainfall, correct wind velocity).

Other characteristics associated with the syndrome are:

- insignificant perianth (reduced, absent or caducous);
- bracts and perianth inconspicuous, ie green to dark brown or red in colour;
- no attractants (odour or scent) or rewards (nectar) to flowers;
- stigmas and anthers on long filaments exerted beyond the perianth;
- anthers open in warm, dry weather;
- pollen bouyant, small in size, usually not in tetrads, smooth and nonadherent surface; low number of ovules per flower; and
- flowers exposed and often unisexual.

ENVIRONMENTAL FACTORS

It was mentioned above that climatic parameters are in a large manner responsible for the efficiency and effectiveness of anemophily as would be expected in a passive mode of pollination. The dispersal capability of pollen is dependent on wind velocity: without air movement pollen moves only by way of force of gravity. The terminal velocity of a pollen grain (a factor of both size and density of the grain) varies from two to six centimetres per second, but average wind velocities range from one to 10 m per second (Whitehead 1969). Small pollen grains therefore have a selective advantage over larger ones, since the smaller grains would be suspended longer and have a lower impaction efficiency.

Atmospheric moisture, whether in the gas or liquid phase, is also a factor controlling the effectiveness of anemophily. Pollen grains absorb moisture from the air and change their density. Heavy, dense pollen grains have a greater chance of impacting against an object, including stigmatic surfaces and other nonpollination surfaces such as branches. Light pollen grains more readily follow the air flow around an obstructing object and avoid capture. Therefore, a high relative humidity will decrease the dispersal capability of pollen grains. It would be expected that wind pollinated plants might release pollen when humidity is low or temperatures high, for maximum dispersibility.

Rain has been mentioned as a pollen removal agent. The ability of a rain drop to capture pollen is dependent on the velocity and size of the droplets (Whitehead 1983). A thunderstorm is less effective at pollen removal than is a fine mist. It is clearly to the advantage of a plant to release its pollen at a time of low or no rainfall to avoid removal of pollen from the air.

ECOLOGICAL FACTORS

The ecological factors that have been correlated with anemophily are altitude, species-richness and floristic association. Anemophily is more common in areas that are floristically low in species diversity. There is also a high frequency of anemophily in island floras (Whitehead 1969). The percentage of anemophilous plants increases from tropical environments to temperate ones.

There appears to be a trend toward an increase in the occurrence of anemophily with an increase in elevation, even in low latitude regions (Regal 1982). This is partly intuitive from the high frequency of anemophily in high latitudes and the presence of temperate floristic elements on high mountains. This trend needs further study, but may reflect the lower availability of potential animal pollinators at higher elevations and latitudes, and the predominance of sedges and grasses in both situations.

Plant associations with reduced species diversity tend to have a high percentage of anemophilous species. Certainly the species poor, north-temperate forests have a high frequency of anemophily. But it is difficult to determine whether the low diversity is a result of the efficiency of wind pollination in closely aggregated (gregarious) populations, or whether the low diversity has been brought about by the harsh seasonal environment of northern climates. The amount of wind pollination can vary greatly even between communities at a single location. Some fynbos assemblages have highly aggregated species populations (eg some Ericaceae) that might be wind pollinated. But wind pollination should not be expected to be prevalent in fynbos because of the high species diversity.

A decrease in anemophily occurs with an increase in aridity. Plants usually are widely spaced in arid environments so the efficiency of anemophily would be very low. In general, wind pollination is low in deserts, as exemplified by the mid-latitude arid zones of North America and Australia, where the percentage of wind pollinated plants is low, contrary to the trend of an increase of wind pollination with increase in latitude. This trend may bear further investigation in the Karoo and Namaqualand regions.

CONCLUSIONS

Anemophily represents the extreme of a continuous variation from no wind pollination (eg Orchidaceae) to obligatory wind pollination (eg conifers) with all conceivable conditions occurring inbetween. There are two basic modes of pollination, anemophily and biotic pollination. Stelleman (1984a) uses the term ambophily for the condition where both modes occur for a particular species with hermaphroditic flowers, whereas Hesse (1981) uses the term amphiphily. Certain species of Plantaginaceae that are normally wind pollinated (eg Plantago lanceolata) contain populations, usually in closed vegetation, in which insect pollination becomes an appreciable contribution to the species' reproduction biology (Stelleman 1984b).

Anemophily appears to be a random, wasteful and imprecise means of pollination. It is neither as effective nor as efficient as animal pollination. Yet this pollination mode has repeatedly evolved from biotic-pollinated ancestors. The reason for the evolution is still unclear and must be hypothesized from the observed trends.

The spacing between individual plants is usually short in anemophilous species. Wetland habitats in particular have a close spacing of plants and many of the species in this habitat type are anemophilous, belonging to the families Cyperaceae, Juncaceae and Typhaceae. There is also a trend toward clumping of species in temperate regions which may be related to a reduction in species diversity. Such close spacing is conducive to wind pollination, since the probability of fertilization decreases rapidly with distance from the pollen source in anemophilous species.

Anemophily can be the dominant pollination strategy in open structured vegetation, especially in the temperate deciduous forests, where flowering often occurs before the annual development of leaves. This permits pollen to move more freely with fewer nonreceptive surfaces to capture pollen. But anemophily also occurs in northern evergreen forests, and only rarely in tropical deciduous forests. Furthermore, most deserts have an open vegetation and windy conditions, yet wind pollination is insignificant in most arid environments.

Genetic diversity is favoured (advantageous) when environmental uncertainty (eg unpredictable rainfall) increases (Regal 1982). In such a situation, the proportion of animal pollination is greater because of the likelihood of outcrossing with nonadjacent neighbours (Regal 1982) and provides a selective advantage (for increased variation). However, Hamrick et al (1979) indicate that populations of anemophilous species have higher levels of genetic variability, higher than animal pollinated species. This might be explained by the long pollen distances conveying less inbreeding and more intrapopulation variation.

There are 8 504 species in 950 genera of 150 families in the Cape flora (Bond and Goldblatt 1984). Of these, 986 species (12%), 156 genera (16%) of 26 families (18%) are potentially anemophilous taxa (Table 6.1). This percentage is comparable (but slightly lower) to the estimate of anemophily in Chile (Arroyo et al 1982) and about equal with that (excluding coniferous vegetation) found in California (Moldenke 1979). The Restionaceae (31%), Cyperacee (21%) and Poaceae (19%) account for the largest proportion of this total figure. The genus Cliffortia (Rosaceae) has the most wind pollinated species (106) although many of these may prove to be apomictic. The aggregated and often patchy distribution of some Ericaceae (Rebelo et al 1985) and Leucadendron (Williams 1972) populations should be investigated to determine whether these species may be wind pollinated. The Cape vegetation might be compared to the sclerophyllous vegetation of Australia which is mostly animal pollinated (Armstrong 1979). Wind pollination must therefore be considered to be of minor importance in the Cape flora pollination spectrum although it is certainly dominant in certain groups (eg Restionacee). More studies are needed to confirm the pollination mode of the potentially wind pollinated species.

TABLE 6.1 The occurence of wind pollination in the Cape flora

Family	Number of species	Family	Number of species	Family	Number of species
CUPRESSACEAE:	(3)	JUNCACEAE:	(18)	Melica	1
Widdringtonia	3	Juncus	17	Merxmuellera	8
		Prionium	1	Microchloa	1
PINACEAE:	(2)			Microsteqium	1
Pinus*	2	JUNCAGINACEAE:	(2)	Miscanthidium	2
		Triglochin	2	Panicum	3
				Pennisetum	2
PODOCARPACEAE:	(3)			Pentameris	4
Podocarpus	3	POACEAE:	(184)	Pentaschistis	38
		Agropyron	1	Phragmites	1
		Agrostis	4	Plagiochloa	6
ZAMIACEAE:	(4)	Aira	1	Poa	1
Encephalartos	4	Andropogon	2	Poagrostis	1
		Anthoxanthum	2	Polypogon	1
		Aristida	2	Prionanthium	2
CYPERACEAE:	(203)	Brachiana	1	Pseudopentameris	2
Bulbostylis	2	Brachypodium	1	Puccinella	2
Carex	5	Chaetobromus	2	Rhynchelytrum	2
Carpha	2	Cymbopogon	2	Schismus	4
Chrysithrix	2	Cynodon	1	Setaria	2
Cladium	1	Digitaria	4	Sporobolus	3
Costularia	1	Diheteropogon	1	Stenotaphrum	1
Cyperus	12	Diplachne	1	Stipa	2
Eleocharis	2	Ehrharta	23	Stipagrostis	1
Epischoenus	8	Elionurus	1	Themeda	1
Ficinia	57	Enneapogon	2	Trachypogon	1
Fimbristylis	3	Eragrostis	11	Triraphis	1
Fuirena	3	Eulalia	1	Tristachya	1
Hellmuthia	1	Eustachys	1	Urochlaena	1
Isolepis	18	Festuca	1		
Juncellus	1	Fingerhuthia	1		
Kyllinga	3	Harpochloa	1	RESTIONACEAE	(310)
Macrochaetum	2	Helictotrichon	6	Anthochortus	6
Mariscus	4	Hernarthria	1	Askidiosperma	10
Neesenbeckia	1	Heteropogon	1	Calopsis	23
Pycreus	3	Holcus	1	Cannomois	6
Rhynchospora	1	Hordeum	1	Ceratocaryum	5
Schoenoxiphium	5	Hyparrhena	2	Chondropetalum	12
Schoenus	1	Karroochloa	3	Dovea	1
Scirpus	21	Koeleria	1	Elegia	32
Tetraria	41	Lasiochloa	4	Hydrophilos	1
Trianoptiles	3	Leersia	1	Hypodiscus	16

TABLE 6.1 (continued)

Family	Number of species	Family	Number of species	Family	Number of species
Ischyrolepis	46	ERICACEAE	(65)	MYRICACEAE	(7)
Mastersiella	3	Coccosperma	3	Myrica	7
Nevillea	2	Coilostigma	2		
Platycaulos	8	Eremiella	2		
Restio	85	Erica (sect.	30	MYRSINACEAE	(3)
Rhodocoma	3	Arsace and		Myrsine	2
Staberoha	9	others)		Rapanea	1
Thamnochortus	31	Nagelocarpus	1		
Willdenowia	11	Philippia	10		
		Salaxis	6	PLANTAGINACEAE	(3)
		Scyphogyne	12	Plantago	3
TYPHSACEAE	(1)				
Typha	1				
		EUPHORBIACEAE:	(8)	POLYGONACEAE	(5)
		Acalypha	4	Emex	1
AMARANTHACEAE	(3)	Ctenomeria	1	Rumex	4
Amaranthus	2	Hyaenanche	1		
Pupalia	1	Lachnostylis	2		
				PROTEACEAE	(13)
				Aulax	3
ASTERACEAE	(6)	FLACOURTIACEAE:	(2)	Leucadendron	10
Artemisia	1	Trimeria	2		
Brachylaena	4				
Tarconanthus	1			ROSACEAE	(106)
		GUNNERACEAE:	(1)	Cliffortia	106
		Gunnera	1		
CHENOPODIACEAE	(17)				
Atriplex	2			THYMELAEACEAE	(14)
Chenolea	1	HALORAGIDACEAE:	(1)	Passerina	14
Exomis	1	Laurembergia	1		
Halopeplis	1				
Manochlamys	1			ULMACEAE	(1)
Salicornia	2	HAMAMELIDACEAE	(1)	Celtis	1
Sarcocornia	7	Trichocladus	1		
Suaeda	2				

SUMMARY:

Total:	986 species (12%)	156 genera (16%)	26 flora families (18%)

REFERENCES

Armstrong J 1979. Biotic pollination mechanisms in the Australian flora - a review. New Zealand Journal of Botany 17, 467-508.

Arroyo M T K, Primack R and Armesto J 1982. Community studies in pollination ecology in the high temperature Andes of central Chile. I. Pollination mechanisms and altitudinal variation. American Journal of Botany 69, 82-97.

Bawa K W and Crisp J E 1980. Wind pollination in the understory of a rainforest in Costa Rica. Journal of Ecology 68, 871-876.

Bond P and Goldblatt P 1984. Plants of the Cape flora: a descriptive catalogue. Journal of South African Botany Supplementary Volume 13.

Dorga P 1964. Pollination mechanisms in gymnosperms. In: Nair P K (editor) Advances in palynology. National Botanical Gardens Lucknow, India.

Faegri K and van der Pijl L 1979. The principles of pollination ecology. 3rd edition. Pergamon Press, Oxford.

Hamrick J L, Linhart Y B and Mitton J B 1979. Relationship between life history characteristics and electrophoretically detectable genetic variation in plants. Annual Review of Ecology and Systematics 10, 173-200.

Hesse M 1978. Entwicklungsgeschichte und Ultrastruktur von Pollenkitt und Exine bei nahe verwandten entomphilen und anemophilen Angiospermensippen: Ranunculaceae, Hamamelidaceae, Platanaceae und Fagaceae. Plant Systematics and Ecology 130, 13-42.

Hesse M 1981. The fine structure of the exine in relation to the stickyness of angiosperm pollen. Review of Palaeobotany and Palynology 35, 81-92.

Lemen C 1980. Allocation of reproductive effort to the male and female strategies in wind-pollinated plants. Oecologia 45, 156-159.

Moldenke A R 1979. Pollination ecology as an assay for ecosystemic organization: convergent evolution in Chile and California. Phytologia 42, 415-454.

Niklas K J 1982. Simulated and empiric wind pollination patterns of conifer ovulate cones. Proceedings of the National Academy of Science of the United States of America 79, 510-514.

Niklas K J 1983. The influence of Paleozoic ovule and cupule morphologies on wind pollination. Evolution 37, 968-986.

Niklas K J 1985. Wind pollination of Taxus cuspidata. American Journal of Botany 72, 1-13.

Phillips J F V 1926. General biology of the flowers, fruits and young regeneration of the more important species of the Knysna forest. South African Journal of Science 23, 366-417.

Rattray G 1913. Notes on the pollination of some South African cycads. Transactions of the Royal Society of South Africa 3, 259-270.

Rebelo A G, Siegfried W R and Oliver E G H 1985. Pollination syndromes of Erica species in the south western Cape. South African Journal of Botany 51, 270-280.

Regal P J 1982. Pollination by wind and animals: Ecology of geographic patterns. Annual Review of Systematics and Ecology 13, 497-524.

Stelleman P 1984a. Reflections on the transition from wind pollination to ambophily. Acta Botanika Neerl. 33, 497-508.

Stelleman P 1984b. The significance of biotic pollination in a nominally anemophilous plant: Plantago lanceolata. Proc. K. Nederl. Akad. Wet. 87, 95-119.

Whitehead D R 1969. Wind pollination in the angiosperms: evolutionary and environmental considerations. Evolution 23, 28-35.

Whitehead D R 1983. Wind pollination: some ecological and evolutionary perspectives. In: Real L (editor) Pollination biology. Academic Press.

Williams I J M 1972. A revision of the genus Leucadendron. Contributions to the Bolus Herbarium 3, 1-425.

CHAPTER 7 GENE FLOW IN PLANT POPULATIONS

A V Hall

Gene flow is the process of transfer of genes within, among and away from populations. In higher plants the genes are transferred in pollen, or in seeds or other kinds of propagule such as bulbils or pieces of stem. The transfer is often aided by a vector such as wind, water or an animal pollinator or seed disperser.

INTRODUCTION

Why is gene flow relevant in a text on pollination biology? An example will show why. Disa cornuta (Orchidaceae) is a thinly dispersed species with most plants a kilometre or more apart (Hall 1959). This is associated with the species' very large numbers of minute, wind dispersable seeds. Why so few individuals develop from these seeds is unknown, but the fact remains that the pollinia must be carried long distances between the plants before cross pollination can take place. This in turn raises the question of the viability of these populations: are they highly inbred due to the rarity of crossing or by the gene pool being shared by so few individuals? Are they therefore more homozygous than other species? How should this species be conserved in nature reserves? Is gene flow so limited that local variants develop and are these lines shifting erratically in response to the random phenomena of genetic drift? What pollinator can fly these distances and detect other plants at such long ranges? Gene flow has so many important interfaces with pollination biology that the two should clearly be reviewed together.

Gene flow has been widely neglected as a research topic in southern Africa, partly because it has been difficult to study with any precision. Even elsewhere there are remarkably few examples of detailed field studies and much of the literature is theoretical. Yet there is no doubt that gene flow is a central field in genetics. In biogeography it influences the distributions of genes. In evolution it is the pathway of genetic communication between individuals, populations and generations.

Gene flow and other genetic biogeography studies have a useful potential for developing a better practical basis for nature conservation. The studies may give valuable insights into the optimal patterns of genetic diversity for critically rare species. Reserve managers can then aim to meet these optima so as to have efficient, long-term conservation of evolutionary lineages (Frankel and Soulé 1981). In the coastal lowlands of the western Cape this may help improve the cost-effectiveness of the nature reserves. The vegetation in this region has been reduced to a patchwork of small remnants among farmlands and carries many plant species threatened with extinction (Hall and Veldhuis 1985; Jarman 1986).

The main aims of this chapter are to review what is known about how gene flow operates in plants and how to go about investigating it in the Cape flora. As the subject is generally under-studied in the Cape flora region, it is introduced by an account of the basic aspects of gene flow, derived largely from standard texts such as those of Endler (1977), Harper (1977) and Grant (1981). It should be cautioned that programmes on gene flow must have prior support from lengthy studies of the details of demography, distribution and breeding systems about which very little is known in the Cape flora.

THE NATURE OF GENE FLOW

Gene flow is the successful transfer of genes to the gene pool formed by another individual, population, genetic neighbourhood or deme, followed by their establishment there. Spatial gene flow results from a transfer over some physical distance. Temporal gene flow results from a transfer from one time period to another. Seeds are an example. Seeds laid down several generations ago may survive to grow into individuals which are then able to breed directly with the plants arising from recent seed, resulting in direct genetic communication between the past and the present.

Much emphasis is given in gene flow studies to the actual transfer of genetic material but it seems just as important to confirm that the genes become established in the recipient population.

Gene flow in seed plants

Gene transfer in seed plants may be by gametophytic pollen grains or by sporophytic propagules. The propagules are usually seeds but may be fragments of the plant, especially stems, rhizomes or specialized units such as bulbils. Long-lived seeds in seed stores may have important genetic influences through temporal gene flow (Harper 1977). The embryos of seeds in the seed store may carry a large proportion of the total gene pool and may only require the right conditions for germination, growth and flowering to become full genetic contributors to the next generation.

A gene flow study should start with a genetically orientated census to show the distribution of the carriers of the gene pool of a species. In this census some account should be taken of the embryo individuals by assessing the number of viable seeds in the seed store and how many individuals they are likely to contribute to the next generation under various expected habitat scenarios. This has to be a crystal ball operation. For example, no-one could foretell when a population of the rare Marsh Rose, Orothamnus zeyheri should be burnt for optimal seed germination. Because of the great difficulty of evaluating the potential of seed stores, they are commonly not counted in ecologically orientated censuses and a population is often only assessed as numbers of adults. In conservation biology, seed store data are vital for planning full use of the gene pool when restoring genetic diversity in small populations which are genetically depleted by increased inbreeding, homozygosity and leakage of alleles (Frankel and Soulé 1981; Hall and Veldhuis 1985).

In theory, seed stores play an important role in local microevolution. Populations without a seed store are likely to vary directly over a number of generations with the amount of gene flow from different gene pools in other areas. In other cases, variation will be damped by germination of seeds from the population's seed store. The seed store acts as a reservoir for the input of past local genotypes to the current population, giving it slower rates of evolutionary change than would be expected from the number of adults present.

Endler (1977), mainly with animals in mind, sees gene flow as only between or within standing populations. Migration or dispersal events are excluded. In animals, migration is the long distance movement of large numbers of individuals at a time in the same direction. In the case of birds, migration often involves return within a year. Endler excludes animal migration from gene flow because it does not result in genetic communication to distant populations.

For plants, it seems better to take a broader view. In many plant species a single propagule may establish a new population, whether there is a potential cobreeder there or not (unlike most animals where at least a pair or a pregnant female is needed for establishment). These newly founded populations are of great interest in genetic biogeography and evolution.

Another reason for using this broader meaning of gene flow is that some flowering plants are apomicts which lack the interbreeding shown by sexually reproducing species (Grant 1981). Dispersal and establishment of apomictic genomes results in new elements appearing in a region, but they cannot breed with the local population as required by Endler's concept but may reproduce themselves asexually. Their arrival in a remote population has much the same end effect as if they had come as cobreeders, so there seems to be no good reason for excluding apomicts from the concept of gene flow.

Gene transfer and establishment differ among pollen, propagules and seeds

The complete process of gene flow involves both the transfer of the bearer of genes and their establishment in a remote site or period. The bearer may be a propagule, a seed, a pollen grain or a pollinium as in the Mimosaceae. Propagules and seeds are much heavier and usually far less numerous than pollen grains and may have correspondingly different means of transfer. Pollen grains are seldom long-lived enough to be effective in temporal gene flow.

Seeds and propagules can arrive and directly establish new individuals in a remote site or population. Especially for seeds, there are a number of ecological hazards in establishment. The seeds must be at the right level in the soil, dormancy must be broken, the habitat conditions must be satisfactory and the young seedlings may meet with competition, predators and fungal attack, all of which severely reduce survival (Harper 1977). A surviving plant may on its own become a founder of a new population, reproducing asexually or by self-fertilization; or, in the case of sexually reproducing species it may breed with the recipient population.

The flowers and fruits of the newly arrived individual are the local base from which its genes may be dispersed as pollen or seeds. Pollen from members of the recipient population may fertilize the newcomer's ovules, strengthening its contribution to the local gene pool.

Processes of genetic establishment are different for pollen. Pollen grains have more obstacles than seeds before their gametophytic genomes become incorporated in the recipient gene pool. For successful incorporation, the pollen grain must germinate and its pollen tube must compete successfully with others from the local plants. Fertilization and ovule development must take place without incompatibility effects (Grant 1981).

Breeding neighbourhood as a unit of genetic biogeography

A population within which there is completely random mating is known as a panmictic breeding unit. However, among stationary plants breeding is seldom fully random so it is more accurate to use the term subpanmictic. Some breeding will occur into a marginal zone lying outside the subpanmictic population's boundary. The area encompassing the subpanmictic population and its marginal zone is loosely termed a breeding neighbourhood (Wright 1946). Neighbourbood size is defined theoretically as the number of plants in an area demarcated by a standard level of observed gene flow. In the rather few plant species studied, gene flow is often so local that the breeding neighbourhood is confined to a small patch within a large and continuous population (Richards and Ibrahim 1978; Grant 1981). The main cause of such localized breeding neighbourhoods is the leptokurtic (mostly near the source) frequency distribution of pollen gene flow events. This distribution is shown in Figure 7.1 for an experimental population of a lupin, Lupinus texensis (Fabaceae: Schaal 1980).

The frequency and mean distances of gene flow events can be evaluated. The resulting pattern shows the effective size of the local breeding unit. This in turn defines the size of the smallest ecotypic unit (Grant 1981; Liu and Godt 1983). Ecotypic units as small as a few square metres have been observed in herbaceous communities (Bradshaw 1959; Jain and Bradshaw 1966; Hamrick and Allard 1972; Hedrick 1985). There are as yet no studies like this in the Cape flora.

Neighbourhood sizes have been found to vary from 75 to 282 plants in Phlox pilosa (Polemoniaceae: Levin and Kerster 1968), to only four individuals in Lithospermum caroliniense (Boraginaceae: Kerster and Levin 1968). Such localization results in phenotypic variants which are in many cases not ecological adaptations to habitats. Wright (1946) showed that if a panmictic unit consists of only 10 individuals, local racial differentiation can develop within a large continuous population by stochastic (random-based) processes, quite apart from the action of natural selection (Grant 1981).

The sizes of genetic neighbourhoods are influenced by a host of factors. Basic among these are the species' density and the effectiveness of the vectors of the pollen or propagules. Influencing these are the season; the seral stage; the availability of food or shelter if the vector is an animal; predation; and finally, all the factors affecting gene establishment such as genetic and habitat compatibility with the new site and its plants.

Patterns of breeding in genetic neighbourhoods are not uniform. One reason for this is that plants at the edge of a patch will have fewer possible cobreeders nearby than those in the middle. In some outcrossing species, cobreeders which produce offspring with the highest fitness occur on average some distance from each other. An optimal outcrossing distance has been proposed at which fecundity (seed production) is maximized (Waser and Price 1983). Crossing between plants closer than this distance

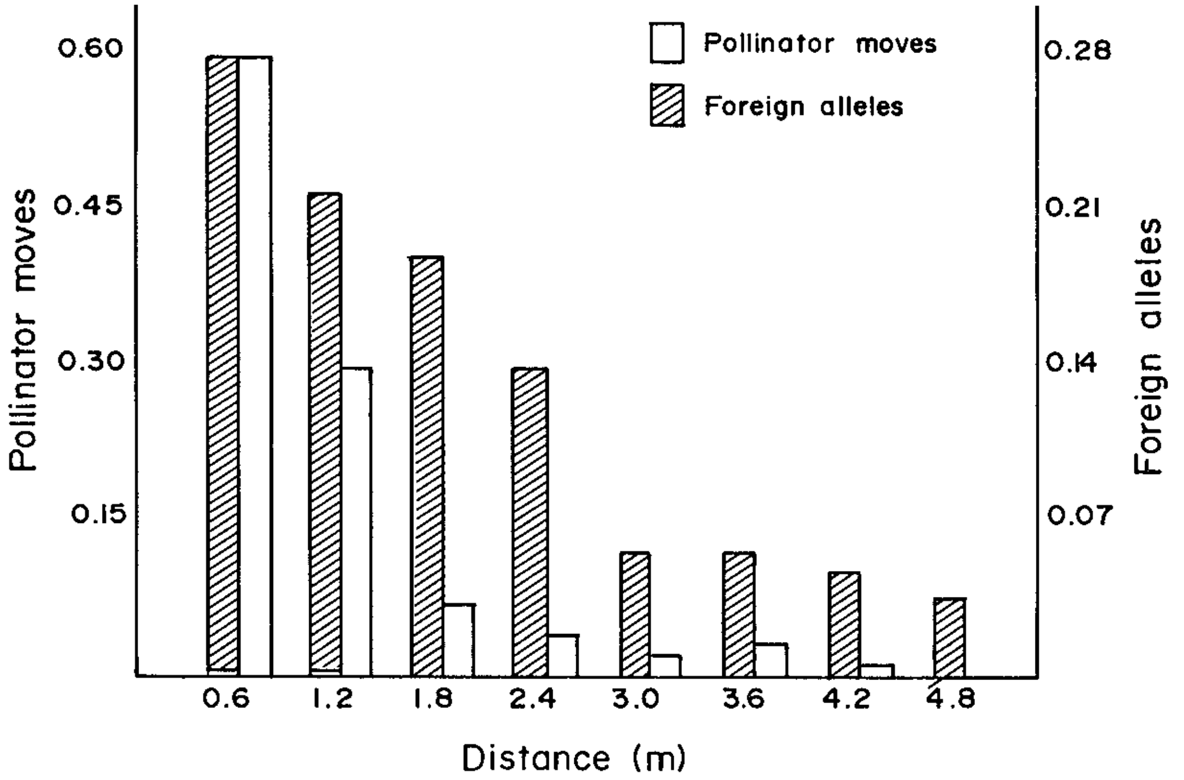


FIGURE 7.1 Bar-chart showing the leptokurtic distribution of gene flow in an experimental population of <u>Lupinus texenis</u> (Fabaceae). Plants grown at the centre of the population were homozygous for alleles not present in the others. The shaded bars show the relative proportion of the foreign alleles in the F1 progeny of plants at various distances after gene flow caused by foraging bees. The clear bars show the proportions of bee movements made over a given distance. From Schaal (1980).

amounts to inbreeding, which may lead to a depression of fitness. Beyond the optimal distance inter-genome incompatibility may increase, resulting in an outbreeding depression of fitness. Although this is an interesting concept, there is as yet no evidence of how common it may be (D Wiens in littera). This could be a profitable line of study in the localized populations so commonly found in the Cape flora.

Gene flow promotes hybridization between seed plants

Gene flow between two or more related taxa may ensue when a barrier to cross-breeding breaks down. The resulting phenotypes are hybrids, which can be recognized in the field by their appearance, intermediate between the parents which are often nearby. Where the hybrids are sterile, the establishment phase of gene flow has failed and the hybrid plants are rare.

The sterility is due to genome incompatibility which is sometimes, as a rare event, corrected by doubling of each genome. Normal pairing can then proceed in meiosis, the duplicated sets of chromosomes of one species behaving virtually independently of those of the other in the dividing cell. Normal sexual reproduction follows. Having achieved this polyploid state there can be no direct breeding back with either of the parents. The new polyploid hybrid is on a separate evolutionary pathway with a highly isolated gene pool. Many of these events have accumulated in some seed plant groups. An example is the grasses (Poaceae) of which 80% of the species are said to be polyploid (Stace 1975). However, it is often uncertain how much of this is due to hybridization or to autopolyploidy (self-doubling) within a species.

Where the hybrids are fertile, hybridization may be marked in the field by the local presence of numerous intermediates, some of which may result from back-crossing with one or both parents. When the hybrid back crosses with only one of the parents, introgressive hybridization may ensue. This may be difficult to detect as it is, in effect a slow or periodic leakage of genes from one species to another through their joint hybrids. When rare hybridization is accompanied by apomixis, a swarm of microspecies may develop (Grant 1981).

Unlike most animal groups, hybridization is of major importance in seed plants, having widely affected the group's evolution by creating complex patterns of reticulation (Stebbins 1974). Examples of this in the Cape flora should be sought in large genera with complex internal relationships, as in Aspalathus (Dahlgren 1960). Another aspect of the importance of hybrids is that some may show more vigour in rate of growth and larger sizes of cells and organs than their parents. This well known phenomenon is termed hybrid vigour or heterosis (Grant 1981). In general, it does not seem to be much in evidence in hybrids in the Cape flora: future studies should be made to evaluate this.

In both obvious and more cryptic forms hybridization is more common in plant species than many older taxonomic treatments would suggest (Raven 1976). For example, nineteenth century British botanists considered plant hybrids to be extremely rare in nature, yet of 2 200 species in the British Isles at least 850 interspecific hybrid combinations are known (Stace 1975). The field work involved in preparing the account of the nearly 2 300 species flora of the Cape Peninsula raised the number of suspected or proved hybrids from 'very few' to 70 (Adamson and Salter 1950).

Gene flow affects the geographical distribution of phenotypes

Populations of a species often have minor phenotypic differences between them. This may be partly due to the effects of habitat factors such as local wind-shears or droughts. The habitat factors will select for some genotypes, raising their frequency against others. Gene flow across the barriers between populations may also alter the frequency of phenotypes, spreading new or foreign alleles and recombinants. One may interpret the resulting patterns of geographical distribution as follows (Endler 1977; Grant 1981):

Clinal variation. This can be seen as a gradient in frequencies of different phenotypes through a series of populations of a species. Some clines may arise from selection which has a gradient ranging from weak in one region to strong in another. Others may be due to the resumption of gene flow between temporarily isolated populations. It is difficult to differentiate between these two origins of clinal variation without historical data. Clinal gradients may be gradual or local and steep or stepped. Even steep gradients may be maintained by strong selective forces in spite of extensive gene flow. There are numerous other factors affecting clines such as heterozygous advantage, fitness components, the presence of partial barriers to gene flow and local reductions in population size. These are discussed in full by Endler (1977).

Hybrid zone. In this case distinct populations have hybrids at their contact zones. A long-standing hybrid population will suggest that intrinsic isolation barriers exist between the parent populations causing hybrid sterility and preventing back-breeding. Gene flow is then effectively blocked.

Overlap or conjunction. These are cases where parts of distinct populations of a species are contiguous or overlap with each other but do not interbreed. They are genetically (but perhaps not competitively) isolated from each other and are on effectively separate evolutionary pathways. They may eventually acquire enough distinctive properties to be worth describing as separate taxa.

Disjunction. In this case the populations occur in spatially separated areas. They may not be distinguishable from each other. Gene flow may or may not be able to bridge the gap between the populations, depending on the amount of separation, the strength of the vectors, the material (pollen or propagules) being carried and the factors affecting establishment. For gene flow to cause the dedifferentiation of distinct populations there must be weak selection and genetic transfer events should have a large mean distance relative to the areas of the populations (Endler 1977).

The importance of gene flow in maintaining genetic diversity

Gene flow causes the dispersal of genetic diversity in the form of new or rare alleles. The maintenance of enough genetic diversity in a population for its long-term survival is a central tenet of conservation biology (Frankel and Soulé 1981).

Small populations can be expected from theory to show specialized genetic effects. In the smallest populations of less than 50 individuals there is a strong chance of uneven sampling of alleles during meiosis for gamete formation. Each generation's alleles may get so unevenly represented in the next that the gene pool soon becomes distorted and alleles may be lost. Randomness rules instead of natural selection and the population may undergo rapid change. This is known as genetic drift, or more explicitly sampling drift. Theoretically this is expected mostly to lead to extirpation of the population but on rare occasions it may generate successful new recombinants (Wright 1943; Levin and Kerster 1974; Grant 1981).

Propagule gene flow may cause a scatter of founder events to occur away from large core populations. This creates a cloud of peripheral neighbourhoods in which high risk genecological experimentation by genetic sampling drift can go ahead without prejudicing the main populations. The sampling errors may occur between the emigrants and their parental gene pools as well as in the small peripheral populations (Endler 1977). These processes may help develop ecotypes adapted to variations in the multidimensional, regional habitat surface (Slatkin 1977; Clegg and Brown 1983). In the fynbos biome, the wide scatter of small populations of many species through the landscape may well provide many cases of natural founder events and genetic sampling drift. Excellent cases may be found in groups such as the Ericaceae, Proteaceae and Iridaceae where there are numerous local endemics.

The occasional transfer of genes between small populations may be an antidote to the loss of genetic diversity (Wright 1951). Without interpopulation gene transfer, the local gene pool is left alone to cope with selective forces. If the population is small, less than the equivalent of about 50 effectively breeding individuals, there is a severely increased risk of fixation of alleles and loss of diversity due to inbreeding (Frankel and Soulé 1981). Enrichment with new mutant alleles developed elsewhere may enhance the survivorship of the local population. The amount of transfer should not swamp local ecotypic adaptation. This has been a strong argument against bringing very remote or ecologically alien genotypes together (Greig 1979).

GENE FLOW AND GENETIC BIOGEOGRAPHY IN THE CAPE FLORA

Gene flow and genetic biogeography are almost untouched fields of study in the Cape flora although there is useful speculation about the significance of the phenomena which can be directly observed (Linder 1985). Indeed almost all evolutionary studies of the biome's plants have had a late start. This is partly because the taxonomic and ecological groundwork has taken so long to lay in such a floristically rich and complex region. Little has been done to use genetic biogeography to understand why the flora is so rich, or to derive the evolutionary principles upon which its species and ecosystems should be conserved (Soulé and Wilcox 1980).

Genetic research is needed for conservation planning

Conservation is especially important in the Cape flora. A recent estimate gave the exceptionally high figure of 1 326 threatened species of vascular plants in the biome west of 26°E longitude (Hall and Veldhuis 1985). Studies on the Cape Peninsula showed that natural rarity has predisposed many plants to becoming threatened (Hall and Ashton 1983). In the western Cape's coastal lowlands the populations of many species have become extinct or reduced to remnants in small patches of natural vegetation surrounded by wheatlands (Jarman 1986).

Many new nature reserves are needed, mainly in these lowlands. The reserves should be planned to be effective for ecosystems and rare and important species, on long-term time scales which will allow evolutionary lineages either to develop, stay as they are or go naturally extinct. Studies in population genetics could help show the viability of nature reserves, especially for rare plants. For example, extensive gene flow and many individuals may be vitally needed by some outbreeders to maintain their genetic diversity which may require large reserves. Most rare species may require at least several populations for survival so that when some patches become extirpated replacements can appear by propagule gene flow from neighbouring areas. Ecological protection for the rare plants and their habitats could be provided with the aid of buffer zones.

This approach may show that some plans for small reserves for rare species may be worthless because of their limited carrying capacity. With the present high prices of rural land, research which will fine-tune reserve size to the needs of conservation is obviously important. Research on gene flow and genetic biogeography should rank at a much higher level of priority than in the past.

Many of the ecosystems which now exist as fragments in the western Cape lowlands would be good examples for studying the reduction or 'relaxation' in the number of species which occupy a remnant of a former large area of natural vegetation. This relaxation is the central hypothesis of island biogeography (Soulé and Wilcox 1980; Diamond 1984). Research on genetic diversity and gene flow between outcrossing populations, isolated at various distances within and between these remnants could throw light on the relationships between isolation and local extinction.

Examples from the Cape flora

The fynbos biome lies in a topographically and climatically varied region. This provides an immense range of selection pressures. The flora contains innumerable cases of localized population variation. Good examples are in the genera:

- Lobostemon (Boraginaceae: Levyns 1934);
- Leucadendron (Proteaceae: Williams 1972);
- Leucospermum (Proteaceae: Rourke 1972);
- Homeria (Iridaceae: Goldblatt 1981); and
- Satyrium (Orchidaceae: Hall 1982).

Cases where gene flow is probably playing a role in a dynamic genetic relationship between related populations include the following:

- Clinal variation: Leucospermum oleifolium (Berg.) R.Br. shows a genetically stabilized altitudinal cline over a distance of 10 km from the coast near Betty's Bay in the Kogelberg mountains (Rourke 1972). Leucospermum cuneiforme (Burm.f.) Rourke shows a cline in leaf width extending over 900 km eastwards from Caledon. This cline is maintained in spite of a background of a great variety of phenotypes reflecting major selection pressures in widely different habitats of the range (Rourke 1972).

- Another long distance cline is found in the flower-sizes of populations of Satyrium retusum Lindl., extending over a distance of 700 km with the gradient steepening in the western 100 km (Hall 1982). Phenotypes varying near the tips of major ranges have been found elsewhere in the Orchidaceae, as in Eulophia odontoglossa Reichb.f. and E streptopetala Lindl. (Hall 1965). This could be as much a result of less gene flow to the terminal populations as a response to adverse habitat conditions causing selection of a narrow range of phenotypes. It is notable in the case of Satyrium retusum that it has a pair of extremely disjunct vicariants, one separated by 1 700 km in the Chimanimani mountains of

Zimbabwe (*S aberrans* Summerh.) and the other in East Africa (*S ecalaratum* Schltr).

- Hybrid zones: *Leucospermum conocarpodendron* (L.) Buek has two subspecies, *conocarpodendron* and *viridum* which are almost contiguous between Little Lions Head and Karbonkelberg on the Cape Peninsula, being separated elsewhere. A hybrid swarm exists in a zone on Little Lion's Head (Rourke 1972). Probable hybrids and backcrossing with partial pollen sterility have been recorded between *Agathosma cerefolium* (Vent.) Bartl. & Wendl. and *A joubertiana* Schlechtd. The species are confined to separate soil types. The hybrids only occur where the soil types abut on one another (Bean in preparation). Other cases of hybridization and possible back-crossing involve *Protea longifolia* (Rourke 1980); and *Erica longifolia* (Rebelo and Siegfried 1985).

Hybrids, hybrid speciation and polypoidy in southern Africa were briefly reviewed by Goldblatt (1978). Studies on hybrids relevant to gene flow in the Cape flora are those of Horn (1962) and De Vos (1972) on Iridaceae; Nordenstam (1968) on *Euryops* (Asteraceae); and Oliver (1986) on *Erica* (Ericaceae).

A guide exists to the rare species which may be suitable for study because of the varying degrees of spatial isolation of their populations (Hall and Veldhuis 1985). Particularly suitable rare species include:

- *Audouinia capitata* (Bruniaceae);
- *Erica fairii* and *E pillansii* (Ericaceae);
- *Gladiolus aureus* (Iridaceae);
- *Leucadendron macowani* (Lloyd 1981) and *L argenteum* (Proteaceae: Wilson 1980);
- *Orothamnus zeyheri* (Proteaceae; Boucher 1981);
- *Protea odorata* (Proteaceae);
- *Staavia dodii* (Bruniaceae: Moll and Gubb 1981); and
- *Witsenia maura* (Iridaceae: Gaiwith 1983).

There are numerous major disjuncts, examples being *Protea coronata* and *P mundii*, where the isolates are so far apart that no gene flow is likely to exist between them.

The state of gene flow research in the Cape flora

There are as yet no reports which precisely document the patterns of transfer of pollen and propagules between or within plant populations in the Cape flora. However, other sections of this report reflect an increasing body of knowledge on the behaviour of the vectors of pollen.

Currently accurate census and distribution data are lacking for both plants and propagules. These are essential supporting components of a gene flow study. Seed store demography has as yet received little attention. Data have been collected on the seed output of a number of rare and threatened species, especially in the Proteaceae (J Vlok personal communication 1986; A G Rebelo personal communication).

As noted by Steiner (this volume) breeding systems are little known in the fynbos biome. Even in important and formerly widely cultivated groups the Ericaceae it is only known that the species are unlikely to be inbreeders (D Wiens in littera). Until precise evidence appears, this gap in knowledge will have a retarding effect as data on the breeding system is the starting point of any gene flow study. For example, the genus Homeria (Iridaceae) is reported by Goldblatt (1981) to be strongly outcrossing and generally self-incompatible. When two or more species occur together, sterile hybrids between them are very often present. Only seven Homeria species were observed to be self-compatible, with the pollen being shed directly onto the stigmas. This suggests the genus would be very suitable for gene flow research.

Apomixis among plants in southern Africa was briefly reviewed by Goldblatt (1978) who noted that apart from the Poaceae this form of breeding seems to be uncommon in the region. He cited a few examples from the fynbos biome of vegetatively reproducing apomicts such as Watsonia bulbifera and Geissorhiza bolusii. Species such as Cliffortia atrata (Rosaceae) and the C ilicifolia complex have populations made up almost entirely of female plants, suggesting parthenogenesis, an interesting case which should be investigated (Adamson and Salter 1950).

The assessment of genetic diversity by isozyme analysis has started recently. The methods have been refined and are being used in a pilot study on the rare plant Audouinia capitata (Bruniaceae: F W Paterson personal communication). If suitably distinctive genetic markers can be found it may be possible to estimate the species' apparently rare gene flow between populations by means of progeny analysis Handel 1983).

A PROGRAMME FOR RESEARCH IN GENE FLOW AND ALLIED TOPICS

Gene flow studies cannot be carried out without extensive support from other fields of study which have been long neglected in southern Africa. These include demography, local distribution patterns, breeding systems, population genetics and island biogeography. These supporting programmes are lengthy but so fundamental to gene flow studies that they cannot be avoided. Methods described in standard texts (Harper 1977; Solbrig 1980; Soulé and Wilcox 1980; Frankel and Soulé 1981; Grant 1981; Morse and Henifin 1981; Schonewald-Cox et al 1983). The tasks for a gene flow programme and supporting studies in the Cape flora are proposed as follows:

Demography and population mapping: The studies should if possible cover gamete and seed productivities; sizes of seed stores; seedlings, adults and their age-classes; and rate of production of genets (sexually produced plants) and ramets (individuals with vegetative origins)(Harper 1977; White 1980).

1. Select a range of plant species optimal for the studies below.
2. Do precise mapping of the species' population boundaries and contents.
3. Lay out fixed sample areas in the populations for long-term study.
4. Carry out census and life-table studies at regular intervals through the fire cycle in populations and sample areas.
5. Hypothesize groups of demographic strategies.
6. Hypothesize dynamics of recruitment, natality and mortality.
7. Relate demographic groupings to ecology and other variables of

interest.

Breeding patterns: Careful selection of species will be needed for cross pollination studies as many Cape flora species have flowers which are too small for removal of anthers without extensive damage. Autogamy may be easily shown by bagging experiments. The effects of seed predation will need to be determined.

1. By experimentation assemble sets of examples of each kind of breeding pattern.
2. Determine the effects on fecundity of selfing various outbreeders.
3. Study the genetic variability of offspring after inbreeding.

Population genetics: There is a large literature on population genetics which should be used for comparison of future results from the fynbos biome (Grant 1981; Schonewald-Cox et al 1983).

1. Investigate patterns of pollen and propagule dispersal.
2. Investigate gene flow between populations under various conditions.
3. Carry out gel electrophoresis studies to show isozyme variation patterns.
4. Make comparative genetic drift studies in small isolated populations.

Insularization effects: The aim here will be to test the hypothesis that gene flow between populations isolated by various distances will critically affect the genetic viability of species in the long term.

1. List a range of cases, ages and origins of insularization in the region.
2. Study impacts such as reduced gene flow affecting insularized populations.
3. Get benchmark data on fecundity and viability for insularized populations.
4. Obtain data as in 3 above for the same species in noninsularized habitats.
5. Get benchmark data for variable properties of populations.
6. Hypothesize on any groupings of population-behaviour after insularization.
7. In future years, compare populations with and without insularization.
8. In future years, test for microevolutionary changes after insularization.

PROPAGULE AND POLLEN GENE FLOW IN THE CAPE FLORA

Local gene flow within a population will usually be by means of both seed and pollen. Over greater distances such as hundreds of metres between populations, there are so many factors involved that it would be risky to generalize on whether seed or pollen are the main carriers of gene flow. For example, in the genus Leucadendron Williams (1972) records a wide variety of potential wind-mobilities of fruits, which vary from nuts lacking wings, to broadly winged samaras or even parachute types, while the pollination syndromes include wind and insects as the pollen vectors. In the coastal flats and mountains of the south western Cape, gene flow by seed may exceed that of pollen in a winged-fruited species of Leucadendron which is pollinated by insects.

Probably over a thousand taxa in the south-western Cape are myrmecochorous, with their seeds dispersed by ants for apparently only up to two to three metres from the parent plant (Bond and Slingsby 1983). Greater distances are recorded elsewhere, mostly up to 10 to 20 m, rarely to 75 m (Beattie 1982). The limited gene flow associated with ant dispersal has been associated with complex patterns of phenotypic variation seen in field populations of ant dispersed species (Beattie 1978). The evolutionary significance of the apparently locally confined gene flow provided by ants in the fynbos biome should be investigated and compared with what may be expected by other mechanisms of propagule dispersal.

In some taxa such as the minute-seeded family Orchidaceae very large numbers of extremely light, wind-borne seeds are produced, several thousand per fruiting capsule. However, the seeds' high potential for propagule-based gene flow may be severely curbed by generally low rates of establishment, as noted in the case of Disa cornuta. This syndrome, coupled with the specialized pollination system of Orchidaceae makes this family especially interesting for comparing pollen and propagule gene flow.

The genetics of founder events should also be assessed in gene flow studies (Slatkin 1977; Carson 1983). A single propagule of a self-compatible species may initiate a new population but pollen cannot. However, subsequent pollen gene flow may be vitally important in supplementing the limited genetic diversity of the founder and its offspring.

The relative significance of pollen or propagules in gene flow will vary according to many factors. These include species characteristics such as the productivity of pollen and propagules, the distances over which they are to be transferred, the kinds and strengths of the pollen and propagule vectors, and local habitat conditions in the season of transfer. For methods for investigating propagule gene flow reference should be made to sources such as Harper (1977) and Cook (1980).

MEASURING POLLEN GENE FLOW

Although descriptive pollination biology has an extensive research history (Richards 1978), methods for measuring pollen gene flow are still under development (Handel 1983; Jones and Little 1983; Real 1983). Most of the past approaches were concerned with the process of transferring pollen. By documenting only the first phase of the gene flow process and omitting genome establishment they are not particularly satisfactory.

Studies of the pollen gene flow associated with the foraging behaviour of pollinators have provided much useful qualitative information. However, many pollinators are so small and move so rapidly they are difficult to observe. It is particularly difficult to assess how much pollen is deposited on each visit. This problem is confirmed by studies such as by Schaal (1980) who found that for an experimental planting of Lupinus texensis an isozyme marker was moved further than actual observations of insect movements had indicated.

The pattern of vector movement has a profound effect on gene flow within and between populations. Although most movements are to very near neighbours, the possibility of longer flights must always be borne in mind. Generalizations from a small sample of populations are risky and should be avoided or at best treated with caution (Handel 1983). It should not be assumed that observations on a single pollinator are enough to give a complete account of the pattern of pollen gene flow for a plant species. The plant may be polylectic, visited by two or more species of pollinator. For example, in a Senecio species in California, quite different patterns of pollen gene flow were given by butterflies and bumblebees. Differences were also found for two other Senecio species (Schmitt 1983).

Traps for airborne pollen have been widely used in studies of wind pollinated forest trees, crops and weeds (Handel 1983). As the traps do not replicate the airflow conditions in inflorescences and in the microclimates of stigmas they may give biased results. Their trapping ability varies with air speed and the shape and size of the collector. Various particle sizes are differentially collected. Their value lies in estimating patterns of pollen movement in relation to wind strength and direction. High winds are an important factor in the climate of the Cape flora and wind pollinated plants such as Restionaceae play such an important role of in the vegetation that they should be a priority target for study in the region.

Dyes and powders offer the simplest way of determining the directions and sources of pollen transfers. Dyes, as solutions or micronized powders are applied to anthers. After a period surrounding plants are studied in the field or collected for ascertaining pollen transfer by examination in the laboratory. The presence or absence of the marker provides a qualitative assessment of whether or not movement of pollen has taken place from the treated anthers to stigmas on the surrounding plants. Particle counts may give an assessment of the relative amounts of transfer: this needs calibration in a test study to yield estimates of pollen grain numbers. Methylene Blue dye is commonly used. Fluorescent powders are easier to see in smaller amounts if the stigmas can be taken to a laboratory with ultraviolet lamps (Handel 1983).

As an example, Waser and Price (1982) used dye particles successfully for measuring pollen transfer in Ipomopsis aggregata (Polemoniaceae). Stigmas were examined and pollen and dye particules were counted under a dissecting microscope. Pollen and dye particle counts showed good correlation, showing that dyes may be accurate analogues of pollen for this species. The experiment was conducted with the anthers of the target flowers removed. This prevented competition from pollen from the target flowers' anthers which would have lessened the external pollen fertilization.

Internal chemical labelling of pollen grains is potentially more accurate than using external dye powders. There are no assumptions needed about the parallel movement of dye particles and pollen grains. One such approach is to use radiochemicals. These have been successfully used for wind pollinated and humming-bird visited plants (Colwell 1951; Schlissing and Turpin 1971). After uptake of the radiochemical and the elapse of a period for pollen transfer, stigmas or pollen traps are surveyed. Autoradiography of pollen grains on stigmas or film is the best method of measuring the amount of transfer. Special licensing arrangements for using radiochemicals must be observed.

A more elaborate method is to apply a solution containing a rare earth element topically to dehiscing anthers. After a period of pollen transfer, the amount of the element on the stigmas is found using neutron activation analysis. Stigmas taken from the field are individually irradiated with a neutron source and placed in a scintillation counter where the levels of gamma radiation associated with the rare earth's decay products are measured. The gamma radiation detected must be related to observed numbers of pollen grains in a calibration experiment, as the amount of uptake of the rare earth solution may vary between species. Very small amounts of transferred pollen can be detected in this way. It has the advantage that the measurements can be conducted long after field collection of the stigmas. It avoids the use of contaminating radiochemicals in the field. However, it is costly and detection cannot be carried out in the field (Gaudreau and Hardin 1974; Handel 1976).

Direct counts of distinctive pollen on stigmas have been possible in rare cases. For example Erythronium americanum has individuals which bear either yellow or red pollen (Handel 1983). Experimental studies could determine rates of transfer from a plant with red pollen to others with a different colour, provided red-pollen individuals are removed from within a likely transfer range. Pollen structure may also be a marker for relating transfer between populations of different but closely related species. Again such cases are very rare.

MEASURING PROPAGULE AND POLLEN GENE FLOW SIMULTANEOUSLY

In this method the amount of transfer of distinctive marker genes to the progeny of plants growing at various distances away is used as a measure of gene flow. A genetic survey is first made to find an allele or suite of alleles in an individual or group which is absent in other plants in the neighbourhood (Handel 1983). The markers may be detected by gel electrophoresis or, rarely, as an isolated dominant allele. Suitable distribution patterns are likely to be rare under natural conditions: if the markers had not appeared recently they are likely to be present in other plants in the neighbourhood where they would contaminate the gene flow experiment by acting as extra sources. The progeny may be seeds removed from fruits, or if further evidence of establishment is needed, seedlings or mature plants.

The advantage of this method is that it can estimate gene flow in the entire process of genome transference from the parent (including factors such as its floral biology) through to the established offspring. In this way it is superior to investigating pollen and pollinator movements which have attracted most attention in past studies of gene flow.

The method has a history of many years of use by plant breeders and agronomists who wish to achieve genetic isolation of pure stocks of cultivars, or arrange plantings of individuals to provide maximum crossing between them. Experimental gardens have been laid out with the individual bearing the genetic marker surrounded by others lacking it (Bateman 1947a,b; Handel 1982). This gives valuable results for the rate, direction and distance of gene flow under controlled conditions.

Progeny analysis is useful for showing very local variation in natural populations where monomorphic patches of a gene are uncommon. Single-locus markers have been used to measure gene flow in experimental gardens and for plants bearing alien genes introduced into natural populations. As illustrated in Figure 7.1, these studies have shown that pollen gene flow is greater than the distances indicated by observations of pollinators (Schaal 1980; Levin 1981; Ennos and Clegg 1982).

A valuable comparison of the dye and progeny methods was given by Handel (1983). A test garden of the mustard Brassica campestris contained a central patch of 16 plants with a dominant marker allele for golden yellow petals, surrounded by 87 plants homozygous for a recessive pale yellow petal colour. Fluorescent dye was applied to anthers of the central plants and after a few days, stigmas were examined under ultraviolet light for the dye. After the plants had set seed in a greenhouse shielded against pollinators, the progeny were examined for the marker. The dye results were different from those with the marker. In 29% of the plants the dye was found but no marker allele and in a further 11% the opposite had occurred. This showed that the dye was unreliable with this species and preference should be given to the more time-consuming method of progeny analysis.

Polymorphic loci make better markers than single-gene differences for gene flow studies. Investigations of isozymes of likely parents and seed or seedling progeny will give an estimate of genetic variability in the populations besides gene flow (Hamrick 1983; Ellstrand 1984; Ellstrand and Marshall 1985). A requirement is that the populations be small enough for analyzing each individual (or at least a large sample of them) so that it can be reliably stated that the associated marker alleles are from immigrant genomes and are not also generated within a destination population (Ellstrand and Marshall 1985). The small populations which are common in the Cape flora are ideal for this, except that there is a risk that genetic polymorphism may be too low to be of experimental value (Prentice 1984; F W Paterson personal communication).

Different ecological factors impinge upon pollen and propagule transfer. Where the animal vectors for pollen and seed transport are essential for the plant's survival, it may be important to isolate and compare the rates of pollen and propagule gene flow. Direct observation of the transfer of seed and pollen may be impractical. Estimates might be obtained by comparing the occurrence of a genetic marker at a destination in plants grown from seeds removed from fruits at the site with that in the young plants there. The plants from the fruits will be influenced by pollen gene flow, while the young plants will in addition show the effect of propagule transfer.

Long-established populations in nature will reflect equilibrium patterns of gene flow to and fro between the original source and destination plants. A new marker will take time to reach this equilibrium. It is at the earliest stage that the dynamics of gene transfer and establishment are revealed. Later, the picture may be complicated by long-lived plants and seed stores damping subsequent gene transfer. Using annual plants with short-lived seeds may help avoid this confusing lag effect. Early gene flow dynamics are probably best observed in an experimental garden.

However, it is as well to note that theoretical extrapolation of experimental garden data to genetically heterogeneous wild plants is difficult as natural competitive patterns may vary from site to site, difficult as natural competitive patterns may vary from site to site, affecting success among the variants in the progeny. Examples of this are the way phenotypes vary in vigour; competition among pollen tubes in the style may suppress the contributions of pollen transferred from elsewhere; and size differences among plants from site to site may influence their rates of pollen capture. Variation in such factors could bias the results away from those predicted by extrapolation. The unique situation of each natural case demands that it should be investigated in nature with a minimum of preconceived generalizations (Handel 1983).

CONCLUSIONS

Gene flow research should help towards providing a long-needed understanding of the genetic biogeography of plant populations in the rich flora of the south-western Cape. The region's many rare species found in small isolated populations are likely to yield valuable insights on the processes of local, short-term evolution and extinction.

Although methods of studying gene flow in plants are still under development elsewhere, several research approaches are described in the literature which would be suitable for use in the fynbos biome. As a part of the programme on gene flow research there should be studies to obtain data on the demography, distribution and breeding systems of the target species.

The results of research in gene flow and other aspects of genetic biogeography are likely to be of practical importance for conservation. The results could be most useful in improving the cost-effectiveness of the planning and purchase of areas for evolutionary conservation in the fynbos biome.

REFERENCES

Adamson R S and Salter T M 1950. Flora of the Cape Peninsula. Juta, Cape Town.

Bateman A J 1947a. Contamination of seed crops. I. Insect pollination. Journal of Genetics 48, 257-275.

Bateman A J 1947b. Contamination of seed crops. III. Relation with isolation distance. Heredity 1, 303-336.

Beattie A 1978. Plant-animal interactions affecting gene flow in Viola. In: Richards A J (editor) The pollination of flowers by insects. Linnean Society symposium series Number 6. Academic Press, London. pp 151-164.

Beattie A J 1982. Ants and gene dispersal in flowering plants. In: Armstrong J A et al (editors) Pollination and evolution. Royal Botanic Gardens, Sydney. pp 1-8.

Bond W J and Slingsby P 1983. Seed dispersal by ants in shrublands of the Cape Province and its evolutionary implications. South African Journal of Science 79, 231-233.

Boucher C 1981. Autecological and population studies of Orothamnus zeyheri in the Cape of South Africa. In Synge H (editor) The biological aspects of rare plant conservation. John Wiley, Chichester. pp 343-353.

Bradshaw A D 1959. Population differentiation in *Agrostis tenuis* Sibth. I. Morphological differentiation. New Phytologist 58, 208-227.

Carson H L 1983. The genetics of the founder effect. In: Schonewald-Cox C M et al (editors) Genetics and conservation. Benjamin/Cummings, Menlo Park, California. pp 189-200.

Clegg M T and Brown A H D 1983. The founding of plant populations. In: Schonewald-Cox C M et al (editors) Genetics and conservation. Benjamin/Cummings, Menlo Park, California. pp 216-228.

Colwell R N 1951. The use of radioactive isotopes in determining spore distribution patterns. American Journal of Botany 38, 511-523.

Cook R 1980. The biology of seeds in the soil. In: Solbrig O T (editor) Demography and evolution in plant populations. Botanical Monographs, Volume 15. Blackwell Scientific Publications, Oxford. pp 107-129.

Dahlgren R 1960. Revision of the genus *Aspalathus*, Part I. The species with flat leaflets. Opera Botanica 4, 1-393.

De Vos M P 1972. The genus *Romulea* in South Africa. Journal of South African Botany Supplementary Volume 9.

Diamond J M 1984. Management for maintenance of species diversity. In: Hall A V (editor) Conservation of threatened natural habitats. South African National Scientific Programmes Report No 92. CSIR, Pretoria. pp 82-94.

Ellstrand N C 1984. Multiple paternity within the fruits of the wild radish, *Raphanus sativus*. American Naturalist 123, 819-828.

Ellstrand N C and Marshall D L 1985. Interpopulation gene flow by pollen in wild radish, *Raphanus sativus*. American Naturalist 126, 606-616.

Endler J A 1977. Geographic variation, speciation and clines. Monographs in Population Biology 10. Princeton University Press, Princeton.

Ennos R A and Clegg M T 1982. Effect of population substructuring on estimates of outcrossing rate in plant populations. Heredity 48, 283-292.

Frankel O H and Soule M E 1981. Conservation and evolution. Cambridge University Press, Cambridge, England.

Gaiwith E 1983. The autecology and conservation of *Witsenia maura* Thunb. (Iridaceae). Honours Thesis, Bolus Herbarium, University of Cape Town, Cape Town. 80 pp.

Gaudreau M and Hardin J 1974. The use of neutron activation analysis in pollination ecology. Brittonia 26, 316-320.

Grant V 1981. Plant speciation. Second edition. Columbia University Press, New York.

Goldblatt P 1978. An analysis of the flora of southern Africa: its characteristics, relationships and origins. Annals of the Missouri Botanical Garden 65, 369-436.

Goldblatt P 1981. Systematics and biology of *Homeria* (Iridaceae). Annals of the Missouri Botanical Garden 68, 413-503.

Greig J C 1979. Principles of genetic conservationin relation to wildlife management in southern Africa. Suid Afrikaanse Tydskrif vir Natuurnavorsing 9, 57-78.

Hall A V 1959. Observations on the distribution and ecology of Orchidaceae in the Muizenberg Mountains, Cape Peninsula. Journal of South African Botany 25, 265-278.

Hall A V 1965. Studies of the South African species of *Eulophia*. Journal of South African Botany Supplementary Volume 5, 1-248.

Hall A V 1982. A revision of the southern African species of *Satyrium*. Contributions from the Bolus Herbarium 10, 1-142.

Hall A V and Ashton E R 1983. Threatened plants of the Cape Peninsula. Threatened-plants research group, Bolus Herbarium, University of Cape Town. 26 pp.

Hall A V and Veldhuis H A 1985. South African Red Data Book: Plants - fynbos and karoo biomes. South African National Scientific Programmes Report No 117. CSIR, Pretoria. 157 pp.

Hamrick J L 1983. The distribution of genetic variation within and among natural plant populations. In: Schonewald-Cox C M et al (editors) Genetics and conservation. Benjamin/Cummings, Menlo Park, California. pp 335-348.

Hamrick J l and Allard R W 1972. Microgeographical variation in allozyme frequencies in Avena barbata. Proceedings of the National Academy of Sciences of the United States of America 69, 2100-2104.

Handel S N 1976. Restricted pollen flow of two woodland herbs determined by neutron-activation analysis. Nature (London) 260, 422-423.

Handel S N 1982. Dynamics of gene flow in an experimental garden of Cucumis melo (Cucurbitaceae). American Journal of Botany 69, 1538-1546.

Handel S N 1983. Pollination ecology, plant population structure, and gene flow. In: Real L (editor) Pollination biology. Academic Press, London. pp 163-211.

Harper J L 1977. Population biology of plants. Academic Press London.

Hedrick P W 1985. Genetics of populations. Jones and Bartlett, Boston.

Horn W 1962. Breeding research on South African plants. III. Intra- and interspecific compatibility in Ixia L., Sparaxis Ker., Watsonia Mill. and Zantedeschia Spreng. Journal of South African Botany 28, 269-277.

Jain S K and Bradshaw A D 1966. Evolutionary divergence among adjacent plant populations. I. The evidence and its theoretical analysis. Heredity 21, 407-441.

Jarman M L 1986. Conservation priorities in lowland regions of the fynbos biome. South African National Scientific Programmes Report No 87. CSIR, Pretoria. 53 pp.

Jones C E and Little R J (editors) 1983. Handbook of experimental pollination biology. Van Nostrand-Reinhold, New York.

Kerster H W and Levin D A 1968. Neighbourhood size in Lithospermum caroliniense. Genetica 60, 577-587.

Levin D A 1981. Dispersal versus gene flow in plants. Annals of the Missouri Botanical Garden 68, 233-253.

Levin D A and Kerster H W 1968. Local gene dispersal in Phlox. Evolution 22, 130-139.

Levin D A and Kerster H W 1974. Gene flow in seedplants. Evolutionary Biology 7, 139-220.

Levyns M R 1934. A revision of the genus Lobostemon Lehm and a discussion of the species problem. Journal of the Linnean Society (Botany) 49, 393-451.

Linder H P 1985. Gene flow, speciation and species diversity in a species-rich area: the Cape Flora. In: Vrba E S (editor) Species and speciation. Transvaal Museum Monograph Number 4. Transvaal Museum, Pretoria. pp 53-57.

Liu E H and Godt M J W 1983. The differentiation of populations over short distances. In: Schonewald-Cox C M et al (editors) Genetics and conservation. Benjamin/Cummings, Menlo Park, California. pp 78-95.

Lloyd J W 1981. Taxonomy, distribution and autecology of Leucadendron macowani, an endangered species. Undergraduate Thesis, Bolus Herbarium, University of Cape Town, Cape Town.

Moll E J and Gubb A A 1981. Aspects of the ecologyof Staavia dodii in the south western Cape of South Africa. In: Synge H (editor) The biological aspects of rare plant conservation. John Wiley, Chichester. pp 331-342.

Morse L E and Henifin M S (editors) 1981. Rare plant conservation: geographical data organization. New York Botanical Garden, Bronx, New York.

Nordenstam B 1968. The genus *Euryops*. Part II. Aspects of morphology and cytology. Botaniska Notiser 121, 209-232.

Oliver E G H 1986. The identity of *Erica vinacea* and notes on hybridization in *Erica*. Bothalia 16, 35-38.

Prentice H C 1984. Enzyme polymorphism, morphometric variation and population structure in a restricted endemic, *Silene diclinis* (Caryophyllaceae). Biological Journal of the Linnean Society 22, 125-143.

Raven P H 1976. Systematics and plant population biology. Systematic Biology 1, 284-316.

Real L 1983. Pollination biology. Academic Press, London.

Rebelo A G and Siegfried W R 1985. Colour and size of flowers in relation to pollination of *Erica* species. Oecologia 65, 584-590.

Richards A J (editor) 1978. The pollination of flowers by insects. Linnean Society symposium series No 6. Academic Press, London. 213 pp.

Richards A J and Ibraham H 1978. Estimation of neighbourhood size in two populations of *Primula veris*. In: Richards A J (editor) The pollination of flowers by insects. Linnean Society symposium series No 6. Academic Press, London. pp 165-174.

Rourke J P 1972. Taxonomic studies on *Leucospermum* R Br. Journal of South African Botany Supplementary Volume 8, 1-194.

Rourke J P 1980. The proteas of southern Africa. Purnell, Cape Town.

Schaal B A 1980. Measurement of gene flow in Lupinus texensis. Nature (London) 284, 450-451.

Schlissing and Turpin R A 1971. Hummingbird dispersal of *Delphinium cardinale* pollen treated with radioactive iodine. Americal Journal of Botany 58, 401-406.

Schmitt J 1983. Density-dependant pollinator foraging, flowering phenology and temporal pollen dispersal patterns in *Linanthus bicolor*. Evolution 37, 1247-1257.

Schonewald-Cox C M, Chambers S M, MacBryde B and Thomas W L (editors) 1983. Genetics and conservation. Benjamin/Cummings, Menlo Park, California.

Slatkin M 1977. Gene flow and genetic drift in a species subject to frequent local extinctions. Theoretical Population Biology 12, 253-262.

Solbrig O T (editor) 1980. Demography and evolution irplant populations. Botanical Monographs Volume 15. Blackwell Scientific Publications, Oxford.

Soulé M E and Wilcox B A (editors) 1980. Conservation biology. An evolutionary-ecological perspective. Sinauer Associates, Sunderland, Massachussetts.

Stace C A (editor) 1975. Hybridization and the flora of the British Isles. Academic Press, London.

Stebbins G L 1974. Flowering plants. Evolution above the species level. Harvard University Press, Harvard, Massachussetts.

Waser N M and Price M V 1982. A comparison of pollen and fluorescent dye carry-over in natural pollinations in *Ipomopsis aggregata* (Polemoniaceae). Ecology 63, 1168-1172.

Waser N M and Price M V 1983. Optimal and actual outcrossing in plants, and the nature of plant-pollinator interaction. In: Jones C E and Little R J (editors) Handbook of experimental pollination biology. Van Nostrand-Reinhold, New York. pp 341-359.

White J 1980. Demographic factors in populations of plants. In: Solbrig O T (editor) Demography and evolution in plant populations. Botanical Monographs Volume 15. Blackwell Scientific Publications, Oxford. pp 21-48.

Williams I J M 1972. A revision of the genus Leucadendron (Proteaceae). Contributions from the Bolus Herbarium 3, 1-425.

Wilson N S H 1980. Recent history and trends of the eight known populations of the Silver Tree, Leucadendron argenteum, on the Cape Peninsula. Undergraduate Thesis, Bolus Herbarium, University of Cape Town, Cape Town.

Wright S 1943. Isolation by distance. Genetics 28, 114-138.

Wright S 1946. Isolation by distance under diverse systems of mating. Genetics 31, 39-59.

Wright S 1951. The genetical structure of populations. Annals of Eugenics 15, 323-354.

CHAPTER 8 POLLINATION AND COMMUNITY ECOLOGY

A G Rebelo and M L Jarman

Whereas species composition of communities is largely the result of historical evolution of populations in a geographical area, the structural features of communities are largely determined by environmental conditions (climate and geology) (Smith 1974). Community structural features are manifested as plant life forms, size, stratification, cover abundance, phenology, and leaf shape, size and texture (Strahler 1975; Orshan 1983). Plant metabolic limitations probably play a major, but intangible, role in determining the morphology of individual plants (eg Cowling 1983). Community structure is also influenced by environmental changes induced by the presence of the community itself, and by the consumer and decomposer components. Fire, environmental factors directly influencing consumer or decomposer components, and interactions between communities also determine the range of potential structural features present. Consequently a branched sequence of possible alternative successional communities results.

Changes in elements influencing communities over time also affect community structure. Species composition in altered environments may change. It is thus difficult to delimit structural features characteristic of specific environmental conditions. Historical stochastic events, coupled with the lack of a uniform baseline spectrum of possible colonizing species, may result in potentially similar communities lacking structural components they should theoretically possess.

The physical environment also determines which pollination syndromes will operate within an area, by influencing plant phenology, structure, cover and primary production. Potential animal pollinators are restricted by the availability of nesting sites, alternative food sources (protein, larval foodplants) metabolic constraints which influence the timing of their life cycles, and the presence of competing flower visitors. Other than for wind pollination (Whitehead 1968, 1983), few community-level studies have been made to determine the factors delimiting pollination syndromes per se (Pleasants 1983).

Despite the current trend away from community studies (Cowling 1987), an understanding of the ecology of the species rich Cape flora may only ever be possible at the community level. The large number of localized interacting plant and animal populations and apparent lack of homogeneity, both on a local and regional scale (Campbell 1985), will complicate understanding of the plant-pollinator interactions in the Cape flora when studied at population and species levels.

In this chapter we review the observed patterns of pollination syndromes worldwide (Part 1); summarize what is known about the patterns of pollination syndromes in the Cape flora (Part 2); summarize what is known about the patterns of pollination syndromes in other Mediterranean-type floras (Part 3); and speculate on the factors which may have been responsible for these patterns (Part 4). Part four is largely speculative, based on impressions gleaned from various colleagues in the field. Whilst quantitative data are urgently required for the Cape flora, this chapter serves chiefly to encourage a more critical examination of pollination in the vegetation assemblages of the Cape flora and the possible role that the physical environment may have played in its evolution.

PART 1: DISTRIBUTION PATTERNS OF POLLINATION SYNDROMES WORLDWIDE

Little research has been undertaken worldwide into the effect of the physical environment on the population dynamics of flower visitors (Kevan and Baker 1983). The interaction beween pollinators and sexual plants is restricted by environmental contraints acting on both components. Important physical factors influencing flower visitors include light (composition, intensity and length of photoperiod), cloudiness, temperature, humidity and wind speed. Similarly, plants are restricted in their use of signals for attracting pollinators by incoming solar radiation and the viscosity, composition, turbulance and temperature of the atmosphere. In addition, floral rewards must be highly correlated to the specific requirements of pollinators: for example, the nectar sugars galactose, lactose and raffinose are toxic to honeybees, but not to other insects, and high nectar potassium levels deter honeybees (Kevan and Baker 1983).

With the exception of wind pollination (Whitehead 1968, 1983), there are no comprehensive reviews on the factors affecting the geographical distribution of pollination syndromes. Additional community-level pollination studies are required worldwide to determine the biogeographical patterns of pollination syndromes. Here we summarize the major research findings to date (Table 8.1) and attempt to draw generalizations.

Wind pollination

Pollen movement is restricted by: wind velocity; air turbulence; vegetation structural complexity; leaf size; plant species richness (correlated with a dispersed distribution of conspecifics); and plant density. Wind pollination predominates in vegetation communities exposed to wind turbulence; which are structurally simple; where leaf size is small or leaves are absent during the pollination period; where there are few species; and where there is a high degree of synchrony in flowering time (Whitehead 1968). Pollen dispersal by wind is restricted to periods of low rainfall, since water droplets remove pollen from the atmosphere. It is also most common in regions where insects are scarce (Procter and Yeo 1973).

It follows that wind pollination is more common in arid regions and at higher latitudes (Arroyo et al 1983) and is largely absent in tropical forests. However, in tropical areas with a distinct summer drought, where deciduous trees and low species richness predominate and insects may become relatively scarce, wind pollination may be more important (Whitehead 1968). Similarly, Eastern Deciduous forests contain a high number of anemophilous taxa, with more anemophilous species in the overstorey than the understorey (Ostler and Harper 1978).

Wind pollination is the dominant pollination mode in the Gynmosperms and certain Angiosperm plant families (Cyperaceae, Poaceae, Restionaceae) (Whitehead 1968, 1983), and tends to be important in communities where these elements dominate. However, it is probable that anemophily has been underreported and zoophily overreported for rare species (Ostler and Harper 1978).

TABLE 8.1 The proportional incidence of pollination syndromes in different vegetation types

Location	Pollination Syndrome												Reference
	Bees[1]			Fly[2]		Butterfly	Beetle	Moth	Bird	Bat	Wind	Autogamy	
Andes	40			37		19	3	2	1	-	17	4	Arroyo et al 1981
Tropical lowland													Bawa et al 1985
forest tree: Total	46			16		5	7	16	4	3	3	-	
Canopy tree	56			23		2	0	13	2	4	0	-	
Subcanopy tree	42			13		6	11	17	5	3	4	-	
Montane Colorado:													Moldenke and Lincoln 1979
Alpine	31	40	0	31	0	12	0	3		0	17	48	
Aspen	25	24	1	18	0	1	1	6		0	21	25	
Sage	31	28	5	1	8	7	1	5		0	12	24	
Fescue grasslands	35	47	1	25	3	5	3	7		0	17	21	
Spruce fen	24	17	4	20	2	6	1	4		0	19	25	
Sierra Nevada:													Moldenke 1979a
Stanford grasslands	10	41	1	7	20	7	16	1	1	0	16	41	
Mathe grasslands	12	40	2	7	16	13	13	2	1		31	42	
Mathe forests	21	30	3	5	17	4	5	0	3	0	12	25	
Tiaga forests	19	19	0	16	2	4	5	0	5	0	29	22	
Chapparal	47	62	7	2	23	20	15	0	12	0	12	7	
Meadow	15	9	0	18	0	2	0	1	2	0	35	19	
Talus	22	20	0	10	5	8	6	1	6	0	20	35	
Alpine	24	27	1	6	0	8	0	2	4	0	25	39	
Annual communities	100		50	88		0	13	0	0	0	-	100	
Early seral communities	100		33	100		33	33	0	0	0	-	100	
Climax communities	100		18	82		27	23	0	0	0	-	32	

[1] Bees: Bumblebees, solitary bees and wasps; combined categories are boxed.
[2] Flies: General fly and beefly; combined categories are boxed.

Insect pollination

In contrast to wind pollination, insect pollination, in terms of the proportion of plant species belonging to particular insect pollination syndromes, occurs in a wide range of habitats. The following trends are discernable among the different insect pollination syndromes:

Moth pollination

Moth pollinated plant species richness is greatest in tropical regions. In North America there are 106 plant species (41 in the Onagraceae), in 40 genera, whereas only three species occur in Alaska. Moth pollination is relatively important in New Zealand, probably due to the paucity of bee species (Arroyo et al 1982). A decline in fruit set with altitude in moth pollinated Calliandra, Oenothera and Yucca has been recorded (Cruden et al 1976). There also appears to be an upper altitudinal limit to moth activity (Grant 1983, 1985). Moth pollination thus decreases with increasing latitude and altitude.

Moths may be diurnal under arctic conditions (where there is no nocturnal period in summer) (Kevan and Baker 1983) and at higher altitudes where it is too cold at night (Primack 1983).

The activity of sphinx moths in Israeli littoral regions is limited to period when wind speeds are at a minimum (at night when onshore-offshore breezes switch), and moth pollinated plant species tend to flower in the least windy season (Eisikowitch 1978).

Butterfly pollination

Butterflies, together with flies, are more important as pollinators in the alpine zone of Europe (Kevan and Baker 1983), the Himalayas and the Andes of Chile, especially above the timber-line (Arroyo et al 1982), than at lower altitudes. Butterflies are also important pollinators in subalpine meadows and in the Chilean Andes they are important at the highest altitudes (Kevan and Baker 1983). Butterflies are not as energy-demanding as bees, do not have to warm or provision nests, and can readily sunbask in order to warm up (Arroyo et al 1982).

In Britain butterfly pollination is most prominent, in terms of butterfly and butterfly pollinated plant species, on calcareous soils (Procter and Yeo 1973). New Zealand has very few butterfly species (Primack 1983).

Fly pollination

Flies are far more effective pollinators than bumblebees in alpine areas, and in Britain, in open heathlands and grasslands (Procter and Yeo 1973; Arroyo et al 1982). Flies are more important in the arctic than bees for the same reasons outlined under butterfly pollination (Kevan 1983). Flies are important as pollinators in New Zealand due to the paucity of bees (Primack 1983).

Primitive Nematoceran flies are typically most abundant in shaded, moist areas in arid regions. Muscoid flies are especially abundant on flowers in high latitudes and high altitudes. Bee- and long-proboscid flies are most abundant in arid areas. In Chile, hoverflies (Syrphidae) are very abundant in matorral, and even more abundant in forests and at high altitudes. This abundance coincides with the abundance of introduced gregarious aphids on which its larvae feed (Moldenke 1979b).

Near cliffs, human habitation, and alongside coasts with nutrient-upwelling, where larval food is more available, flies may also predominate (Procter and Yeo 1973; Rebelo 1987). Flies were found to pollinate a coastal bluff population of Nemophila, where oligolectic bees were inexplicably absent (Cruden 1972a).

Bee pollination

The distribution of bee faunas is reviewed by Michener (1979). Bees attain their maximum species richness in the warm temperate, xeric regions of the world. The greatest richness occurs in California (1 985 species), with the majority of bees in the Chaparral areas (676) and sparse forest of the southern mountains. The Californian desert is nearly as rich (668), with the boreal forest (589), grasslands and coastal zone (129) progressively poorer in species. In decreasing order of importance, other important xeric bee faunas are: southern Europe and Asia, central Chile and Argentinia, western southern Africa, and Australia. Mesic temperate areas such as eastern USA and central Europe have markedly fewer species than their adjacent xeric regions, and bee faunas decrease rapidly in arctic areas. Tropical areas do not have as large a bee fauna as xeric and temperate regions, although the Neotropics rank second only to California. Tropical and temperate deserts have very poor bee faunas as do savannas. Grasslands have moderate bee faunas.

Bee faunas vary between alpine areas: eg Chile has a large bee fauna, whereas that of New Zealand is small.

Mellitophily is the dominant pollination syndrome below 2 600 m in the Chilean Andes, whilst above 2 600 m specialist feeders decline, leaving the larger more opportunistic bee species (Arroyo et al 1982). It has been suggested that the longtongued honeybees in Europe may be ecologically equivalent to hummingbirds in North America (Inouye 1976).

The richness of bee faunas does not relate to that of their floras. Two hypotheses are proposed to explain the above pattern of bee species richness (Michener 1979). Firstly, bees store their highly perishable larval food (pollen and nectar) underground in wax or cellophane cells. In areas of high humidity the larvae and their food stores are susceptible to fungal attack and hygroscopic liquifaction which may drown larvae. The successful bee species in the tropics are those which no longer nest in the soil. Secondly, social bees are highly successful in the tropics: being highly-active, aseasonal, generalist foragers, they may have excluded other bees species.

High temperatures, above 40 and 35°C, inhibit honeybee and bumblebee foraging, respectively (Kevan and Baker 1983). In hot environments bees avoid the heat by being nocturnal and matinal or by flying well above the ground. Honeybees stop foraging when wind speeds exceed 24 to 34 km h^{-1}, or less in exposed environments (Kevan and Baker 1983).

In northern temperate regions, small bees are more common in open heaths and grasslands than bumblebees (Procter and Yeo 1973). In the mountains of New Mexico, bee activity is curtailed by rain during the rainy season, so that bee pollinated plants at higher altitudes are not as effectively pollinated as bird pollinated species.

In the eastern United State bumblebees appear to be more important pollinators in harsher alpine environments. They tend to predominate in cool environments, for example at high altitudes, high latitudes and certain (foggy?) coastal areas, where their ability to thermoregulate allows them to forage at lower ambient temperatures than other bees (Pleasants 1983). Bumblebees are unable to breed in areas where the flowering season lasts for less than nine weeks (Pyke 1982). In Britain, bumblebees are more common in hedges, banks, wood-margins, and ground flora of open woods (Procter and Yeo 1973). In New Zealand there are no bumblebees, but many plant species conform to the bumblebee pollination syndrome. These species are, however, not visited by introduced bumblebees (Primack 1983).

Owing to competition, only three or four bumblebee species can coexist in an area: a short tongue; medium- and long-tongue species; the fourth species being a short-tongued robber. While segregation is determined by tongue length, the designation of tongue length is not rigid, but usually involves a series with a factor of 1,3. Exceptions to this rule typically involve specialization on specific plant species and diurnal segregation (Pleasants 1983).

Eusocial bees in the Neotropics tend to be aseasonal, whereas solitary bee species tend to occur during the dry season. In New Zealand there are no social bees (Kevan and Baker 1983).

In Australia, introduced honeybees consume 30 to 60% of the nectar produced by Eucalyptus, Callistemon, Amyema and Grevillea - all ornithophilous species (Paton 1986b). Their effect on nectarivorous bird populations is unknown.

Wasps have a greater species diversity in the tropics than in the temperate zones (Procter and Yeo 1973). Nevertheless, flower-visiting wasps are far more diverse than currently reported for temperate habitats (Kevan and Baker 1983).

Flower mites

Hummingbird flower mites live and feed in flowers (especially species in the Vaccinieae (Ericaceae) (Colwell 1973)). Adults frequent nectaries of flowers, while larvae and nymphs frequent the stamens and style. Being phoresic on hummingbirds, they occur wherever there are hummingbirds. They reach their greatest diversity in lowland Neotropical forests. They are also present in Aloe introduced to California (Colwell 1985).

Flower mites have been recorded from sunbirds, bumblebees, butterflies and honey possums in Australia (from Naeem et al 1985); on Rhododendron in the subalpine zone of Papua New Guinea (Stevens 1976); from Protea, Aloe, beetles and birds in the Cape flora (Ryke 1954, 1964; A G Rebelo personal observation).

Bird pollination

Birds are effective pollinators under conditions of cloudy and rainy weather at high elevations, when other pollinators are unable to forage. Birds are more effective pollinators than bees at high altitudes in Mexico, with bird pollinated plant species replacing bee pollinated species (Cruden 1972b). A large proportion of high altitude plant species in New Guinea are bird pollinated: there are more bird pollinated plant species in subalpine forest than in lower montane forest (Stevens 1976).

Typically nectarivorous bird communities are organized by relatively large aggressive species which exclude smaller species from the dominant sources of nectar. Larger species may be restricted to a narrow resource spectrum at the upper end of the scale. The smaller species are more efficient and exploit a greater variety of poorer, more scattered resources. Four strategies of nectar feeding were recognized by Snow and Snow (1980):

- high reward trapliners which visit scattered resource-rich plants unavailable to other nectarivores and occurring over a wide area;

- low reward trapliners which also trapline, but are excluded by territorial birds;

- territorial birds, which defend an area-bound rich nectar resource; and

- territorial parasites of three types: large aggressive birds which displace territory holders; small sneaks which surreptitiously feed within other birds' territories; and groupies which swamp territory holders by feeding in large flocks.

Traplining is only known to occur in hummingbirds and flocking is confined to Australia, occurring in both honeyeaters and lorikeets. Hermit hummingbirds (ie high energy foragers) drop out with increasing altitude faster than nonhermits (Stiles 1981).

Most communities tend to have a period when nectar is scarce (Wolf and Gill 1980). Birds only partition nectar resources when they are in short supply (Feinsinger and Swarm 1982). Nectar is not a limiting resource in parts of Australia (Paton 1986b). In contrast on Hawaii, nectar resources (chiefly Metrosideros) may be limiting in certain summers, whereas on Peru and Colombian mountains, nectar is consistently and severely limiting (Carpenter 1978). Sunbirds may segregate by behaviour at the same plant species in Ericaceous and Proteaceous Moorland where they compete for nectar throughout the year (Cheke 1971).

Hummingbirds are very similar in morphology and size throughout temperate North America. Species are interspecifically territorial on plant species which have also converged towards a common morphology. By contrast, patterns on tropical islands suggest that where two hummingbird species cooccur, the larger will be twice the size of the smaller. In the Antilles, there is close evolution between birds and flowers. Whereas competition occurs between bird species of similar sizes, there is little competition between species of different size classes (Brown and Kodrik-Brown 1979).

In eastern North America, the Ruby-throated hummingbirds and Yellowbellied sapsuckers migrate north as summer flowers begin blooming, apparently following the northward movement of the 35°C isotherm (Austin 1975; but see Bertin 1982). Earliest migrants feed on sap from tree stems (Miller and Mero 1983).

There appears to be a trend for Ericaceae to be important bird pollinated plants in mountainous areas; Stevens (1976) records Vaccinieae in Central and Tropical America, Rhododendron and other genera in the Himalayas, Java and Papau New Guinea; and Erica is important in South Africa (Rebelo et al 1985).

It has been suggested that long-tongued bumblebees and social bees may replace birds as pollinators in north America (Inouye 1976) and Europe (Ford 1985). Whilst introduced social bees may consume up to 60% of the nectar produced by ornithophilous plants in Australia (Paton 1986a), bird pollination has evolved together with social bees in all the tropical regions and in southern Africa. These comparisons with the Southern Hemisphere suggest that Eurasia and North America probably lost most of their ornithophilous species during the Pleistocene glaciations. Although North America has migrant hummingbirds, no parallel exists in Europe. No ornithophilous taxa are known to exist in northern Europe and the European Mediterranean region (Ford 1985).

Mammal pollination

Mammal pollination, as a successful syndrome, appears to be predominant in south temperate mediterranean regions and Madacascar. Sussman and Raven (1978) maintain that it once was more widespread, but has been usurped by bat pollination and is now restricted to refugia.

Bat-pollination is largely confined to canopy trees in savanna and forest habitats, and appears to be more common in South America and Asia than in Africa (Sussman and Raven 1978).

Autogamy

Self fertilization may be favoured over cross pollination under a variety of circumstances (Wells 1979): when constant rain, drought or cold weather prevents pollen dispersal; in new populations founded by a single individual; when homozygous recessive alleles produce the most environmentally fit individuals; in sterile hybrids; and when a gene for self pollination arises and spreads by pollen transfer.

Species on edges of distribution ranges tend to be autogamous (eg Scottish and Scandanavian mountains and Timbaktu), whereas apomixis tends to occur in open unstable habitats (Procter and Yeo 1973). Similarly autogamy may be higher on islands where pollinators are likely to be absent (Woodell 1979). Agamospermy increases in arctic and alpine habitats, although some of the most common plants are obligate outcrossers (Kevan and Baker 1983). Obligate selfers are more dominant in coastal areas, where fog inhibits insect activity, than in adjacent inland communities in California and Chile (Moldenke 1979b).

Kevan (1972) suggests that many Eurasion diploid plant species may have survived the glaciations in refugia together with their pollinators. Following retreat of the ice, polyploid species moved into the arctic together with their pollinators. However, many arctic plant species are autogamous, apomictic or anemophilous. Insects do, however, pollinate some of these species and thus provide outcrossing.

Flower colour

The range of floral colours (in terms of plant species) present in local floras is not uniform among geographical regions or plant communities (Scogin 1983) (Table 8.2). White is the most frequent floral colour in most communities, especially in forest and mixed shrub and streamside vegetation. However, the most frequently encountered colour on a worldwide basis is yellow, which is more common in grassland and pine forest understorey vegetation.

On a geographical scale, high altitude, alpine and arctic floras are rich in white and yellow flowers, whereas the tropics are rich in red and orange flowers (Kevan 1983). Temperate regions show a more uniform balance, but exhibit a wider range of floral colorations (Scogin 1983). For example, the dominant colour of herbaceous plant species in Californian grasslands, deserts and open-woodlands (where bees are common) is yellow; whereas white and pink dominate in fir and redwood forests (where flies and moths are common) (Kevan 1973). The proportion of yellow and blue flowers decreases with increasing latitude in the high Andes. The frequency of blue flowers is relatively high in the high Andes at low latitudes and in alpine communities.

Alpine flowers are less colourful in Australia than in the European Alps; in the Japanese flora, white and yellow flowers are more common in the north, and several plant species become paler with increasing altitude, while others become more intensely coloured (Kevan 1983).

Most comparative studies of floral pigments have been based on taxonomic rather than ecological surveys. Results of floral pigment studies are shown in Table 8.3 and reveal a high proportion of plant species with delphinidin pigments in temperate regions and pelargonidin in tropical regions. Investigations of the pattern of plant pigments between plant communities are nonexistant (Scogin 1983).

Weevers (1952) maintained that floral colours are harmonically distributed geographically - therefore the evolution of flower colour must be independent of environment and pollinators; the single exception being blue, which is more prevalent at high elevations and depauperate in tropical regions.

Gottlieb (1982) points out that only species belonging to advanced plant families have blue flowers, presumably due to the evolution of certain metabolic pathways. Pure blue flowers are rare, occurring in only 385 genera belonging to 66 plant families. Pure blue-coloured flowers are not simply due to the presence of a delphinidin or cyanidin, but usually involve copigments, tannins and other compounds which form a 'pigment complex'. The chelatogenic interaction of metal ions (K^{1+}, Mg^{2+}, Al^{3+}, Fe^{3+} and Mo^{3+}) is essential to avoid transformation of the pigment to a colourless pseudobase. In evolutionary terms, the hydrophobic-hydrophilic

TABLE 8.2 Proportional incidence of colours of plant species in different vegetation types

Locality	No of plant species	Colours											Reference
		Red	Pink	Orange	Yellow	Green	White	Blue	Purple	Violet	Ultra-violet	Brown	
World	18 000	15		0	31	8	27	6	7	7	?	0	Kevan 1972
Arctic Havencamp	73	5		0	41	6	44	0	6	0	14	0	Kevan 1972
Arctic Sweden	1 350	13		0	33	8	26	6	4	11	?	0	Kevan 1972
Arctic Taimyr	156	0		0	33	0	41	2	10	13	?	0	Kevan 1972
High Andes 18°S		7	8	0	32	10	37	12			?	0	Arroyo et al 1983
High Andes 19°S		5	8	0	35	9	14	14			?	0	Arroyo et al 1983
High Andes 22°S		5	7	0	39	13	29	15			?	0	Arroyo et al 1983
High Andes 30°S		1	15	0	35	9	38	9			?	0	Arroyo et al 1983
High Andes 33°S		8	17	0	31	13	32	7			?	0	Arroyo et al 1983
High Andes 40°S		5	22	0	27	8	52	2			?	0	Arroyo et al 1983
High Andes 52°S		1	8	0	21	19	47	11			?	0	Arroyo et al 1983
High Andes 55°S		0	7	0	17	17	57	3			?	0	Arroyo et al 1983
BP Andes	47	13	19	13	9	11	28	9			?	0	Snow and Snow 1980
BP Trinidad	(?)	35	10	8	8	4	31	4			?	0	Snow and Snow 1980
Z Alpine Meadow USA		0	17	0	22	1	53	4	5		?	0	Ostler and Harper 1978
Z Upland Meadow USA		0	16	4	14	0	43	22	0		?	2	Ostler and Harper 1978
Z Alpine Fell-f USA		4	6	0	22	0	43	10	15		?	0	Ostler and Harper 1978
Z Alpine Grassland USA		7	2	1	38	0	39	13	0		?	0	Ostler and Harper 1978
Z Limber pine USA		12	11	0	45	0	15	8	8		?	0	Ostler and Harper 1978
Z Juniper USA		0	22	0	54	0	24	0	0		?	0	Ostler and Harper 1978
Z Grassland USA		0	28	0	49	0	18	0	5		?	0	Ostler and Harper 1978
Z Aspen USA		0	7	0	12	0	55	10	8		?	7	Ostler and Harper 1978
Z White fir USA		12	6	1	15	0	76	2	4		?	0	Ostler and Harper 1978
Z Oakbrush USA		5	18	3	22	0	46	1	5		?	0	Ostler and Harper 1978
Z Mixed shrub USA		7	10	0	9	0	63	5	7		?	0	Ostler and Harper 1978
Z Streamside USA		0	9	0	12	0	71	8	0		?	0	Ostler and Harper 1978
Maqui, Israel	45	0	7	0	20	31	40	0	0	0	?	2	Dafni 1986

BP = Bird pollinated; f = field; Z = Zoophilous

TABLE 8.3 Proportional distribution of plant pigments in different geographical areas (Scogin 1983)

Geographical area	Anthocyanin plant pigments (flavinoids)		
	Delphinidin	Pelargonidin	Cyanidin
Himalayan plants	61	2	-
Trinidad plants (tropical)	41	17	-
Australian flora	63	2	47
Worldwide survey: tropical	-	38	-
subtropical	-	31	-
temperate	59	6	34

stabilization theory (cf Gottlieb 1982) explains the absence of blue flowers in primitive woody angiosperms, which lack C-glycosylflavones. Rebelo et al (1985) proposed that blue as a flower colour may be scarce in *Erica* as it typically occurs on nutrient-poor substrata, where metal cations necessary for chelation of blue pigments are relatively unavailable.

However, these patterns may reflect the relative abundance of different pollination syndromes in different areas (Kevan and Baker 1983; Kevan 1983), and thus reflect the colour preferences of pollinator groups (Table 8.4). Flowers reflecting blue and purple tend to be obligately insect pollinated, often structurally adapted to bee pollination, and are frequented more by bees than any other pollinator group. Blue as a colour is especially attractive to bees and bee-flies. Nocturnally pollinated flowers are generally pale and contrast against dull backgrounds. Yellow flowers attract an almost unlimited variety of insects. Some unspecialized Coleoptera, Diptera and Lepidoptera show a strong preference for yellow. White flowers are also widely visited. Pink flowers have a strong association with butterfly pollination. Green is largely absent from zoophilous plant species in the western United States. Red is the dominant ornithophilous blossom colour in the tropics, while white and pink dominate the ornithophilous species of the Andes (Scogin 1983). Although some red flowers have butterfly and carpenterbee pollinators, red flowers are dull to most insects. There are only a few recorded examples of pure ultraviolet (UV) flowers, (eg *Papayer rhoeas* which reflects red (a component not perceived by most insects) and UV). It is pollinated by bees (Kevan 1983). Utech and Kawano (1975) suggest that the reduced frequency of UV-reflectant plants with increasing latitude may be related to the supposedly (cf Kevan 1983) reduced intensity of UV at high latitudes. At high altitudes, the reflection or absorption of harmful UV radiation may serve a protective function.

Baker and Hurd (1968) suggest that the dominant flower colour is related to ecological processes. Trends based on plant communities are (Kevan 1983): flowers in dense forests are more frequently white than those in less dense woodlands; the flora of coniferous forests have pale flowers whereas those in open areas and forest margins have yellow and purple flowers, respectively (paler flowers are more visible in the dimmer forest shade); and the frequency of yellow flowers tends to decrease, whereas blue increases, with increasing species richness (greater importance of specialized bee pollinators in species-rich habitats).

TABLE 8.4 Colour preferences and qualities of different pollinator classes (Scogin 1983)

Pollinator	Preferences
Wasps	Brown (dull)
Carrion/dung flies	Brown, purple (dull)
Bats	Cream, green, purple (drab)
Beetles	Cream, green (drab)
General flies	Cream, white
Nocturnal moths	White
Bees	Yellow, blue (bright)
Diurnal moths	Red, pink, purple (bright)
Butterflies	Red, yellow, pink, blue (bright)
Birds	Red, green yellow (bright)

Flower odour

Little comparative work has been done on floral odours in different floras or geographical regions. The only generalization that can currently be made is that production of scent as a primary reward is confined to the tropics where Neotropical male euglossine bees visit species in the Orchidaceae, Araceae, Gesneriaceae, Solanaceae and Euphorbiaceae to collect scents used to attract females (Williams 1983). Doubtlessly, other generalizations must be possible. If the musty smell of bat pollinated blossoms (due to diacetyl and other compounds) is exclusive to the syndrome, then it must be largely confined to the tropics.

Both of the above examples apply to cases where the odour is part of a pollination syndrome limited by the distribution of the pollinator. The diurnal absence of the odours characteristic of moth pollinated blossoms suggests that the effectiveness of odours may be reduced under certain environmental conditions. Factors likely to restrict the effectiveness of certain odours include temperature, humidity and wind. Thus floral fragrances used to attract euglossine bees are only produced in quantity on hot, sunny days, as a high temperature is needed to produce and disperse the odours (Williams 1983). Similarly, certain members of the Araceae volatilize floral odours by producing heat (Meeuse 1978).

Synthesis

The geographical distribution of pollination syndromes can be understood in terms of three parameters: pollinator energy requirements, pollinator dependence on flowers and plant productivity. The trends outlined below require refining with regard to pollinator and plant species richness, abundance and biomass. In this preliminary outline, these will be regarded as synonymous.

Regular flower visitors (anthophiles) can be divided into three categories with regard to their energy requirements: obligate endotherms ('warm-blooded' with very high energy requirements, eg birds and mammals); facultatively endothermic poikilotherms (heterotherms: 'cold-blooded', but able to produce heat endogenously to maintain a higher body temperature when active, eg certain hummingbirds, bees, moths, beeflies, long-proboscid flies, and larger beetles); and obligate poikilotherms ('cold blooded', but which regulate body temperature by changing environments, eg flies, beetles, and butterflies). These categories are not discrete and overlap considerably.

Obligate endothermic (OE) anthophiles theoretically could exist in most terrestrial environments. However, their high energy requirements limit their coevolved food plants to areas of year-round, high photosynthetic productivity and adequate water-supply for the production of copious nectar. OE-pollination is thus scarce at high latitudes and in drier areas (deserts and grasslands). At high altitudes in tropical and subtropical regions the seasonal constancy (relative to equivalent latitudes) permits the near year-round growth of perennial plants. This, together with the proximity of lower altitude OE-pollinator source areas, results in high altitudes possessing a higher proportion of OE-pollination than equivalent latitudes. OE-pollination is more abundant in habitats where poikilothermic pollinators are disadvantaged, eg lower temperatures at high altitudes and fog-prone areas. For the same reasons annual plants are rarely OE-pollinated, whereas OE-pollination is more abundant in perennial shrubs and trees.

Heterothermic anthophiles may be divided into two categories: those which require nectar and pollen throughout their life cycle (eg bees), and those which only utilize pollen and nectar as adults.

The distribution of bees is limited by temperature and rainfall. Where plant productivity is high year-round (tropical rainforests), social bees dominate bee communities. A minimum period of flowering is required for solitary bees to provision broods and for social bees to build up numbers or gather overwintering supplies. Where temperature and rainfall limit plant phenology to shorter periods (eg savannas, deserts and alpine regions), smaller solitary bees dominate. Where temperatures are lower and flowering seasons are sufficiently long (eg artic and lower alpine regions), larger solitary bees, which are able to thermoregulate better, are dominant. Bees are the dominant pollinators in winter-rainfall areas and associated deserts, where annual forbs tend to replace the grasses of summer-rainfall areas. High summer humidity liquifies bee larval food reserves, limiting ground-nesting bees in the tropics.

The distribution of non-OE anthophiles which only use nectar as adults (NA-pollinators) is complicated by restrictions due to larval requirements. Except where larval requirements are uniform for a taxonomic group it is difficult to explain the geographical patterns observed. However, not having to provision nests allows NA-pollinators to visit flowers with too low a reward to be visited by bees. Populations of NA-pollinators are unlikely to be limited on the abundance of NA-pollinated flowers, but rather on the productivity and detritus component of neighbouring communities, whichever influences larval populations the most. However, this may not hold for some heterothermic anthophiles, such as some moths and specialized flies which defend territories against other nectar-feeders, and may rely on nectar to provide the energy required to locate mates and nesting sites. The distribution of pollination syndromes involving these specialized species should, subject to larval-restrictions, parallel that of OE- and bee pollination more closely than NA-pollination.

PART 2: PLANT ASSEMBLAGE PATTERNS IN THE CAPE FLORA

Community patterns in the Cape flora are largely related to parent geology and rainfall (Table 8.5; Figure 8.1).

Mountain Fynbos (including Grassy Fynbos) (sensu Moll et al 1984) is a heathland vegetation type which occurs on nutrient-poor, well leached, acid, sandy soils derived from sandstones and quartzites of the Cape Fold belt and from the Cape granites. It is further divided into six major series (Grassy, Proteoid, Asteraceous, Restoid, Ericaceous and Riverine) based on rainfall, altitude, aspect, soil depth and soil texture (Campbell 1985). Moll et al (1984) combine these into three subdivisions (wet, mesic and dry) based on a moisture gradient which determines the density of the canopy cover.

Lowland Fynbos (Moll et al 1984) comprises the remainder of the heathlands and is subdivided into three types based on substratum: (1) Sand Plain Lowland Fynbos on deep acid sands; (2) Elim Lowland Fynbos on lateritic soils; and (3) Limestone Lowland Fynbos restricted to calcareous, neutral to alkaline, shallow sands.

Fynbos communities are characterized by a lack of species dominance, a lack of perennial herbaceous and annual plant species, and a dominance of sclerophyllous evergreen shrubs (Bond and Goldblatt 1984).

There is a preponderance of bird pollinated and mammal pollinated plant species in Mountain and Lowland Fynbos communities (Rebelo and Breytenbach this volume; Rebelo this volume). These Proteaveld (Proteoid Fynbos) and Heath (Ericaceous Fynbos) communities tend to occur on southern aspects on deeper soils, under relatively mesic situations (Campbell 1985). In addition, wind pollinated plant species, mainly Restionaceae, tend to dominate communities (Restioid Fynbos or Restioveld) on shallow, rocky soils, under moderately xeric conditions, with a northerly aspect, especially at high altitudes (Campbell 1985). Asteraceous Fynbos, which typically is dominated by Asteraceae and other insect pollinated plant species, tends to occur in the most xeric communities.

In contrast to Mountain and Lowland Fynbos, which appears to have evolved in situ, Renosterveld (Moll et al 1984), the other dominant vegetation type in the Cape floral region, contains fewer endemic species, and no endemic families. Renosterveld has strong karroid, subtropical and temperate grassland affinities. The four types of Renosterveld, differentiated by the relative abundance of different grasses, are restricted to fine-grained dystrophic soils derived from Malmesbury and Cango phyllites, Bokkeveld and Karroo shales and Cape granites. Microphyllous shrubs especially of the Asteraceae and Thymeliaceae predominate, and annuals, herbs and perennial grasses are relatively important in the understorey.

A substantial portion of the total species richness in Renosterveld is due to the high incidence of deciduous geophytes (Asphodelaceae, Iridaceae, Hyacinthaceae, Oxalidaceae) (Bond and Goldblatt 1984). Renosterveld contains relatively few bird pollinated and no mammal pollinated plant species. The majority of plant taxa appear to be insect pollinated, with wind pollination being largely confined to the graminoid element in the understorey.

TABLE 8.5 Major vegetation communities of the mediterranean regions in relation to substratum nutrient status. 'Fynbos' = heathland. Compiled from Beard (1983), Groves et al (1983), Specht and Moll (1983), Moll et al (1984), Moll (1986)

Substratum	Cape flora	Australia	Chile	California	Mediterranean
Sandstone, quartzite and well leached granite	Mountain Fynbos Grassy Fynbos	Banksia Woodland	-	Sclerophyllous Forest	Sclerophyllous Forest Maquis
Acid sands	Sand Plain Fynbos	Banksia Woodland Scrub Heathland	-	-	-
Limestone	Limestone Fynbos	Limestone Heaths	-	-	-
Lowland laterite	Elim Fynbos	Scrub Heathland?	-	-	-
Dystrophic shales and granites	Renosterveld	Wandoo Woodland Gimlet Woodland (Mallee)	Matorral	Manzanita Chaparral Savanna Woodland	Matorral Savanna Woodland Grassland
Meso-eutrophic shales and granites	Karroid shrublands	Wando Woodland Gimlet Woodland (Mallee)	Matorral	Manzanita Chaparral Savanna Woodland	? - extinct
Calcareous sands	Strandveld Dune Fynbos	Mallee?	Matorral	-	Garrigue Batha Phrygana
Serpentine soils	-	-	-	Serpentine Chaparral	
Independent of substratum: (high rainfall)	Afromontane Forest	Jarrah-marri Forest	-	-	-

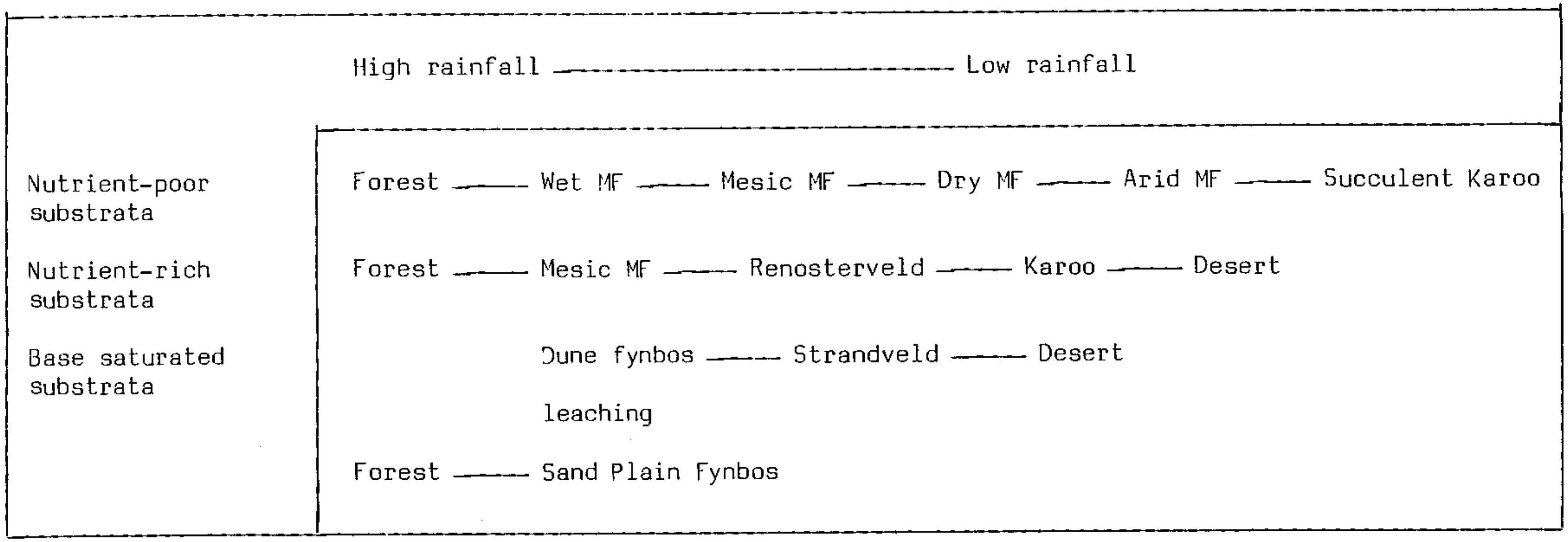


FIGURE 8.1 The apparent sequence of climax communities on different substrata, as determined by rainfall in the Cape flora.

Under drier conditions, principally to the north, Renosterveld is replaced by karroid shrublands (Moll et al 1984) on eutrophic soils. Karroid communities are characterized by their lower plant cover, greater proportion of succulents, and an abundance of annual plant species which appear subsequent to heavy winter rains. Heavy summer rains appear to favour the growth of grasses and shrubs, rather than annuals (A G Rebelo personal observation). Karroid shrubland communities are dominated by insect pollinated species today, but under conditions of less overgrazing the graminoid component may have been important. Wind pollination is apparently largely absent among the shrubs, perhaps because of the relatively large distances between plants. Bird pollination is confined to river courses (*Nicotiana* (Solanaceae)), plant parasites (*Septulina* and *Moquiniella* (Loranthaceae)), or to isolated pockets of stem-succulent plants, mainly *Aloe*, and *Tylecodon* species (Asphodelaceae and Crassulaceae), which appear to favour specific geological or relief formations.

Strandveld communities (Moll et al 1984), similar in structure and generic composition to subtropical thicket communities of the east coast of South Africa, but with a strong karroid component, are confined to deep, well drained, base saturated, sand/shell soils of the south and west coast regions of the Cape flora. A large proportion of species appear to have inflorescences adapted for the generalist fly pollination syndrome (Rebelo 1987). Succulents, geophytes, annual herbs and climbers are important insect pollinated understorey components.

Afromontane forest communities (Moll et al 1984) occur under conditions of high rainfall, and in certain areas Wet Mountain Fynbos may be seral to forest. Afromontane forest is poor in species and low in endemism. Few members of the forest communities are bird pollinated (*Burchellia*, *Halleria*) or wind pollinated (Rebelo this volume; Koutnik *this volume*). The majority of species are insect pollinated.

Published accounts of the relative importance of pollination syndromes in the different plant assemblages in the Cape flora are not available. Preliminary work on the plant communities in the Hangklip (based on combined species and abundance data from Boucher (1978)), are presented in Table 8.6 (A G Rebelo unpublished). In all the Hangklip communities, with the exception of marsh communities (Marsh and Seepage Marsh), insect pollination is the predominant pollination syndrome, with a higher incidence in Afromontane Forest, Strandveld and Limestone Fynbos. Wind pollination is predominant in Restionaceae- and Poaceae-dominated Seepage Marsh and Marsh (adjacent vleis). Elsewhere, wind pollination is most prominent in Riparian communities and Inland Mountain Fynbos (= Renosterveld). Bird pollination seldom accounts for more than 12% of the species in any community, but often comprises the dominant plants in the Plinthic, Coastal, Inland Mountain Fynbos and Sand Plain Fynbos communities. The high proportion of bird pollination in Riparian and Afromontane Forest communities is largely due to the high incidence of bird pollinated Mountain Fynbos species in the bordering ecotonal areas. These include *Protea mundii* and *Protea cynaroides*, which, due to protection from fire, are being overgrown by forest species (Boucher 1978). By contrast, in the interior of these two communities bird pollination is scarce, comprising less than five per cent of the species. Whereas bird pollination is scarce in Marsh, Strandveld and Limestone Fynbos communities, the incidence of bird pollination remain consistently high in Mountain Fynbos communities, irrespective of substratum. Mammal pollination parallels the incidence of ornithophily in Mountain Fynbos and Sand Plain Fynbos, but is absent from Limestone Fynbos.

TABLE 8.6 Proportion of pollination syndromes for the dominant plant species in the Hangklip area (34°15'S; 18°45'E), South Africa. Data and community names are from Boucher (1978)

Community	Number of species	Proportion of species per pollination syndrome			
		Insect	Wind	Bird	Mammal
Marsh	14	36	64	0	0
Strandveld	97	73	24	3	0
Limestone Fynbos	119	70	25	4	1
Forest	43	75	16	9	0
Riparian	96	53	36	11	0
Sand Plain Fynbos	115	57	30	12	1
Mountain Fynbos:					
Seepage marsh	75	41	49	8	0
Inland north aspect	186	54	37	9	0
Coastal slopes	179	60	28	10	2
Yellow plinthic soils	237	54	33	11	2
Inland south aspect	208	49	37	12	2

PART 3: PATTERNS OF POLLINATION SYNDROMES IN MEDITERRANEAN REGIONS

Because climate is the driving force influencing soil formation and leaching from parent material, mediterranean regions should contain a similar suite of soil and landform types (Paskoff 1973). However, south-western Australia and the Cape flora are characterized by deep acid sands and laterites which do not occur in the other mediterranean regions (Table 8.5).

Mediterranean floras must be understood in terms of the continuing evolution of subhumid to semi-arid plant communities at the margins of the tropics (Solbrig et al 1977). The alteration of climate during the Pleistocene (which produced the cold ocean currents, with dry summers and wet winters) is largely responsible for the present mediterranean vegetation structure. However, whereas the increase in orogenic activity of both the Sierra Nevada of North America and the Andes of South America contributed to the rapid speciation of plants in those areas (Solbrig et al 1977), the mediterranean areas of southern Africa and Australia did not experience any orogenic activity, yet also have large floras. The evolution of mediterranean floras also must be viewed in terms of the Tertiary floras from which they originated, and the floras which displaced them during the Pleistocene glaciations (Solbrig et al 1977). The movement of the Cape and south-western Australian floras during the Tertiary, relative to the continental drift northward across climatic belts after the breakup of Gondwana, must also be considered.

Research in the different floras has focused on their most important pollinator components. Thus the rich bee faunas of the Chilean mattoral and Californian chaparral have been extensively studied, although virtually no research has been undertaken on pollination biology in the Mediterranean region, which also has a rich bee fauna. Pollination studies in the Cape flora and Australian heathlands and shrublands have concentrated on pollination by birds and mammals. Unfortunately, comparative data on both bird and bee pollination are thus not currently available for mediterranean floras. In this section we summarize some of the pollination research undertaken in the various mediterranean floras.

Mediterranean Maquis

The pollination environment of the Mediterranean Maquis has been outlined by Dafni (1986). Despite a very high abundance of bee species and a wealth of plant species, the Mediterranean region has been ignored by pollination biologists.

The Mediterranean Maquis is characterized by a preponderance of small flowers: one third of the plant species have flowers less than 10 mm long. This can be explained in terms of the major pollination syndromes: the majority (80%) of the nonherbaceous flora is pollinated by flies, hoverflies and small solitary bees; 24% is wind pollinated (two species are both wind and insect pollinated). Predominant flower colours are white (40%), green (31%), and yellow (20%). There is a paucity of colourful flowers, including blue. A fair proportion of the nonherbaceous plants are unisexual (18%) or dioeceous (24%).

The dense shade of the maqui may limit the abundance of solitary bees, which prefer to nest in well illuminated environments. Wasps and Syrphidae flies are important active pollinators in maqui.

There are two distinct flowering seasons: 54% of species flower in the period March to May (spring), when insect abundance peaks, although several species flower in autumn.

The maqui is dominated by wind pollinated trees. Two thirds of these flower in spring and comprise 29% of the total spring-flowering component. Leaf-deciduous species (42% of anemophilous taxa) flower before the leafbuds break.

The maqui lacks any specific 'maqui flowers' or endemic pollination syndromes. This may perhaps stem from its being composed of a mozaic of species evolved elsewhere. If any trend can be drawn, it is towards one of a generalist pollination syndrome.

Chaparral and Matorral

Patterns of pollination syndromes and pollinator species between the Mediterranean plant communities of California and Chile have been studied by Moldenke (1979b,c) and summarized in Cody et al (1977) (Tables 8.7 and 8.8).

Both the Californian chaparral and the Chilean matorral (collectively named mediterranean scrub below) are fire-adapted ecosystems. In chaparral the fire periodicity is about eight years. Whereas their is no understorey beneath the shrubs in mature chaparral communities, a dense cover of annual and geophyte species characterizes the early seral stages. However, annuals form a conspicuous element of mature matorral communities, which differ little from early seral communities in species content and relative cover.

The peak blooming period in vegetation types in southern California is restricted, relative to northern California, by a lack of summer moisture. The matorral has a peak blooming period similar to that of chaparral. However, Chilean coastal scrub communities bloom for much longer, possibly because of moisture supplied by summer fogs.

Mediterranean scrub and desert scrub communities show a close correspondence in plant species number and floral biomass between California and Chile. However, in coastal scrub Chile has a much higher floral biomass, which is largely due to three mass-blooming species: *Puya chiliensis*, *Baccharis linearis* and *B concava*. *Puya* is hummingbird pollinated (by *Patagonia gigas*) and *Baccharis*, the only floral resource available in late summer, is pollinated by bees and flies.

A significantly larger number of species, individuals and biomass of flower-herbivores occurs in the mediterranean scrub than in any other Californian or Chilean vegetation community. The presence of enormous numbers of several minute, flower-visiting species boosts insect numbers in both mediterranean scrub communites. However, they are probably ineffective pollinators, even though they specialize on visiting certain plant taxa.

TABLE 8.7 The relative contribution of plant species to the different pollination syndromes in vegetation communities in California (Moldenke 1979b)

Vegetation type	Total number of species	Proportion (%) of species per pollination syndrome											
		Solitary	Halictine	Beefly	Wasp	Beetle	Butterfly	Hoverfly	Muscoid	Hummingbird	Water	Wind	Selfers
Coastal scrub	140	27	7	2	1	3	2	2	1	3	3	15	33
Desert scrub	140	29	2	2	4	3	2	4	3	3	0	11	38
Chaparral (burned)	157	24	5	7	5	2	3	2	1	5	4	11	24
Oak-Pine forest	84	41	1	9	3	4	1	0	1	8	0	20	13
Chaparral	72	41	7	6	3	0	1	0	3	14	0	10	9

TABLE 8.8 The relative contribution of plant species to the different pollination syndromes in vegetation communities in Chile (Moldenke 1979b)

Vegetation type	Total number of species	Proportion (%) of species per pollination syndrome											
		Solitary	Halictine	Beefly	Wasp	Beetle	Butterfly	Hoverfly	Muscoid	Hummingbird	Water	Wind	Selfers
Desert	180	36	0	9	5	4	0	1	4	0	1	7	32
Succulent scrub	105	16	0	6	2	5	1	4	3	4	2	10	48
Coastal scrub	154	22	5	5	1	5	2	4	5	5	1	17	32
Matorral	158	53	14	1	2	1	3	12	2	8	1	21	30

Fog in coastal communities results in a significantly lower flower herbivore biomass than in other plant communities, especially in Chile. Only large, heavy-bodied facultatively homeothermic pollinators, such as hummingbirds, nemestrinid flies and large bees, can economically visit flowers under fog conditions. At higher latitudes Bombus comprises 99% of the community pollinator biomass in coastal scrub. In desert communities bees account for less than half of all pollinators. This may reflect the importance of water, via nectar, in these communities.

Butterflies are equally important as pollinators in mediterranean scrub communities in Chile and California, although species richness is greater in California, with Asteraceae their preferred resource.

Wasps are important in both mediterranean and desert scrub communities on both continents, where they may visit plant species ignored by other pollinators.

Diverse families of beetles are frequent visitors to flowers, favouring Asteraceae. Convergent evolution of a long-proboscid pollinator from different beetle families has occurred in Chile and California.

The primitive Nematoceran flies appear to be important pollinators only in communities characterized by a large amount of shade and moist microhabitats in arid regions. Beeflies and long-proboscid flies are diverse and abundant in arid communities.

Forty per cent of the flora of mediterranean scrub and forest communities rely upon solitary bees as pollen vectors, whereas for coastal and desert communities the figure is 25% and 27%, respectively. In both California and Chile the percentage of specialist-bee feeders increases with aridity.

Alpha-diversity for bees is highest in mediterranean scrub (171 chaparral, 116 matorral) and lower in coastal scrub (80 California, 64 Chile). Desert scrub (87, 29) and montane forest (135, -) are intermediate in California, and Chilean coastal desert scrub (0, 29) has the lowest diversity.

Halictine bees are especially important in the mediterranean scrub communities. The deep-roots and water-storing ability of halictine-pollinated shrub species permits an extended blooming season, which, because of nonoverlapping blooming peaks, results in efficient pollination.

The guild of large, fast-flying, high-energy, long-lived pollinators (hummingbirds, sphinx moths and large, heavy-bodied bees) accounts for eight to 14% of plant species in mediterranean scrub. The abundance of bird pollinated plant species in California accounts for the ubiquity of hummingbirds in mediterranean scrub. By contrast in Chile, bird pollinated plant species are scarce (although conspicuous, eg Lobelia and Sophora), and the giant hummingbird is far more local in its occurrence.

In summary, analagous physiognomic plant communities in Chile and California are more similar in terms of pollination ecology than adjacent, physiognomically different communities. In desert communities small solitary bees, bombyliid flies and wasps predominate. In coastal communities, large thermoregulatory bees, long-tongued flies and hummingbirds predominate. In evergreen scrub all groups are abundant, and butterflies and hoverflies are additionally present.

Extrinsic factors affecting resource utilization in pollinators result in the following trends in both California and Chile: whereas feeding generalists by species and individuals dominate in mediterranean scrub, feeding generalists by species and biomass predominate in coastal communities, and feeding specialists occur in deserts. At higher latitudes a few species of supergeneralist nectar-feeders dominate the food web in forests and coastal regions.

South-western Australia

Fifteen per cent (610) of the 4 000 plant species in south-western Australia are estimated to be bird pollinated. The most prominent plant families visited by birds are Proteaceae, Myrtaceae and Haemodoraceae. Some 58 bird species have been recorded as feeding on indigenous flowers, with honeyeaters (Meliphagidae), lorikeets (Loriidae) and silvereyes (Zosteropdae) being the most important families (Hopper and Burbidge 1986).

A feature of the nectarivorous avifauna is the lack of specificity in foraging. Most honeyeaters visit a wide range of plant taxa. Adenanthos (Proteaceae) is, however, visited exclusively by the smaller honeyeaters in forest communities, and lorikeets display a marked preference for Eucalyptus (Myrtaceae) (Hopper and Burbidge 1986). Larger honeyeaters feed at rich, clumped nectar sources and exclude smaller, energetically more efficient species to poorer sources of nectar (Paton and Ford 1983; Paton 1986b).

The possible mechanism and steps by which bird pollination may have evolved is reviewed by Paton (1986a). Honeyeaters continuously saturate plant communities in south Australia, consuming all the nectar and responding rapidly to changes in local nectar abundance. Areas in New South Wales may, however, be populated at an abundance too low to prevent nectar from accumulating and dripping to the ground (Paton 1986b). In moister, coastal areas, with adequate soil-moisture, there is a continual cycle of flowering in bird pollinated plant species (Keighery 1983; Paton 1986b).

In contrast to the southern heathlands, subtropical rainforests and the adjacent deserts of southern Australia have few bird pollinated plant species (Keighery 1983; Ford 1986). The southern heathlands (encompasing the Stirling and Eyre Phytogeographical Provinces) have twice as many bird pollinated plant species as any comparable area in temperate Australia (Keighery 1983). Bird pollinated plants are most abundant in Banksia and Jarra Woodlands and Limestone heaths - nutrient-poor substrata, and are uncommon in foreshore regions, swamps and saltlakes (Keighery 1983; Table 8.9).

Although 25 of the 119 species of Australian marsupials occasionally visit flowers, only 10 species regularly feed on nectar. Twenty-three plant genera are visited by mammals, eight in the Myrtaceae and six in the Proteaceae (Turner 1983). However, Banksia and Eucalyptus species are the most important nectar sources for mammals. As with bird pollination, the

TABLE 8.9 The proportion of different pollination syndromes occurring (by plant species) in various habitats in temperate western Australia (Keighery 1983)

Habitat	Total number of species	Pollination Syndromes		
		Insect	Bird	Wind
Paperback swamp	27	66,7	0,0	33,3
Sedgeland swamp	40	72,5	2,5	25,0
Fore dunes	30	66,7	3,3	30,0
Stable dunes	88	83,0	4,5	12,5
Island: (dunes)	104	67,3	5,7	27,0
Tuart woodland	182	80,8	6,6	12,6
Limestone heath	131	78,6	8,4	13,0
Banksia woodland	96	74,0	10,4	15,6
Jarrah	32	62,5	12,5	25,0

species richness of mammal pollinated plants tends to peak on nutrient-poor substrata. Tarsipes rostratus is the most specialized mammalian nectarivore in Australia, and is confined to the sand-plain heath vegetation (Turner 1983).

Australia has a depauperate social bee fauna (Michener 1979). The incidence of insects using Eucalyptus (Myrtaceae) and Amyema (Loranthaceae) varies considerably between years, and is probably related to movements of apiaries, since introduced honeybees are the most common insects at these flowers (Paton 1986b).

Moth and butterfly pollination are relatively rare in south-western Australia (Keighery 1983).

Wind pollination predominates in foreshore regions, swamps and salt lakes (Keighery 1983; Table 8.9).

PART 4: POSSIBLE DETERMINANTS OF POLLINATION SYNDROME FREQUENCIES IN THE CAPE FLORA

Various explanations may be attributed to the observed patterns of pollinator abundance in the Cape flora. By contrast to California and Chile, where the apparent dominant factor influencing pollination syndromes is climate and fire frequency (Moldenke 1979b), the major patterns in the Cape flora relate to substratum. Rainfall, wind, fire and altitude are factors which also play a role in determining patterns.

Soil nutrient status

The dominant physical and structural characteristics of vegetation in the fynbos biome are intimately linked to soil nutrient status (Moll 1986) (Table 8.5). Economic theory predicts that plants should adjust resource allocation to ensure that all resources equally limit growth. Thus, plants under nutrient (ie resource) stress on infertile soils tend to accumulate high concentrations of carbon-rich compounds such as carbohydrate, resin and lignin, but have low nutrient contents (Bloom et al 1985). Nutrient-poor environments present a relatively homogeneous resource imbalance, resulting in plants with genetically fixed high root:shoot ratios. This allows for better exploitation of changes in nutrient levels through storage, than by changes in allocation responses.

Plants characteristic of nutrient-rich environments are highly plastic in their response to environmental stress, allowing them to dominate the limiting resource (Bloom et al 1985). With greater nitrogen availability, they may store nitrogen as amino acids, nitrate, or alkaloids in the leaves. Consequently, there is a dichotomy between resource allocation in nutrient-rich renosterveld/karroid shrublands and nutrient-poor fynbos communities.

Fynbos communities thus have excess carbon which can be channelled into leaves and the production of lignins and tannins (as antiherbivore devices), and is also available for the production of large, robust inflorescences and copious nectar (Milewski 1983). Since nectar production may consume twice as much energy (carbon) as the seed crop, and can equal that of flower production (Southwick 1984), energy considerations are important in determining possible pollination syndromes. In addition, the production of serotinous and myrmecochorous fruits ensure that limiting nutrients, which occur at high concentrations in seeds, are effectively protected against generalist seed predators. Since nutrient input into seeds apparently only occurs well after flowering has ceased (Brits et al 1986), flower abortion and predation can be tolerated with little net expense.

Thus, extensive nectar secretion and robust flower structures, conducive to rodent and bird pollination, may be economically feasable to plants in nutrient-poor fynbos communities. Another feature selecting for alternative pollination strategies to insect and wind pollination is the high species diversity. This places a premium on exploiting alternative pollen vectors, such as birds and mammals.

In nutrient-rich communities (renosterveld, strandveld and karroid shrublands), economic theory predicts that carbon is relatively more limiting and the production of large inflorescences or copius nectar is economically unfeasable. Smaller, more common pollen vectors, such as bees, flies and butterflies, which potentially produce a higher degree of gene flow per gram flower, are utilized as pollinators. Relatively large inflorescences are confined to annuals and geophytes, which tend to sink proportionately more resources into reproduction. In addition, water may be a limiting factor which prevents the secretion of copious nectar.

The high productivity of nutrient-rich communities also results in high herbivore and detritivore populations. These provide a source of alternative pollen vectors, mainly Diptera and Lepidoptera, whose larvae occupy these niches. Herbivore and detritivore populations are considerably lower in nutrient-poor communities, where the high ratio of carbon to nitrogen inhibits herbivore utilization of plant materials. Nitrogen is a limiting resource for insect herbivores, and there appears to be a lower limit to the proportional nitrogen content of foods beyond which nitrogen is lost by excretion faster than ingestion can occur (Mattson 1980). This may be further enhanced by the production of non-nitrogen-containing allelochemicals (tannins and lignins) which prevent bulk feeding by smaller herbivores. These qualitative defences, which include tough sclerophyllous leaves, are nitrogen-cheap. By contrast, quantitative defences, although effective at low concentrations, are nutrient-expensive, and may readily be neutralized by specific coevolved herbivores (Feeny 1975). Quantitative defences are therefore probably not important in nutrient-poor situations, but are chiefly found in ephemeral plants (which are scarce in nutrient-poor communities) and in young growing tissues (Cottrell 1985).

Low-nutrient soils may explain the near-absence of butterfly species which utilize fynbos plants as larval food sources, and their scarcity as pollen vectors in Mountain Fynbos (Cottrell 1985). Only the Lycaenidae have shown any extensive speciation within the south-western Cape, and the majority of species are aphytophagus, feeding off Homoptera and Hymenoptera (ants) (Cottrell 1985; Henning 1985). However, the moth fauna is far more extensive than the butterfly fauna in the south-western and southern Cape (Vogel 1954). Insufficient data are available to ascertain whether moths contradict the above hypothesis, but it is conceivable that the majority of species may have larvae which forage in nutrient-rich communities.

Similarly, the high incidence of fly pollination in the Strandveld may be due to fly larvae utilizing the large quantities of kelp washed up on beaches after storms along the coast. It is interesting that the inland extent of strandveld is greatest (ie the middle west coast between 32°00"S and 33°00"S) where upwelling of the highly productive Benguella current also appears to be greatest (Andrews and Hutchings 1980).

The low insect herbivore biomass in nutrient-poor fynbos communities limits the potential biomass of insect pollen vectors and insectivorous consumers. In moister areas, where the production of copious nectar is possible, the availability of energy in the form of nectar sugars has allowed an increase in biomass of those pollinator species which are able to procure their own nitrogen. Thus the biomass of avian nectarivores may account for 50% of the avian biomass in Protea-dominated Mountain Fynbos communities, whereas it seldom exceeds five per cent in nutrient-rich communities (Siegfried 1983). During the breeding season avian nectarivores apparently utilize nectar as an energy source to enable the exploitation of, otherwise energetically unprofitable, insects for protein (Skead 1967).

Data on the proportional biomass or species numbers of insect nectarivores to total insect biomass have not been collected in the Cape flora. It is likely that nectar feeders might also account for the majority of insect biomass in nutrient-poor vegetation types. It is possible that populations of some Dipteran species, which obtain nitrogen for egg production from vertebrate blood, may be partly limited by nectar available to adults. Certainly many specialist, fly pollinated plant species occur in Mountain Fynbos, where they appear to have filled the vacant butterfly niche (Vogel 1954; Rebelo et al 1985).

Rainfall and temperature

The effects of rainfall on the climax communities in relation to substrata are shown in Figure 8.1. Pollination syndromes of these vegetation communities are discussed in the previous section. The effects of rainfall and temperature on pollination biology are most readily manifested in plant phenology, especially in drier areas.

In karroid vegetation in Namaqualand annual composites bloom in profusion following winter rains sufficient to allow germination. Simultaneously, bees, flies and beetles pupate and visit the flowers. The stimuli required for germination and pupation in these taxa are largely unstudied in the Cape flora, and factors affecting pollination phenology in most communities are poorly known.

In Mountain Fynbos, the majority of bird pollinated plant species encountered at low altitudes, flower during winter, while the majority of insect pollinated species flower in summer (Rebelo et al 1984). This may be related to the greater water resources required for nectar secretion in bird pollinated species, which limits flowering to period of high water abundance. Insect species tend to flower during the warmer spring and summer, when insects are most active.

At high altitudes, both insect and bird pollinated plant species tend to bloom for short periods in summer. This is presumably because cold conditions limit insect activity. In ornithophilous plants the cold (or frozen) nectar might cool birds, and thus nullify the energy gained from the nectar. Summer nectar production by bird pollinated plant species can be maintained due to precipitation in the form of mists, which provide considerable water to high altitude communities during summer (Marloth 1905).

In Lowland Fynbos communities water-logging during winter may result in bird pollinated species blooming in spring, relative to the winter peak which occurs at low altitudes in Mountain Fynbos (Rebelo this volume).

Nevertheless, there is an apparent dearth of nectar available to birds in early summer in the south-western Cape, when large numbers of avian nectarivores may be found in gardens. Whether this is a natural phenomenon, or may due to the destruction of early-summer nectar sources (eg Protea repens) in the lowlands by urban expansion, is unknown. Conservation recommendations based on these data are hampered by the lack of data on nectarivorous bird movements in the south-western Cape. This is partly due to the altitudinal migration of birds to remote mountain peaks and a lack of knowledge concerning possible geographical migration.

The pattern of bee diversity also appears to follow gradients of temperature and rainfall, although an overriding factor may be the role of humidity which hinders the storage of pollen and nectar over long period. Water-logging may also detrimentally affect overwintering in solitary bee species (Michener 1979). The Cape flora possesses a rich bee fauna, with species less numerous on the Cape Peninsula and increasing towards the interior (Michener 1979). While bee species richness is apparently greatest in the Namaqualand region (V B Whitehead personal communication), species abundances within plant communities in the Cape flora are not known. Nor are there adequate data on the phenology of bees or flies within the region.

The distribution of the two subspecies of Apis mellifera (Hymenoptera) may be determined by climate. The occurrence of the Cape Honeybee (A mellifera capensis) in the Cape flora may be due to its more efficient use of energy in breeding and foraging in the cold, rainy winters and windy summers of the south-western Cape. By comparison the African bee A mellifera adansonii) has a higher metabolic rate, produces more brood, and is a more opportunistic breeder, all of which may limit it to warmer climates north of about latitude 32°00'S (P W Worswick personal communication).

Vogel (1954) proposed that butterflies were scarce in the Cape flora due to the lack of water in the dry areas of the Karoo and the frequent high wind speeds of the fynbos biome.

Wind

The winds in the Cape flora are influenced by the subtropical anticyclones and cold fronts associated with the circumpolar westerly wind system (Fuggle 1981). The gale force, south-easterly summer winds are due to an extremely stable anticyclone, which also causes the hot dry summers by displacing the westerly system to the south of the continent. During winter, the westerly system moves northwards, bringing gale force north-westerly winds, which immediately precede the rain-bearing cold fronts, backing to south-westerly winds after fronts pass. As cold fronts approach the continent, a sympathetic coastal low develops, which moves from east to west along the coast and may result in cyclonic rain. Hot, dessicating, gusty 'Berg winds' (north-easterlies), associated with the southern and eastern edge of coastal lows, are caused by air subsiding from inland plateau regions and may result in temperature rises of 10 to 15°C.

All these winds are manifest all year round, their seasonal dominance determined by the seasonal interplay of the westerly wind belt and the South Atlantic anticyclone. North-easterlies give way to north-westerlies as cold fronts approach, veering to south-westerlies as the fronts pass, giving way to south-easterlies as anticyclonic conditions prevail.

Local winds are highly variable due to the high relief over much of the area. Light sea breezes occur regularly in coastal areas, especially in the early afternoon. Land breezes are absent over most of the west coast due to the very cold west coast sea temperatures, but are common on calm nights along the east coast (Fuggle 1981).

Wind may affect the incidence of pollination syndromes in communities in a number of ways. For instance wind, depending on its speed and frequency, may:

- reduce pollinator activity due to a lowering of body temperature;
- reduce the efficiency of pollinators by limiting flight;
- reduce the amount of water available for nectar by increasing transpiration;
- provide water for nectar secretion, during an otherwise dry summer period, in the form of mist at high altitudes;
- necessitate that flowers have structural adaptations to ensure that they are not destroyed;
- restrict the growing and flowering season of certain plants (eg by 'burning' and pruning young buds).

These effects will apply differentially to different pollination syndromes, depending on the characteristics of pollinator locomotion and the plants' pollination syndromes. In extreme conditions, insects may become brachypterous or unwilling to fly and plants may have strong flower stalks and have a decumbent, sprawling or cushion habit (Kevan and Baker 1983).

Vogel (1954) attributed the paucity of butterlies relative to moths in southern Africa as being due to the diurnal south-easterly winds, and the susceptability of butterfly flight to high winds. Cottrell (1978) attributed the lack of butterfly species to a lack of larval food plants. Since Cottrell's arguments must hold for moth larvae as well, the ratio of butterfly to moths, if valid, might be attributable to diurnal differences in wind frequency and speed.

Average wind speeds are higher diurnally (Figure 8.2), but strong winds seldom occur before noon (Weather Bureau 1975). The diurnal differences in wind speed are the greatest along the coast, with maximum wind speed in the afternoon in accordance with the Espy-Kopper theory of diurnal variation. Inland, however, maximum wind speed occurs at noon in winter, but varies in summer, depending on orographic and open air stream movements (Weather Bureau 1960). The possibility that wind limits butterfly diversity in the Cape flora is thus not plausable, since butterflies could theoretically fly during the morning.

However, Vogels' statement is based on Seitz (1930 quoted by Vogel (1954), who gives a one to three ratio for diurnal to nocturnal Lepidoptera in the 'sonnebrattende Wustern und Steppen" of Africa, and a one to three ratio Vogel (1954) observed between diurnal and nocturnal lepidopteran pollinated plant species in southern Africa. Data on the ratio of diurnal

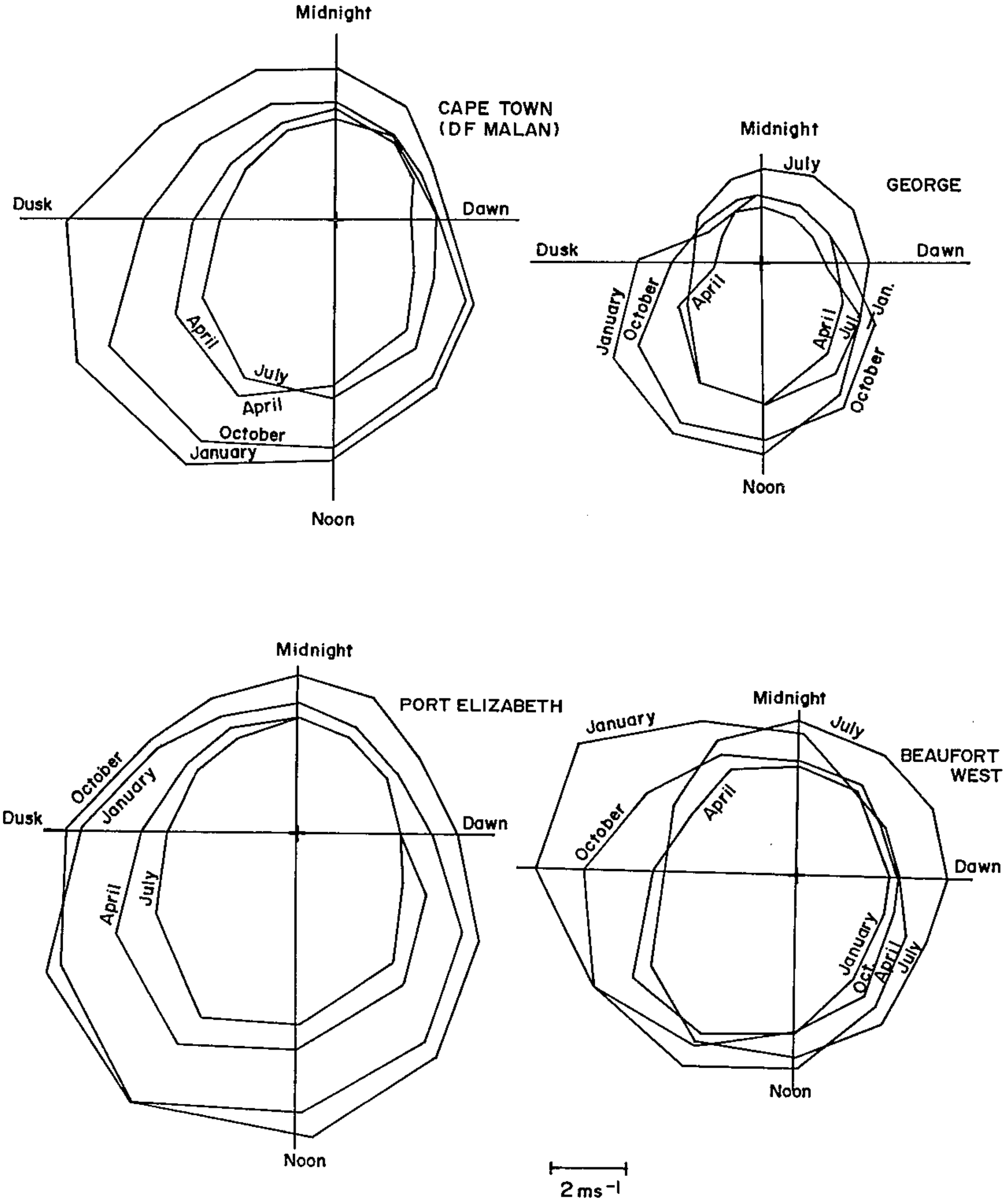


FIGURE 8.2 Mean wind speed, including calms, (ms-1) for every two hours through the day. Data from Weather Bureau (1976).

to nocturnal lepidopterans are not available. An estimated ratio calculated from Henning (1985) for southern Africa is one to 10, although the proportion for anthophilous Lepidoptera is unknown.

The hypothesis that wind may be a factor in the high incidence of bird and mammal pollinated plant species (by hindering insect flight) in the Cape flora may be relagated as secondary to the nutrient-poor substratum hypothesis, as both pollination syndromes occur in nonmountainous areas, where winds are not as frequent or as strong.

It is possible, however, that the flowering phenology of wind pollinated species may be influenced by the frequency and speed of wind. Wind pollinated plant species at Hangklip showed bimodal peaks in flowering (in autumn and spring) (A G Rebelo unpublished). This pattern is negatively correlated to the standard deviation of the mean wind speed, suggesting that flowering may occur when steady winds are most predictable (ie low in summer when the high velocity south-easterlies occur, and low in winter when the north-westerlies are accompanied by rain). However, there are insufficient regional data on plant flowering phenology to test this hypothesis.

The small flowers of most wind and insect pollinated plant species are largely unaffected by wind. Blossoms of bird pollinated species are usually robust, especially in sclerophyllous Proteaceae where they tend to be woody. Structural adaptations of flowers to resist destruction by high wind speeds are perhaps most conspicuous in coastal and high altitude, large-flowered geophytes. The flowers of Watsonia, Homoglossum, Gladiolus, Chasmanthe and Anomalesia (Iridaceae) appear to twist within their floral bracts and face downwind, while the peduncle (inflorescence stalk) is robust enough to resist the wind. Other species, also with robust peduncles, have robust flowers which are firmly seated within their floral bracts (Anapalina, Witsenia, Micranthus (Iridaceae)), or have flowers with short stalks which allow them to point downwind and reduce wind-resistance (Aloe (Asphodelaceae), Drimia (Hyacinthaceae)).

Fire

Whilst the dominant pattern of plant assemblages in the Cape flora is determined by soil nutrient status and rainfall, the most dramatic determinant of vegetation communities is fire (van Wilgen 1987). In regions of high rainfall, fire is effectively excluded and Afromontane Forest develops as a climax seral community. A major dichotomy between nutrient-poor and nutrient-rich substrata becomes apparent with increased summer drought and lower annual rainfall. In Renosterveld the rapid growth of the vegetation allows for annual fires and tends to favour grasslands, but in the slower growing, nutrient-poor fynbos communities fires only occur at five to 60-year intervals. Thus, whereas Renosterveld has many annuals and geophytes, fynbos is characterized by schlerophyllous shrub species having a single-aged cohort turning over at fire-mediated intervals of five to 60 years.

With decreasing rainfall the fire interval increases owing to the decline in plant productivity. Fire is infrequent in karroid shrublands, and in Xeric Mountain Fynbos the fire interval may increase to well over 60 years. Under these situations winter-flowering annual species (especially Asteraceae) increase. The effect of fire on the pollination syndromes is thus inextricably bound with substratum and climate. Similarly, the flowering phenology of plants may also be geared to ensuring that seeds are released prior to potential late summer fires, although other influences, such as ant activity in myrmechochorous species (Lamont et al 1985), undoubtably apply.

Fires do, however, reset seral succession. When protected from fire, Mesic and Wet Mountain Fynbos may change to Afromontane forest. However, with the exception of geophytes and nitrogen-fixing legumes, there is little evidence of succession within the plant communities of the Cape flora. No data are available for pollinator seral succession in the Cape flora.

Fire stimulated flowering is recorded in the Amaryllidaceae, Iridaceae, Liliaceae, Orchidaceae, Poaceae (Kruger 1977), Ericaceae (Boucher 1978) and Proteaceae (Rourke 1978, 1980; Williams 1972). The pollination of certain geophytes only found flowering in the immediate post-fire environment is not known.

Siegfried (1983) proposed that a succession of bird pollinators occurred in Mountain Fynbos: Malachite sunbirds Nectarinia famosa predominate in young vegetation dominated by geophytes, followed by Orangebreasted sunbirds N violacea and Cape Sugarbirds Promerops cafer, when Erica and Protea begin flowering three to five years after the fire. In addition, nectarivorous bird populations increase with post-fire age of vegetation. Since old stands of fynbos begin senescing after 30 to 40 years (Moll and Hoffmann 1984), nectarivorous bird populations presumably also decline. Rebelo and Breytenbach (this volume) proposed that rodents replace birds in older vegetation as the dominant pollinators of certain Protea species which bloom profusely following fires. In Strandveld, some early seral species appear to be bird pollinated (Rebelo this volume), whereas older communities appear dominated by fly pollinated plant species.

A low-nutrient status, together with a regular pyric perturbation cycle, (as in fynbos communities) are ideal conditions for maintaining high species richness. The high number of plant species competing for potential pollen vectors may have influenced the pollination strategies available to plants. Likewise, pollen vectors may have had a major impact on plant speciation and hybridization. The environmental, populational and genetic factors generating and maintaining such a high plant species diversity are poorly understood, and provide an exciting avenue for research in pollination biology.

Population structure

Pollination of plant species may be affected by three parameters of population structure: the number of plants in the population; the area over which the population occurs; and the distribution pattern of plants within the population. Virtually no research has been undertaken looking at the effect of population structure on gene flow and pollination in the Cape flora. Wiens et al (1983) reflected on the small population sizes of rodent pollinated Protea species, and a relationship between wind pollination and dense populations has been recorded (Whitehead 1968). Rebelo and Siegfried (1985) recorded a high degree of colour polymorphism in some bird pollinated Erica species. They attributed this to low levels of gene transfer between discrete populations by bird pollinators, and suggested that insect pollinators, with a shorter gene transfer distance, might have resulted in more speciation between insect pollinated populations.

Whereas the population structure within certain pollination syndromes may be highly variable (eg ornithophilous Protea species vary from dense monospecific stands to plants spaced hundreds of meters apart) this may not be true in wind pollinated species, for which there may be a minimum population density beyond which pollen transfer becomes unlikely. This may account for the paucity of wind pollination in karroid shrublands and desert areas.

Population density also has a bearing on rare species which may be neglected by pollinators. Thus the relatively rare orchid Disa fasciata mimics the more common flowers of Adenandra (Rutaceae) species amongst which it grows (Wiens 1978). Pollination studies on either the mimic or the model have, however, not been undertaken.

Patterns of gene dispersal by pollinators probably vary considerably depending on population structure. Thus a gene flow 'neighbourhood' of five plants may cover an area of one metre in a dense stand of Protea lepidocarpodendron or 500 m in a sparse stand. Similarly, isolated populations of the same species may comprise a few plants in one area and several thousand in another. Should we wish to understand speciation in the Cape flora, it may be necessary to consider founder effect, genetic drift, periferal populations, sympatric evolution and stasis in terms of the effect these changes may have on the pollination of these entities. Thus a fragmented bird pollinated plant population might effectively be far less fragmented than a relatively compact mammal pollinated population. However, pollination is only one component of gene flow: an obligate serotinous reseeder may have a much smaller effective gene pool, with a much higher, more discrete genetic turnover rate (once every fire cycle), than a fire-resprouter with long-lived, soil-stored seeds.

Competition

The Cape flora is characterized by a high plant species richness. While the role of competition in determining community structure can be debated, the role of competition in pollination is more clear cut. Either pollinators are abundant and compete with one another for the use of available plant resources, or else pollinators are scarce and plants compete with one another for pollinators. This applies at both the individual and species levels. This is especially important for plants as nonlegitimate foragers may prevent seed set. The role of competition in pollination has been reviewed by Pleasants (1983). There are no comparative data in the Cape flora.

CONCLUSIONS

Geographical and environmental patterns in the distribution of pollination syndromes are readily apparent. The description of these patterns, although alluded to in the literature, has seldom been studied intensively. The Cape flora offers a unique opportunity to study the effects of rainfall, temperature, geology, altitude, and human activity on the distribution of pollination syndromes within a small geographical area. To date little such research has been undertaken. Moreover, knowledge of the patterns of distribution and movements of pollinators is essential. Without a knowledge of these interrelationships between communities in the Cape flora, conservation of this rich flora may not be possible.

REFERENCES

Andrews W R H and Hutchins L 1980. Upwelling in the southern Benguella current. Progress in Oceanography 9, 1-81.

Arroyo M T K, Armesto J J and Villagran C 1981. Plant phenological patterns in the high Andean cordillera of central Chile. Journal of Ecology 69, 205-223.

Arroyo M T K, Primack R and Armesto J 1982. Community studies in pollination ecology in the high temperate Andes of central Chile. I. Pollination mechanisms and altitudinal variation. Amercian Journal of Botany 69, 82-97.

Arroyo M T K, Armesto J and Primack 1983. Tendencuas altitudinales y latitudinales en macanismos de polinazacion en la zona andina de los Andes templados de Sudamerica. Revista Chilena de Historia Natural 56, 159-180.

Austin D F 1975. Bird flowers in the Eastern United States. Florida Science 38, 1-12.

Baker, H G and Hurd P D 1968. Intrafloral Ecology Annual Review of Entomology 13, 385-414.

Bawa K S, Perry D R and Beach J H 1985. Reproductive biology of tropical lowland rain forest trees. I. Sexual systems and incompatibility mechanisms. American Journal of Botany 72, 331-345.

Beard J S 1983. Ecological control of the vegetation of southwestern Australia: Moisture versus nutrients. In: Kruger F J, Mitchell D T and Jarvis J U M (editors) Mediterranean-type ecosystems. Springer-Verlag, Berlin. pp 66-73.

Bertin R I 1982. The ruby-throated hummingbird and its major food plants: ranges, flowering phenology, and migration. Canadian Journal of Zoology 60, 210-219.

Bloom A J, Chapin F S and Mooney H A 1985. Resource limitation in plants - an economic analogy. Annual Review of Ecology and Systematics 16, 363-392.

Bond P and Goldblatt P 1984. Plants of the cape flora. A descriptive catalogue. Journal of South African Botany Supplement 13.

Boucher C 1978. Cape Hangklip area. II. The vegetation. Bothalia 12, 455-497.

Brits G J, Jacobs G and Steenkamp J C 1986. The pruning of proteas for cut flower production. Farming in South Africa: Flowers and ornamental shrubs: B.15.

Brown J H and Kodric-Brown A 1979. Convergence, competition, and mimicry in a temperate community of humming-bird-pollinated flowers. Ecology 60, 1022-1035.

Campbell B M 1985. Montane vegetation structure in the fynbos biome: Structural classification and adaptive significance of structural characters. PhD Thesis, Rijksuniversiteit te Utrecht, Utrecht.

Carpenter F L 1978. A spectrum of nectar-eater communities. American Zoology 18, 809-819.

Cheke R A 1971. Feeding ecology and significance of interspecific territoriality of African montane sunbirds. Review Zoology/Botany Africa 84, 50-64.

Cody M L, Fuentes E R, Glanz W, Hunt J H and Moldenke A R 1977. Convergent evoltion in the consumer organisms of mediterranean Chile and California. In: Mooney H A (editor) Convergent evolution in Chile and California. Dowden, Hutchinson and Ross, Stroudsburg. pp 144-198.

Colewell M C 1973. Competition and coexistence in a simple tropical community. American Naturalist 107, 737-760.

Colwell R K 1985. Stowaways on the hummingbird express. Natural History 7, 56-63.

Cottrell C B 1978. Aspects of the biogeography of southern African Butterflies. Zambezia supplement 5.

Cottrell C B 1985. The absence of coevolutionary associations with Capensis floral element plants in the larva/plant relationships of southwestern Cape butterflies. In: Vrba E S (editor) Species and speciation. Transvaal Museum Monograph 4, 115-124.

Cowling R M 1983. The occurrence of C3 and C4 grasses in the fynbos and allied shrublands in the south eastern Cape, South Africa. Oecologia 58, 121-127.

Cowling R M 1987. Current and future trends in ecology: the 1986 INTECOL experience. South African Institute of Ecologists Bulletin 6, 1-16.

Cruden R W 1972a. Pollination biology of Nemophila menziesii (Hydrophyllaceae) with comments on the evolution of oligolectic bees. Evolution 26, 373-389.

Cruden R W 1972b. Pollinators in high elevation ecosystems: relative effectiveness of birds and bees. Science 176, 1439-1440.

Cruden R W, Kinsman S, Stockhouse R E and Linhart Y B 1976. Pollination, fecundity and the distribution of moth-flowered plants. Biotropica 8, 204-210.

Dafni A 1986. The Mediterranean maqui as a pollination environment. Invited paper at the 5th OPTIMA meeting, Istanbul.

Eisikowitch D 1978. Insect visiting of two subspecies of Nigella arvensis under adverse seaside conditions. In: Richards A J (editor) The pollination of flowers by insects. Academic Press, London. pp 125-132.

Feeney P 1975. Biochemical coevolution between plants and their insect herbivores. In: Gilbert L E and Raven P H (editors) Coevolution in animals and plants. University of Texas Press, Austin.

Feinsinger P and Swarm L A 1982. "Ecological release", seasonal variation in food supply, and the hummingbird Amazilia tovaci on Trinidad and Tabago. Ecology 63, 494-506.

Ford H A 1985. Nectarivory and pollination by birds in southern Australia and Europe. Oikos 44, 127-131.

Ford H A 1986. Use of fruit and nectar by birds in the rainforests of southern Australia. In: Ford H A and Paton D C (editors) The dynamic partnership: birds and plants in southern Australia. Handbook of the flora and fauna of south Australia, Australia.

Fuggle R F 1981. Macro-climatic patterns within the Fynbos biome. NPES final report.

Gottlieb O R 1982. Micromolecular evolution, systematics and ecology. Springer-Verlag, Berlin.

Grant V 1983. The systematic and geographical distribution of hawkmoth flowers in the temperate North American flora. Botanical Gazeteer 144, 439-449.

Grant V 1985. Additional observations on temperate North American hawkmoth flowers. Botanical Gazeteer 146, 517-520.

Groves R H, Beard J S, Deacon H J, Lambrechts J J N, Rabinovitch-Vin A, Specht R L and Stock W D 1983. Introduction: the origins and characteristics of mediterranean ecosystems. In: Day J A (editor) Mineral nutrients in mediterranean ecosystems. National Scientific Programmes Report No 71. CSIR, Pretoria. pp 1-18.

Henning S F 1985. Lepidoptera. In: Scholtz C H and Holm E (editors) Insects of southern Africa. Butterworths, Durban.

Hopper S D and Burbidge A H 1986. Honeyeaters and their plants in south-eastern Australia. In: Ford H A and Paton D C (editors) The dynamic partnership: birds and plants in southern Australia. Handbook of the flora and fauna of south Australia, Australia.

Inouye D 1976. Resource partitioning and community structure: a study of bumblebees in the Colorado Mountains. PhD Thesis, University of North Carolina.

Keighery G J 1983. Bird pollinated plants in western Australia and their breeding systems. In: Armstrong J A, Powell J M and Richards A J (editors) Pollination and evolution. Royal Botanical Gardens, Sydney. pp 77-89.

Kevan P G 1972. Floral colours in the high arctic with reference to insect-flower relations and pollination. Canadian Journal of Botany 50, 2289-2316.

Kevan P G 1973. Flowers, insects, and pollination ecology in the Canadian high arctic. Polar Record 16, 667-674.

Kevan P G 1983. Floral colours through the insect eye: what they are and what they mean. In: Jones C E and Little R J (editors) Handbook of experimental pollination biology. Van Nostrand Reinhold, New York.

Kevan P G and Baker H G 1983. Insects on flowers. In: Huffaker C B (editor) Ecological entomology. Wiley, New York. pp 3-30.

Kruger F J 1977. Ecology of the Cape Fynbos in relation to fire. USDA Forest Services General Technical Report W03, 301-307.

Lamont B B, Collins B G and Cowling R M 1985. Reproductive biology of the Proteaceae in Australia and South Africa. Proceedings of the Ecological Society of Australia 14, 213-224.

Marloth R 1905. Some aspects in the vegetation of South Africa which are due to prevailing winds. South African Journal of Science 3, 215-218.

Mattson L J 1980. Herbivory in relation to plant nitrogen content. Annual Review of ecology and systematics 11, 119-161.

Meeuse B J D 1978. The physiology of some sapromyophilous flowers. In: Richards A J (editor) The pollination of flowers by insects. Academic Press, London.

Michener C D 1979. The biogeography of bees. Annals of the Missouri Botanical Garden 66, 277-347.

Milewski A V 1983. A comparison of ecosystems in Mediterranean Australia and southern Africa: Nutrient-poor sites at the Barrens and the Caledon Coast. Annual Review of Ecology and Systematics 14, 57-76.

Moldenke A R 1979a. Pollination ecology within the Sierra Nevada. Phytologia 42, 223-282.

Moldenke A R 1979b. Pollination ecology as an assay for ecosystem organization: Convergent evolution in Chile and California. Phytologia 42, 415-454.

Moldenke A R 1979c. Host-plant coevolution and the diversity of bees in relation to the flora of North America. Phytologia 43, 357-419.

Moldenke A R 1979d. The role of host-plant selection in bee speciation processes. Phytologia 43, 433-459.

Moldenke A R and Lincoln P G 1979. Pollination ecology in Montane Colorado: a community analysis. Phytologia 42, 349-379.

Moll E J and Hoffman M T 1984. An evaluation of a post-fire regeneration model for fynbos. Proceedings of the fourth International Conference on Mediterranean Ecosystems, 115-116.

Moll E J, Campbell B M, Cowling R M, Bossi L, Jarman M L and Boucher C 1984. A description of major vegetation categories in and adjacent the fynbos biome. National Scientific Programmes Report No 83. CSIR, Pretoria. 29 pp.

Naeem S, Dobkin D S and Oconner B M 1985. Lasioseius mites (Acari: Gamasida: Ascidae) associated with hummingbird-pollinated flowers in Trinidad, West Indies. International Journal of Entomology 27, 338-353.

Orshan G 1983. Approaches to the definition of Mediterranean growth forms. In: Kruger F J, Mitchell D T and Jarvis J U M (editors) Mediterranean-type ecosystems. Springer-Verlag, Berlin. pp 86-100.

Ostler W K and Harper K T 1978. Floral ecology in relation to plant species diversity in the Wasatch mountains of Utah and Idaho. Ecology 59, 848-861.

Paskoff R 1973. Geomorphological processes and characteristic landforms in the Mediterranean regions of the world. In: di Castri F and Mooney H A (editors) Mediterranean type ecosystems: Origin and structure. Springer-Verlag, New York. pp 53-60.

Paton D C 1986a. Evolution of bird pollination in Australia. In: Ford H A and Paton D C (editors) The dynamic partnership: birds and plants in southern Australia. Handbook of the flora and fauna of south Australia, Australia. pp 32-41.

Paton D C 1986b. Honeyeaters and their plants in south-eastern Australia. In: Ford H A and Paton D C (editors) The dynamic partnership: birds and plants in southern Australia. Handbook of the flora and fauna of south Australia, Australia. pp 9-19.

Paton D C and Ford H A 1983. The influence of plant characteristics and honeyeater size on levels of pollination in Australian plants. In: Jones C E and Little R J (editors) Handbook of experimental pollination biology. Van Nostrand Reinhold, New York. pp 235-248.

Pleasants J M 1983. Structure of plant and pollinator communities. In: Jones C E and Little R J (editors) Handbook of experimental pollination biology. Van Nostrand Reinhold, New York. pp 375-393.

Primack R B 1983. Insect pollination in the New Zealand mountain flora. New Zealand Journal of Botany 21, 317-333.

Procter M and Yeo P 1973. The pollination of plants. Collins, London.

Pyke G H 1982. Local geographic distributions of bumblebees near Crested Butte, Colorado: Competition and community structure. Ecology 63, 555-573.

Rebelo A G 1987. Mass emigration of kelp flies (Coelopidae). Journal of the Entomological Society of southern Africa 50, 257-258.

Rebelo A G and Siegfried W R 1985. Colour and size of flowers in relation to pollination of Erica species. Oecologia 65, 584-590.

Rebelo A G, Siegfried W R and Crowe A A 1984. Avian pollinators and the pollination syndromes of selected Mountain Fynbos plants. South African Journal of Botany 3, 2285-2296.

Rebelo A G, Siegfried W R and Oliver E G H 1985. Pollination syndromes of Erica species in the south-western Cape. South African Journal of Botany 51, 270-280.

Rourke J P 1980. The Proteas of southern Africa. Purnell, Cape Town.

Ryke P A J 1954. Two new predatory mites (Acarina: Phytoseiinae) in the western Province. Journal of the Entomological Society of southern Africa 17, 241-245.

Ryke P A J 1964. Acarina associated with Protea flowers in the Cape Province. Journal of the Entomological Society of southern Africa 26, 337-354.

Scogin R 1983. Visible floral pigments and pollinators. In: Jones C E and Little R J (editors) Handbook of experimental pollination biology. Van Nostrand Reinhold, New York. pp 160-172.

Siegfried W R 1983. Trophic structure of some communities of fynbos birds. Journal of South African Botany 49, 1-43.

Siegfried W R and Rebelo A G 1986. Sunbird-Erica pollination systems in Mountain Fynbos. Final Report. Foundation for Research Development, CSIR.

Skead C J 1967. Sunbirds of southern Africa. Balkema, Cape Town.

Smith R L 1974. Ecology and Field Biology. 2nd edition. Harper and Row, New York.

Snow D W and Snow B K 1980. Relationships between hummingbirds and flowers in the Andes of Colombia. Bulletin of the British Museum of Natural History 38, 105-139.

Solbrig O T, Cody M T, Fuentes E R, Glanz W, Hunt J H and Moldenke A R 1977. The origin of the biota. In: Mooney H A (editor) Convergent evolution in Chile and California mediterranean climate ecosystems. Dowden, Hutchinson and Ross Incorporated, Stroudsburg. pp 41-65.

Southwick E E 1984. Photosynthate allocation to floral nectar: a neglected energy investment. Ecology 65, 1775-1779.

Specht R L and Moll E J 1983. Mediterranean-type heathlands and schlerophyllous shrublands of the world: an overview. In: Kruger F J, Mitchell D T and Jarvis J U M (editors) Mediterranean-type ecosystems. Springer-Verlag, Berlin. pp 41-65.

Stevens P F 1976. The altitudinal and geographical distributions of flower types in Rhododendron section Vireya, especially in the Papuasian species, and their significance. Botanical Journal of the Linnean Society 72, 1-33.

Stiles F G 1981. Geographical aspects of bird-flower coevolution, with particular reference to central America. Annals of the Missouri Botanical Garden 68, 323-351.

Strahler A N 1975. Physical Geography. Wiley, New York.

Sussmann R W and Raven P H 1978. Pollination by lemurs and marsupials: an archiac coevolutionary system. Science 200, 731-736.

Turner V 1983. Marsupials as pollinators in Australia. In: Armstrong J A, Powell J M and Richards A J (editors) Pollination and evolution. Royal Botanical Gardens, Sydney. pp 55-66.

Utech F H and Kawano S 1975. Spectral polymorphisms in angiosperm flowers determined by differential ultraviolet reflectance. Botanical Magazine Tokyo 88, 9-30.

Van Wilgen B W 1987. Fire regimes in the fynbos biome. In: Cowling R M, Le Maitre D C, McKenzie B, Prys-Jones R P and van Wilgen B W (editors) Disturbance and the dynamics of fynbos biome communities. National Scientific Programmes Report No 135. CSIR, Pretoria. pp 6-12.

Vogel S 1954. Blutenbiologische typen als elemente der Sippengliderung: dargestellt aanhand der flora sudAfrikas. Gustav Fischer Velag, Jena.

Weather Bureau 1960. Climate of South Africa Part 6 Surface winds. WB 26. Weather Bureau, Pretoria.

Weather Bureau 1975. Climate of South Africa Part 12 Surface winds. WB 28. Weather Bureau, Pretoria.

Weavers T 1952. Flower colours and their frequency. Acta Botanica Neerlandica 1, 81-92.

Wells H 1979. Self-fertilization: advantageous or deletrious? Evolution 33, 252-255.

Whitehead D R 1968. Wind pollination in the angiosperms: evolutionary and environmental considerations. Evolution 23, 28-35.

Whitehead D R 1983. Wind pollination: some ecological and evolutionary perspectives. In: Real L (editor) Pollination biology. Academic Press, London. pp 97-109.

Wiens D 1978. Mimicry in plants. Evolutionary Biology 11, 365-403.

Wiens D, Rourke J P, Casper B B, Rickart E A, LaPine T R, Peterson C J and Channing A 1983. Nonflying mammal pollination of southern African Proteas: a non-coevolved system. Annals of the Missouri Botanical Garden 70, 1-31.

Williams I J M 1972. A revision of the genus Leucadendron (Proteaceae). Contributions from the Bolus Herbarium 3.

Williams N H 1983. Floral fragrances as cues in animal pollination. In: Jones C E and Little R J (editors) Handbook of experimental pollination biology. Van Nostrand Reinhold, New York. pp 50-72.

Wolf L L and Gill F B 1980. Resource gradients and community organization of nectarivorous birds. Acta 17th Congress International 2 Ornithology, 1106-1113.

Woodell S R J 1979. The role of unspecialized pollinators in the reproductive success of Aldbran plants. Phililisophical Transactions of the Royal Society of London 286, 99-108.

CHAPTER 9 MANAGEMENT IMPLICATIONS

A G Rebelo

Management considerations are becoming more prominent in conserving vegetation in the Cape flora, with only 31% of the original lowland vegetation types remaining and 24% of these reduced in conservation value by the invasion of alien woody plant species. In the mountains management has been largely orientated towards maintaining a water supply.

Whereas the importance of management in conserving the Cape flora is hampered by a lack of sound ecological understanding, some aspects of management are known to be incorrect or deleterious. Thus flower pickers often overexploit fynbos plants, many managers overstock their reserves with exotic large herbivores and many reserves are burned at frequencies known to eliminate certain plant species. Coupled with our lack of knowledge of the importance of size of burnt area, the effect of introducing exotic plants and herbivores, and the impact of high levels of honeybees on natural communities, the pressure faced by pollinators and plants in a fragmental, dwindling ecosystem are largely unknown.

In this chapter the effects of the commercial wildflower trade, the bee industry, the role of fire, herbivory and alien plants on pollination biology are reviewed, and implications for management of the remnants of the Cape flora are sketched.

THE COMMERCIAL WILDFLOWER TRADE

The indigenous wildflower trade in the southern and south-western Cape earns over R10 million annually, 85% of which is derived from plants in natural vegetation, usually Mountain, Sand Plain and Elim Fynbos (sensu Moll et al 1984) (Davies 1984). Three major categories of material are utilized: fresh cut flowers, fresh foliage and dried material. All three differ in their potential effects on seed production and pollinator dynamics.

Picking techniques

Techniques of flower removal practiced by pickers influence both plant growth and production of flowers in subsequent years. Hence the pruning method employed by wildflower pickers might influence pollinator dynamics and seed production for several years after picking has ceased.

In the Proteaceae, cutting of wood older than two years, results in reduced shoot formation or death of the branch (Brits et al 1986). Incorrect pruning results in unproductive stubs which have a tendency to become diseased. However, long flower stems are required for trade purposes, which especially in Protea, may leave the branches too short to produce new growth. The pruning programme recommended by Brits et al (1986) requires intensive training of staff, which is not often given to pickers operating outside commercial plantations.

Casual observations of veld utilized by the cutflower trade usually reveals a large proportion of dead branches and a substantial number of dead plants. This is especially marked in stands of *Brunia albiflora* and *Erica pinea* (Kleinmond Nature Reserve), *Protea compacta* (Bredasdorp), and *Paranomus capitatus* (Riviersonderend). Rebelo and Holmes (in preparation) found that during 1985/86, levels of mortality induced by picking of *Brunia albiflora* in the Kleinmond Nature Reserve varied between 14% and 33% of the population. There was at the same time a two per cent natural mortality, with a further 16% to 24% of the population having over 50% of the plants' foliage removed annually. The high mortality (up to 50% of the plants picked were killed) evident in the Kleinmond Nature Reserve is significantly higher than that of eight per cent on an adjacent area, where the owner picked intensively. This suggests that high mortality is largely due to incorrect picking techniques.

Little is known about effects of large scale removal of material for 'greens', although it is unlikely that young growth is utilized, since in many species these tend to be soft and collapse on dessiccation. The utilization of greens probably results in a higher mortality rate than the picking of cut flowers, especially in plant species with monopodial growth forms, short lived leaves and an inability to regenerate from old epicormic buds (Table 9.1). The tolerance of fynbos plant species to pruning has not been investigated (except for commercial cultivars of Proteaceae), despite such data being the first stage in determining to what degree a plant may be pruned without adversely affecting its growth and flower production. Research is urgently needed to determine the optimum picking procedures for both flowers and greens. This is especially important in species which are picked in natural veld, since population decreases under natural conditions are not as detectable as in commercial plantations.

Picking of material to be dried is often more destructive than picking fresh flowers or greens. The inflorescences used are often below the current year's growth, and the long stems required by the trade may extend well into wood with dead epicormic buds. Picking for dried material may also significantly reduce the seed banks of serotinous species (eg the wind pollinated *Leucadendron salicifolium* which is utilized for its attractive seedheads). The significant reduction in population sizes in successive generations may affect pollination of wind pollinated species, for which dense populations may be optimal (Koutnik this volume).

The use of female *Leucadendron platyspermum* for dried cones from natural stands in the Bredasdorp region has significantly skewed the sex ratio towards male plants in natural populations, both by reducing the number of female flowers produced and by killing female plants (personal observation). Seed production and the canopy stored seed bank appear to have been reduced despite the large numbers of male plants which remain as seemingly healthy populations. The effects of such harvesting on seed banks will only become apparent following a fire.

Guidelines for assessing the degree of veld utilization, especially in cases where veld is hired by independent collectors, are urgently needed. Several farmers in the Bredasdorp area who had previously hired out their land to independent picking operators prior to commencing picking themselves, have expressed shock at the 'high rates and ruthless methods (of utilization) applied'. In cases this has resulted in near elimination of seed banks and extensive plant mortality.

Guidelines for recommended maximum utilization levels should allow inexperienced laymen, such as land owners, to rapidly assess the degree of utilization on land hired out to picking companies. This can perhaps best be achieved by educating land owners as to the actual value of the plants on the land, such that otherwise 'useless' land is viewed in a more favourable light.

TABLE 9.1 Plant taxa which are likely to have a high mortality rate when heavily picked. This list is compiled from field observations and extrapolation to similar taxa. It will not necessarily apply to all variants of the species concerned. The list is by no means comprehensive, and examples were selected primarily from an unpublished list of plants utilized by the wildflower trade compiled by M Simpson (Cape Department of Nature and Environmental Conservation). The list also includes examples not utilized by the trade, which display high mortality rates, even if only lightly picked (eg for flower shows)

Family	Genus	Examples
Asteraceae	Edmondia	fasciculata, pinifolia, sesamoides
	Euryops	abrotanifolius
	Helipterum	affine
	Othonna	quinquedentata
	Ursinia	eckloniana
Bruniaceae	Berzelia	abrotanoides
	Brunia	albiflora, alopecuroides
	Staavia	dodii
Ericaceae	Erica	corifolia, elimensis, fascicularis, longifolia, patersonia, pelilifera, placentiflora, thomae
Fabaceae	Priestleya	vestita
Proteaceae	Leucadendron	concavum, diemontianum, elimense, flexuosum, linifolium, thymifolium, verticillatum
	Leucospermum	trunculatulum, utriculosum
	Mimetes	hottentoticus, stokoei
	Orothamnus	zeyheri
	Paranomus	adiantifolius
	Protea	compacta
	Serruria	confragosa, florida, heterophylla
	Sorocephalus	alopecurus, clavigerus, imbricatus, scabridus, tenuifolius
Santalaceae	Thesium	euphorbioides
Scrophulariaceae	Agathelpis	angustifolia
Thymeliaceae	Gnidia	oppositifolia
	Struthiola	tomentosa

Nutrients

The degree to which picking activities may remove nutrients from communities with low levels of available nutrients (viz Mountain Fynbos, Sand Plain Fynbos and Limestone Fynbos) is unknown. Circumstantial evidence suggests that nutrient reserves in the plant may only be shunted into seeds late in the life cycle of the inflorescence (Brits et al 1986). However, Jongens-Roberts and Mitchell (1986) showed that up to 20% of the phosphorus in *Leucospermum parile* accumulated in the mature inflorescences. It is important that the nutrient requirements and allocation to inflorescences be investigated in commercially utilized plant species, so that the amounts of nutrients removed from these communities can be evaluated.

Furthermore, methods for fertilizing areas in order to maintain soil nutrient-levels, or to increase plant production, need to be investigated (application techniques, quantities, and nutrient complexes used).

Pollinator dynamics and seed set

The effect of flower removal from natural plant populations on pollinator populations, the resulting changes in pollinator dynamics, and its effect on seed set and seed quality in the remaining inflorescences are not known. Research is urgently needed to investigate the effect of flower picking on the quality of pollination in natural stands, as determined by seed set and seedling vigour. The removal of flowers could change the energy reward to expenditure ratio of foraging pollinators. Foraging strategies used by pollinators are not simply related to resource density, but may vary with energy requirements, behavioural limitations, and population levels of pollinators and their competitors.

Current recommendations on wildflower picking in mountain catchment areas suggest that picking should not exceed 50% of blooms or foliage each year, provided that no picking be undertaken for one year prior to a planned fire. The current lack of knowledge concerning seed dynamics and the unpredictability of fires are cited by Van Wilgen and Lamb (1986) as reasons for discouraging the picking of wild populations in favour of cultivation.

The effect of a 50% annual reduction in flowers on pollinator dynamics is unknown (Figure 9.1). However, unless a reasonable (and currently unknown) proportion of flowers is retained annually in plant populations, the ability of pollinators to colonize stands of previously exploited veld in the years between picking and burning may not be sufficient to obtain a sustainable seed set. This may be more critical at some times of the year than at others, and during critical periods, may influence population sizes of pollinators available at other times of the year, when resources may be more abundant. A further complication is that problems associated with pollination may not manifest themselves until areas of natural veld, which act as a buffer and reserve supply of pollinating insects and birds, are reduced in extent to below critical levels.

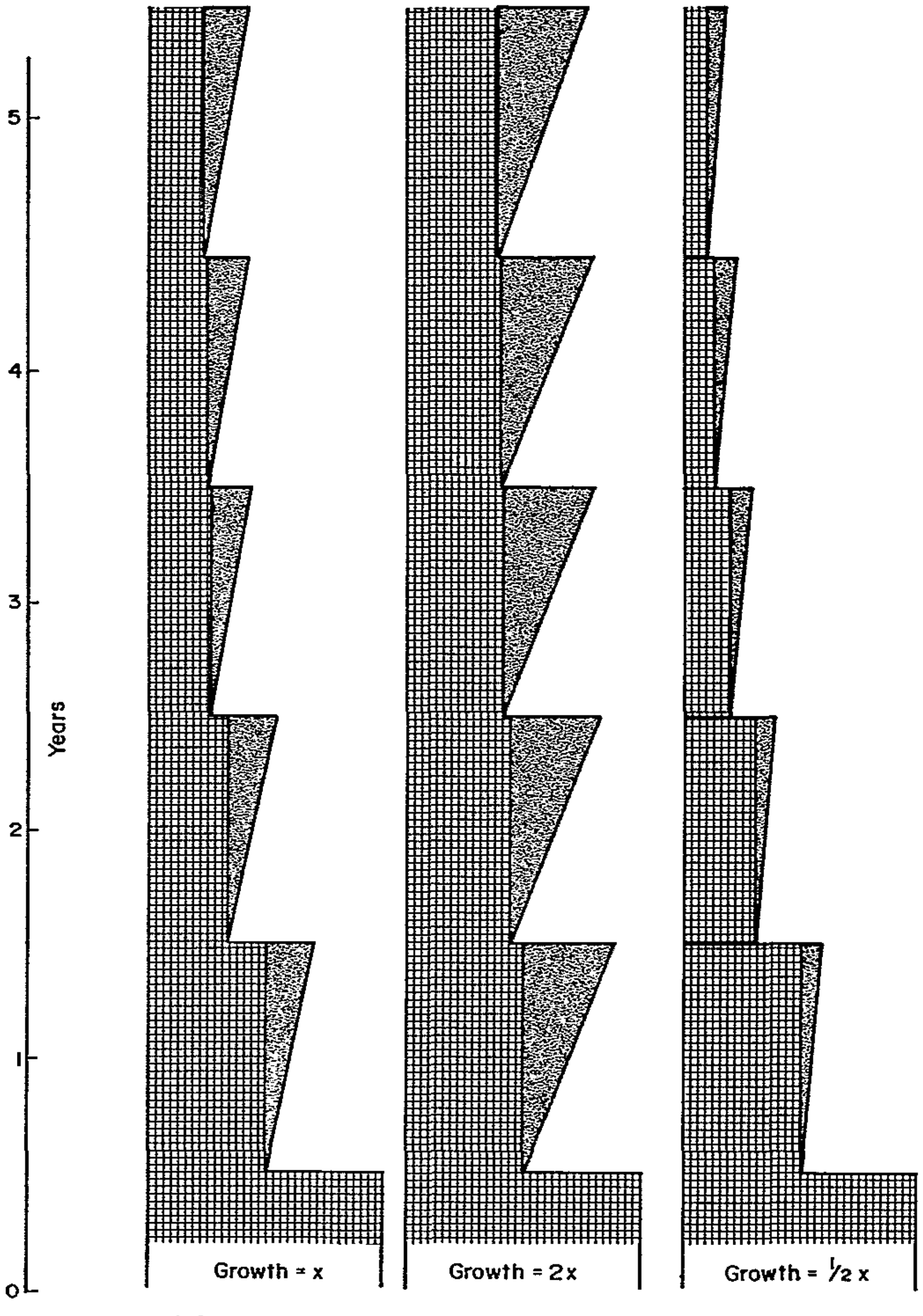


FIGURE 9.1 A model of exploitation of a 'green' at 50% annual removal after four years growth. Annual growth (shaded) of the plant is assumed to be constant, and not affected by plant size, nutrient removal or pruning effects. In the model the plant biomass will stabilize at twice the growth increment, fluctuating annually by one half the maximum biomass. Should annual growth be affected by plant size or if plants are not able to grow from stems due to pruning methods utilized, then stabilization may not occur, and the species may be exterminated before the following fire cycle.

Pests

The current trend in the wildflower trade is to produce 'quality flowers' (ie large blooms, free of blemishes and scars) which can compete with the high standards achieved by *Protea* growers in other countries. This can only be done by growing selected cultivars on a large scale (Brits, Protea farmers day 1986). Blooms from natural areas are often smaller than those obtained from commercial plantations, but in both cases blooms may be commercially reduced in value by the presence and action of natural pollinators.

Certain insect pollinators are regarded as 'pests' by the cutflower industry, since the export market demands insect-free produce. 'Their (the insects) mere presence in exported flowers is unacceptable' (Coetzee and Latsky 1986). The genus *Protea* has a particular problem in this regard, as it has large numbers of beetles and mites in its inflorescences, many of which are probably pollen vectors (Gess 1968; Annecke and Moran 1982; Coetzee and Giliomee 1985; Coetzee 1986; Coetzee et al 1986). Insect control in natural areas is impractical, but insect levels in cultivated plantations can be controlled to a certain extent. However, levels of insect infestation in commercial plantations appear to be inversely related to their distance from natural vegetation, and few plantations approach the insect-free flowers demanded by importers (J Coetzee personal communication).

Unconfirmed reports of the shooting of Cape sugarbirds *Promerops cafer*, because of damage to *Protea* and *Leucospermum* inflorescences, require investigation. In a casual survey at the 1986 Protea Farmers day meeting eight out of the 10 farmers approached considered *P cafer* a problem in cultivated plantations. Six farmers volunteered an easier more effective approach than shooting to solving the sugarbird problem: staking poisoned *Protea* inflorescences as prominent perches in plantations. There are no known recorded instances of such poisonings, and the effects of such treatments on insects and other nectar-feeding birds are unknown.

The Cape sugarbird is mainly a problem in *Leucospermum* and *Protea* plantations where it breaks the florets and scars the involucral bracts. The problem is more acute in those *Protea* species (*grandiceps*, and potentially *stokoei*, *speciosa*, *coronata*) where sugarbirds perch on the involucral bracts in preference to the florets, but some damage is caused to young inflorescences (eg *compacta*) as well. In addition, taller bushes are visited at a higher frequency and suffer more damage. As a rule, however, damage by birds is confined to older inflorescences, whereas newly opened inflorescences are preferred by the trade.

Leucospermum cultivars prone to sugarbird damage can be picked just before the first florets open, and thus before nectar flow and bird visits commence. Bird and insect damage to *Protea grandiceps* can be eliminated by enclosing buds in stockings or plastic-mesh bags. This is feasible in *Protea grandiceps* because 'quality' flower production requires that competing buds be pruned from adjacent young inflorescences. However, enclosing the young inflorescences is considered labour intensive and expensive.

Other solutions to the insect and bird problems of the wild flower trade need to be sought. Methods applicable in plantations may be totally unacceptable in natural areas.

Conclusions

While some research on insect and bird pollination in fynbos plants has been undertaken, little is known about the resilience of plant populations to commercial picking, and currently there are no projects investigating this aspect. The optimal and maximum levels of utilization which may still ensure sufficient pollination and seed set to maintain plant populations are not known for any plant species. The possible application of these levels of utilization is complicated by the unpredictable occurrence of fires, which may prevent the planning of a period of nonpicking for a few years prior to burning. There are currently no established techniques to allow owners to gauge the extent of veld utilization, despite the urgent need to monitor utilization.

The South African Protea Producers and Exporters Association (SAPPEX) has as one of its aims 'to uphold the cause of nature conservation, where applicable, and especially in connection with optimal utilization of floral veld as a sustained natural resource' (Middelmann 1984a). Hopefully, SAPPEX will contribute (eg by providing funds or staff) to the research needed to understand exploitation levels, and to investigate legal avenues of curtailing illegal picking. Since certain members of SAPPEX are alleged to have been involved with illegal picking from time to time (Greig 1984; Middelmann 1984b), it will be interesting to observe what progress can be made by the association to develop and enforce a "wildflower-picking ethic".

FIRE REGIME

Fire is recognized as the major disturbance influencing plants and animals in fynbos and renosterveld vegetation types of the fynbos biome. However, the effect of fire on the life cycle of pollinators is largely unknown.

Succession

Most reseeding fynbos plants do not flower for three to eight years following a fire. While this has been interpreted as an adaptation to a nutrient-poor environment (with plants building up nutrient reserves before seeding), it may be equally well related to the low fire risk due to the low fuel loads present in early seral stages, or may serve to reduce levels of seed- and flower-parasite infestation and predation through consecutive fire cycles. This absence of flowers of many plant species from early seral stages must be paralleled by either a lack of adult insect pollen vectors, or a shift in foraging preferences to those plants which flower in the early seral stages (geophytes, early seral Asteraceae and Fabaceae). While some data are available for seral phenology of certain plant species, little data exist on the seral biology of insect species or their foraging preferences.

Whereas most fynbos plant families include resprouting species, these are probably unable to maintain the pollinator biomass of mature vegetation in situ. Following a fire, most nectarivorous birds leave the burn area, while a few return to forage on the resprouting species. A succession of nectarivorous bird species appears to occur with Nectarinia famosa predominant in the immediate postfire environment, when geophytes and resprouters are dominant. This is followed by *N violacea* and *Promerops cafer* when *Erica* and *Protea* species begin flowering respectively. However, no data on the biology of anthophilous insect or mammal pollinators exist with regard to the effects of fire on population dynamics and movement. Thus the blooming of many putatively rodent pollinated *Protea* species (eg *acaulos*, *angustata*, *restionifolia* and *scabra* in the Hangklip area) is incongruent with the suspected behaviour of rodents in the early seral post-fire environment. These species bloom most profusely in the first three to four years following a fire, and produce relatively fewer flowers in older veld. Rodent abundance is correlated with density of plant cover, apparently because predation is high where cover is scarce (Breytenbach and Rebelo this volume). These species, therefore, flower during the period when rodent populations can be expected to be at their lowest. Birds visit these proteas extensively, and rodent runs lead directly to inflorescences in older veld. In contrast, other rodent pollinated Protea species (eg *amplexicaulis*, *humiflora* and *subulifolia*), which only begin flowering four to five years following the fire, appear to be more exclusively rodent pollinated (Breytenbach and Rebelo this volume).

In marked contrast are those species which bloom only in the post-fire environment, including many Orchidaceae and other geophytes. Many of these appear to have highly specialized pollination syndromes. While most have alternative means of regeneration, their pollinators must survive in mature vegetation. It is conceivable that some insect species may have diapausal larvae or pupae surviving the periods between fires. However, no examples are known and this survival strategy seems unlikely.

Since flower production of early seral plant species may be largely confined to a period of a year or two after fires, pollination may be effected only once every fire cycle (five to forty years). Neither the pollinators of most of these species, nor their natural flowering densities in mature vegetation are known. Research is urgently required to determine what effects long fire cycles have on the population dynamics (including seed banks and other dormant stages) of early seral plants and animals.

Burning regime

While historical management of fynbos has oscillated between complete protection (1920 to 1970) and management based on the effects of burning on prominent plant species (eg *Orothamnus zeyheri* (Boucher 1981), *Staavia dodii* (Moll and Gubb 1981) and *Serruria florida*) nothing is known about the effects of burning regime on the associated (anthophilous) fauna. However, the effects of management have probably not had as dramatic an affect on insects as on plants for the following reasons:

- Insects, unlike plants, are relatively mobile and can readily restock depleted areas by emigrating from neighbouring areas.

- Firebreaks have provided refugia and may perhaps have increased the population sizes of insect species relying on postfire environments.

- Insect species adapted to plants with long maturation periods before flowering would probably survive short fire cycles if their food plants survived.

Where food plants survive only as seeds for one fire cycle, survival of their dependent insect species may depend on the factors influencing larval survival. Similarly, insect species with a long larval life may be adversely affected if the interfire interval is too short to allow maturation to egglaying adults. For example, the role of dead wood in senescent vegetation or unburned stems in the immediate postfire seral stages as nesting sites for solitary bees is unknown, nor is there any data on the effect of season of burn or fire intensity on insect populations in postfire vegetation.

Paradoxically, the same management practices which allow seed predators to maintain high biomass at the expense of seed reserves, will probably favour anthophilous insect species. In addition the motility and resilience of insects probably ensures that very few insect species have been extinguished by current or past management practices, except where populations of larval food plants have decreased extensively.

The patterns of possible insect recolonization differ substantially in the complex mountain islands of the south-western Cape and the isolated, linear mountain chains in the southern Cape (Figure 9.2). To date, very little research has been undertaken on the effects of size of burn on recolonization and regeneration of vegetation in the Cape flora. While this has implications for early seral pollinators, which might possibly be outcompeted by species with less efficient dispersal abilities, its main implications occur in other fields:

- How far are wind dispersed seeds transported into burned areas?
- How far do birds and mammals move into burned areas to forage on seeds and seedlings?
- At what rate do seed parasites infest burned areas?
- Do small compartments for burning increase the local herbivore biomass by providing easily accessible young veld for long time periods?

These influences, although not directly related to pollination biology, might affect pollination through their effects on population sizes, flower production and pollinator colonization.

Despite insect resilience, data on the life histories of anthophilous insects are required if sound management of viable ecosystems is intended. This might be especially critical for some rare plants (eg *Erica jasminiflora* and *Erica junonia*, and many Orchidaceae) which are apparently pollinated by highly adapted insects which may, in turn, rely extensively on these plant species for their survival. This will be more important in those ecosystems which have been reduced to islands (eg Renosterveld and Elim Fynbos) than those which still consist of large tracts of natural veld. In the future, viability of nature reserves may depend on the ability of pollinators to move between different vegetation types and reserves within the Cape floral region.

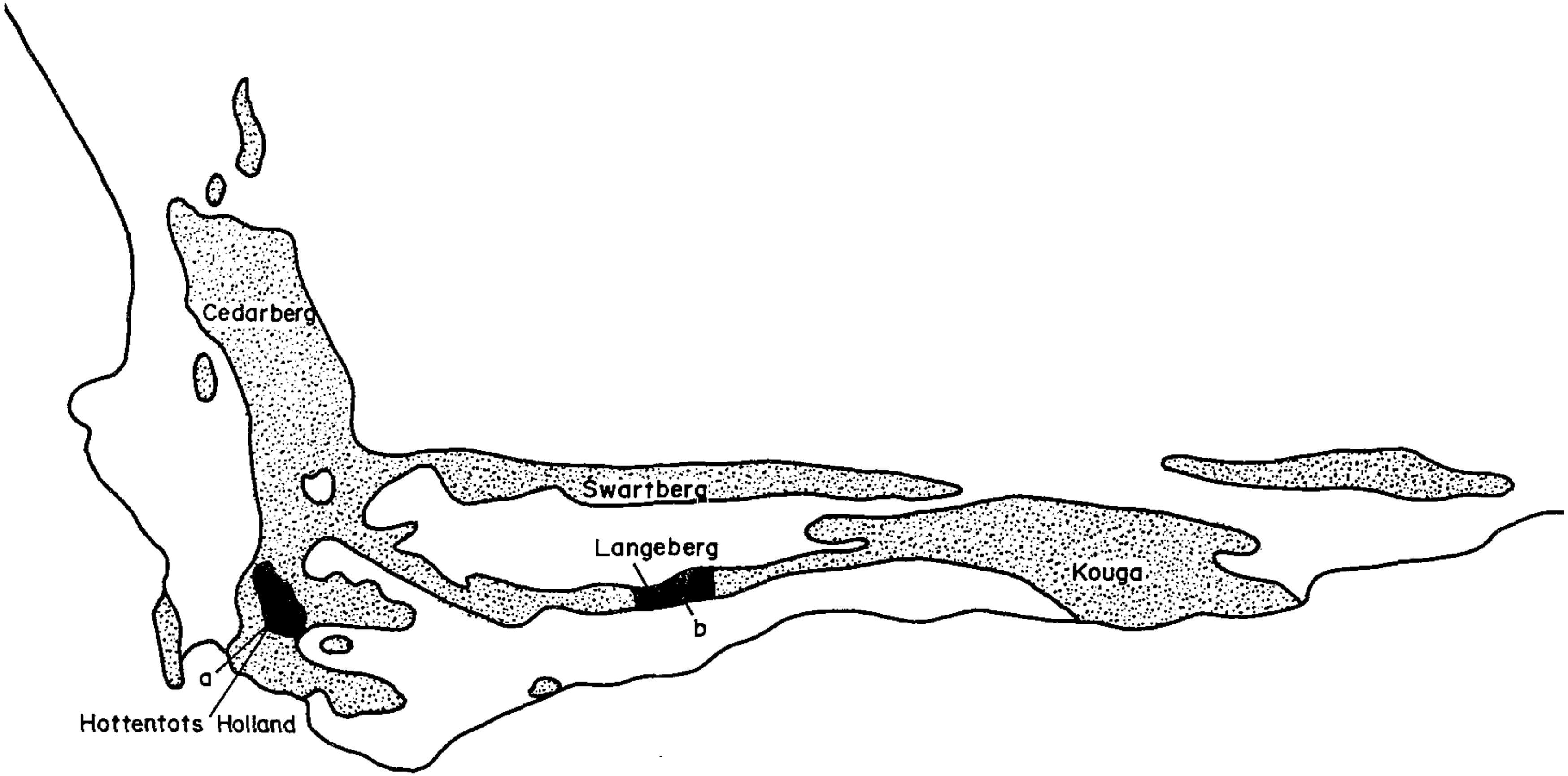


FIGURE 9.2 Recolonization of burned areas by pollinators. The south-western Cape with its island topography (a) would allow survival of entire islands, which would allow colonization of burned areas from relatively nearby. By contrast, the linear mountain chains of the Langeberg (b) and Swartberg Mountain ranges do not allow as ready colonization from similar habitats. The specificity of pollinators to vegetation communities will also determine the rate of recolonization.

Conclusions

There are currently no data on fire regime, frequency, season, intensity, or spatial configuration as concerns pollination biology, to suggest possible options available to reserve managers. Since the insect fauna may probably be more resilient to changes in fire regime than many plant species, management practices should, for the present, be based on what data there are for the effects of fire on plant demography.

Spatial configuration of burning compartments, and the effect of size of compartments, may play an important role in determining colonization rate of pollinators (and seed predators and parasites, herbivores and plants). The effect of size and spatial configuration of fires on regeneration and colonization is currently the least understood aspect of fire ecology.

Research is perhaps most urgently needed on the pollination, breeding systems and demography of exclusively early seral plant species, while the patterns of seral phenology of both plants and their pollinators are also required for sound ecosystem management. Data on the effects of season of burn, fire intensity, fire area, and time of day of burning are most conspicuously wanting.

ALIENS

Alien plants

Alien plants could affect pollination of plants in several ways:

- They might reduce the number of pollinator visits to indigenous plants by competing for pollinators.

- The effective pollen load carried by pollinators which is accessible to the stigmatic surfaces of indigenous plants might be reduced when pollinators are covered with alien pollen.

- Alien plants may reduce the population size of indigenous plant populations so that oligolectic pollinator populations might decrease, thereby reducing pollination of indigenous plants at critical seasonal or annual stages.

- They may increase the effective distance between indigenous plants so that the energy costs of nectar/pollen exploitation might increase to beyond the break-even level of reward/expense.

- They may also conceal, shade and camouflage indigenous plants, possibly increasing the time spent by pollinators in finding flowers.

There are no data on the effects of aliens on pollination of indigenous plants in the Cape flora. The pollinators utilizing alien plants, and their abundances, in uninvaded vegetation have also not been determined. It is also not known what effects shading or concealing indigenous plants by taller alien plants have on flower and seed production or pollinator visitation.

Alien animals

Alien invertebrates could disrupt pollination systems in several ways (Howarth 1985):

- They might change the pattern of outcrossing among plant species, leading to a possible reduction in seed viability or an increase in hybridization.
- Alien invertebrates may rob plants or nectar, reducing the chances for pollination by legitimate visitors.
- Alien invertebrates might compete with indigenous pollinators for nectar resources, leading to a decrease of native species.
- Alien invertebrates might reduce (to extinction) the population levels of pollinators, leading to the decrease of coevolved plant species dependent on them.

In Hawaii, it is postulated that the high incidence of hybrid swarms present among native floral groups is the result of the introduction of Apis mellifera, a catholic forager (Howarth 1985). By contrast, in New Zealand, A mellifera forages predominantly on introduced plants (Donovan 1980). On both these islands, indigenous bees are exclusively solitary, and the plant species, not having evolved with colonial bees, are either disrupted or ignored by social bees.

Competition between indigenous and alien pollinators is difficult to assess, and few direct studies have been undertaken, primarily since the original population densities of the animals involved are not known. An alarming decrease in abundance of Drosophila and Lepidoptera occurred in Hawaii between 1977 and 1983, corresponding to a population increase of Vespula pensylvanica following its introduction (Howarth 1985).

Alien invertebrates can be important pollinators of alien plants, including weeds. Fig trees have escaped from cultivation in Hawaii, which would not have occurred had their pollinators, fig wasps, not been introduced (Howarth 1985). In South Africa, Drosophila flavohirta has colonized Eucalyptis grandis flowers in which it breeds, the larvae living off nectar. This has resulted in a reduced and unpredictable honey crop from this species, since honeybees avoid fly-infested flowers (Herrmann 1984).

No catalogue of introduced insects is available for the Cape floral region, nor are there any records of alien invertebrate species affecting pollination of indigenous plants for the Cape flora. Only two introduced insect species probably have a major effect on pollination biology in the Cape flora: Vespula germanica and Iridomyrmex humulis.

The European Wasp Vespula germanica apparently arrived in Cape Town during 1970 via nests built on freight containers. Unconfirmed reports suggest that it has recently expanded its range from the Peninsula into the Hottentots Holland area, and can therefore be envisaged as potentially spreading its range throughout the south-western Cape. It can be expected to compete directly with many indigenous wasps for floral nectar, but will probably pollinate most of the 'wasp pollinated' plant species. However, with its strong biting jaws *V germanica* is an accomplished nectar thief, and it remains to be established whether fynbos plant species are preadapted to withstand the effects of such an efficient nectar robber.

Vespula germanica is a social wasp which builds a subterranean paper-nest. Although annual in Europe, in milder climates colonies may persist throughout the year (Whitehead and Prins 1975; Cooke 1984). Colony sizes are largest in autumn, when foraging for proteins and nectar is most avid. The larvae are fed proteinaceous food consisting largely of larval insects but including adult insects as well. In New Zealand *V germanica* raids and exterminates weak bee hives (Line 1965), but there is no literature on its effects on nonsocial bees.

The Argentinian Ant *Iridomyrmex humilis* was probably introduced to South Africa during the Anglo Boer War (Arnold 1926), and has since spread to urban and agricultural areas throughout the southern and western Cape (De Kock 1985). *Iridomyrmex humilis* disperses by establishing minor nests near food sites, as both reproductives and workers may trail to food sources; nuptial flights do not occur, as in most other ant species (Smith 1936). The major impact of *I humilis* in the Cape flora is the displacement of seed-dispersing ants, with a resultant increase in predation of seeds of myrmecochorous plant species, which, it is hypothesized, could change the composition and structure of invaded plant communities (Bond and Slingsby 1984) and, therefore, potentially their pollination biology.

Iridomyrmex humulis is a frequent visitor to the flowers of many plant species in the areas in which it occurs. Most local indigenous plants have, however, coevolved with nectar-thieving ants and have probably evolved effective protection for their nectar resources. However, *I humulis* may prey on the nests of some indigenous pollinators, as it is a major pest to the local bee industry, causing bees to desert (Anderson et al 1983). In Hawaii, nests of the ground-nesting bee *Nesoprosopis*, one of the more important pollen vectors on the island, were found to be absent from areas invaded by *I humulis* (Loope et al 1986). Paton (1986) found significantly fewer insect visitors in *Protea eximea* inflorescences when these contained *I humilis*.

Conclusions

While alien plants are notable in their visual impact during colonization, alien animal invasions pass relatively unnoticed. Similarly, indigenous vegetation threatened by alien plants has been better studied than its associated anthophilous fauna: the effects of alien insects on indigenous plant populations are currently almost completely unknown.

The first step in assessing changes that might occur in vegetation invaded by aliens is the study of interactions between plants and animals in pristine communities. Without this data, which relies heavily on the level of taxonomical understanding of the groups concerned, it will be impossible to predict what effects alien invaders may have on the pollination of plants in an area. These data are essential if the characteristics of species which may comprise a future potential threat to natural pollination systems are to be identified. Unless steps are undertaken to prevent the introduction of potentially deleterious alien insects, their control, once naturalized, may come too late for restoring natural pollination systems.

HERBIVORY IN CONSERVATION AREAS

The effects of herbivory on flower production

Many herbivores may prevent flowering, either by grazing or browsing the flower buds and flowers or by lowering plant production below the threshold of reproduction. In this regard herbivory resembles flower picking. Grazing levels in nature reserves, under pressure to display large ungulates for attracting tourists, may often far exceed that sustainable under natural conditions.

Preliminary data from the Cape of Good Hope Nature Reserve reveal that 70% of food items in the diet of ostriches (*Struthio camelus*) consists of flowers of 121 plant species, of which the Asteraceae comprise 28% (G H Bradley unpublished). Similarly, flowers comprise 24%, 14% and 35% of recorded food items eaten by Grey Rhebok *Pelea capreolus*, Grysbok *Raphicerus melanotis* and Steenbok *R campestris*, respectively (D Clarke unpublished). However, flowers and new shoots are often very important in terms of frequency of exploitation. In reserves which are overstocked with ungulates the effects of grazing on flowering may be fairly serious. This is aggravated on firebreaks and recent burns, where animals may concentrate at much higher levels than in older vegetation. Fire related overgrazing and erosion has, for instance, been recorded for the alien Himalayan Tahr *Hemitragus jemlahicus* on Table Mountain (Smithers 1983). This overutilization may be critical in rare species: for example, in *Protea odorata*, an endangered species (Hall and Veldhuis 1985), cattle were found to be significant consumers of inflorescence buds, reducing flowering from 10,5 inflorescences per plant to 4,8 (R N Cunliffe and A G Rebelo unpublished).

With the destruction of larger mammalian and avian predators in and adjacent to urban and agricultural areas, some indigenous herbivores appear to be increasing in numbers. For instance, during four years of monitoring five populations (totalling over 300 plants) of *Satyrium odorum* in the Kleinmond Nature Reserve, grazing by Rock Hyraxes (*Procavia capensis*) resulted in a total of only five inflorescences being produced (all in a single year) (Rebelo in press).

Effects of herbivores on pollinator populations

Hoof action of ungulates may damage topsoil and plants. Trampling by sheep may destroy the nests and nesting habitat of solitary bees, as has been recorded in the United States (Sugden 1985). No similar data are available for the Cape floral region, although stocking rates of ungulates may be high. The effects may perhaps be more deleterious under sandy conditions of the Sand Plain Fynbos, than in the more clayey soils of the karoo and renosterveld.

Possible similar effects may be imposed on nesting bees by the removal of dead wood for fuel. Until more studies are undertaken on pollinator life cycles, it will not be possible to predict potential threats to pollinator abundance.

Conclusions

Herbivores should be maintained below carrying capacity if plant production, pollination and seed set are to be maintained in nature reserves. Population control of herbivores must be undertaken to ensure that the carrying capacity of the vegetation is not exceeded. This applies equally to small herbivores, such as Procavia capensis, and larger herbivorous mammals and birds.

Localized overgrazing should be minimized, especially in habitats containing rare plant species. Localized overgrazing may occur near watering points or salt licks, which should be located well away from areas containing rare plant species. Localized overgrazing also frequently occurs in areas of relatively young veld, such as firebreaks and recent burns (R Prys-Jones and D Clark personal communication) in which the carrying capacity might be exceeded for several consecutive years, although the average carrying capacity for the reserve may be well within limits. In this regard the size of fire compartments may play an important role in influencing the grazing levels present in reserves. Fire compartments should be large enough to ensure that the area burned regenerates normally, despite animals foraging preferentially in it.

In Mountain, Sand Plain and Limestone Fynbos, which probably did not support large resident herbivore populations, special care must be taken to ensure that pollination and seed set take place before the following fire, since, in contrast to grasslands and savannas, many plant species are unable to regenerate by means other than seeds. In these habitats, where herbivores may often be found only in burned areas, research is needed to ascertain whether carrying capacity should be adjusted to the average fire compartment size.

BEE INDUSTRY

The extent of the bee industry

The local bee industry is expanding. This is partly due to the increase in deciduous fruit orchard plantations, but mainly due to the recognition of the need for cross pollination in modern fruit production. Although no survey of the extent of the industry in the south-western Cape has been undertaken, it is estimated that 12 000 hives currently exist in the south-western Cape, whilst the 1985 demand for pollination of deciduous orchards was estimated at 52 000 hives (R H Anderson personal communication). The current value of the industry, including the increased yield of bee pollinated orchards, honey production and amateur bee keepers, can be conservatively estimated at R50 million annually. In 1979, revenue received from honeybee pollinated crops in South Africa exceeded R334 million (Anderson et al 1983).

In winter large quantities of hived colonies, which are required for the short spring pollination period, must be maintained in prime condition for the following pollination season. Because honey production is an integral part of the industry a substantial proportion of the hives' reserves may be removed, principally in spring and summer. Consequently, in order to maintain the hives, bee colonies either have to be fed, or else must be located where abundant winter flowers can supply nectar to the hives.

Since, artificial feeding of honeybees is not economic, due to the high cost of cane sugar, bees are overwintered, either in *Eucalyptus* plantations or in natural veld where nectariferous plants are available. The favoured indigenous plants include *Acacia* species (pollen and nectar), *Aloe* species (pollen, occasionally nectar), *Euclea* species (nectar, pollen from male flowers, female flowers are often not visited), *Scutia* species and many Mesembryanthemaceae species (Anderson et al 1983). However, flower production and nectar secretion is influenced by temperature, rainfall and fire, and is often not a predictable resource. For instance, rain dilutes *Protea* nectar. In addition, contamination and tainting of honey with pollen from other species may reduce the value of the honey crop produced by bees in natural veld: *Brabejum* honey is bitter and unpalatable, *Euphorbia* honey causes intense irritation of the throat and nose, *Helichrysum* honey may be bitter and very dark, *Senecio* honey may vary from an unpleasant odour to a sour taste.

In the past hives were occasionally overwintered in Mountain Fynbos (*Arctotheca*, *Aspalathus*, *Blaeria*, *Erica*, *Grubbia*, *Protea*), karoo shrublands (*Acacia*, *Aloe*, *Drosanthemum*, *Lampranthus*, *Malephora*, *Melianthus*, *Mesembryanthemum*, *Portulacaria*, *Psilocaulon*, *Rhus*), forests and strandveld (*Asparagus*, *Diospyros*, *Pterocarpus*), or more usually on forestry land amidst *Eucalyptus* plantations. The Department of Environment and Water Affairs is currently removing plantations for the re-establishment of fynbos, as well as discouraging the placement of hives on State land. Hives have to be overwintered elsewhere. Consequently, beekeepers are using private land abutting natural vegetation to overwinter their hived bees.

The effect on natural pollination systems

Apis mellifera capensis occurs naturally in the south-western Cape, but is limited in distribution and population size by the availability of suitable nest sites (hollow tree trunks, small caves, etc) and access to water. Because of the lack of suitable nesting sites for social bees in Mountain Fynbos, solitary bees might possibly be more important as pollinators under natural conditions than *A mellifera*.

By swamping the ecosystem with an unnaturally high biomass of *A mellifera* in hives, available nectar resources in natural vegetation might be heavily reduced. At high densities *A mellifera* may even forage extensively on bird pollinated flowers (eg *Leucospermum oleifolium*, *L conocarpodendron*, *L cuneiforme*, *L cordifolium*, *L tottum*, *Protea repens*, *P eximea*, *P nitida* and *E perspicua*) as occurred at Kirstenbosch when hives were introduced into the area. These species were seldom visited by bees before hives were introduced (A G Rebelo personal observation). Since the majority of plants visited by *A mellifera* are probably also pollinated, plants with a diverse pollination spectrum are probably not adversely affected by the high bee density, and may even benefit. However, those plant species adapted for specific pollinators, may be adversely affected for several reasons:

- *Apis mellifera* bees may thieve nectar and not pollinate the flowers of the plants, thus reducing the energy reward to legitimate pollinators.

- *Apis mellifera* may utilize pollen, thereby reducing potential gamete availability for pollination in plant species which rely on otherwise infrequent effective pollinator visitation.

- By stealing nectar from oligophilic plant species and exploiting polyphilic plant species, *A mellifera* may reduce the populations of solitary bees, specialized anthophilous flies, or even lepidopterans, to below the levels required for efficient propagation of oligophilic or monophilic plant species.

- *Apis mellifera* may change the pattern of outcrossing among plant species, leading to a possible reduction in seed viability or an increase in hybridization.

Research into natural population levels and fluctuations of indigenous pollinators should be urgently undertaken, before the overwintering of honeybees in natural vegetation is initiated on a large scale. Because bees may regularly forage for up to 4 000 m from the hives, the effects of overwintering hives may extend well into seemingly natural stands of vegetation. The large number of bees overwintered adjacent to nature reserves (eg Kogelberg State Forest - see photograph South African Bee Journal 58, 112) is a cause for concern.

However, the increase in *A mellifera* hives overwintered in natural vegetation may primarily have affected natural populations of *A mellifera*, and the effects on other anthophilous insect species may not be as severe as postulated above. What then is the impact of the reduced natural *A mellifera* populations on the pollination of plant species flowering during spring and summer, when hives have been removed to the fruit orchards? Without baseline data on natural pollinator population dynamics, it is impossible to predict the effects of introducing hived bees into an area.

Problems with overwintering hived bees

Several problems associated with the overwintering of bees affect both the management of the area concerned and the bee industry:

- Adequate access roads are required as hives are transported in bulk on lorries in order to keep down costs.

- The area must be secluded and out of the public eye in order to prevent vandalism or danger to the public.

- Vandals robbing hives usually use smoke in the process, and may increase the fire risk to the surrounding veld.

- Overwintering areas must be protected from fire, and hives may be located in borrow pits, or on firebreaks for this purpose.

- The area should be free of the Argentinian Ant (*Iridomyrmex humilis*) which may cause absconding.

Conclusions

Research is needed to identify the plant species which are visited by A mellifera in fynbos. More importantly, the abundance of indigenous bees and insect pollinators in different vegetation associations needs to be assessed. For the adequate conservation and maintenance of indigenous communities data are required on a maximum stocking level of A mellifera so as to minimally influence the standing biomass of indigenous solitary bee and anthophilous fly populations. On a more academic and evolutionary level, the effect of A mellifera on the quality of seed produced relative to those produced by other indigenous pollinators needs to be studied. The feasibility of alternative strategies for the overwintering of A mellifera, such as the possibility of replacing pines as windbreaks in fruit orchards with winter flowering nectariferous plant species or the planting of Eucalyptus groves (as a dual function crop in woodlots and parks) requires evaluation. In addition, there is a shortage of legume pastures in the south-western Cape, which would provide nectar and pollen during winter and reduce the need to overwinter bees in natural areas.

REFERENCES

Anderson R H, Buys B and Johannesmeier M F 1983. Beekeeping in South Africa. Department of Agricultural Technical Services Bulletin 394.

Annecke D P and Moran V C 1982. Insects and mites of cultivated plants in South Africa. Butterworths, Durban.

Arnold G 1926. A monograph of the formicidae of South Africa. Annals of the South African Museum 14, 144-145.

Bond W and Slingsby P 1984. Collapse of an ant plant mutualism: The Argentine ant (Iridomyrmex humilis) and myrmecochorous Proteaceae. Ecology 65, 1031-1037.

Boucher C 1981. Autecological and population studies of Orothamnus zeyheri in the Cape of South Africa. In: Synge H (editor) The biological aspects of rare plant conservation. Wiley, Chichester. pp 343-353.

Brits G J, Jacobs G and Steenkamp J C 1986. Farming in South Africa. Flowers and ornamental shrubs. B 15. The pruning of proteas for cut flower production. Horticultural Research Institute, Pretoria.

Coetzee J H 1986. Insects - a hazard to the protea industry. Acta Horticulturae 185, 209-216.

Coetzee J H and Giliomee J H 1985. Insects in association with the inflorescence of Protea repens (L) (Proteaceae) and their role in pollination. Journal of the Entomological Society of southern Africa 48, 303-314.

Coetzee J H and Latsky L M 1986. Faunal list of Protea repens (L.) L. Acta Horticulturae 185, 241-246.

Coetzee J H, Rust D C J and Latsky L M 1986. Acari (mites) on proteas. Acta Horticulturae 185, 247-251.

Cooke M J 1984. The European Wasp - a new alien invader in South Africa. African Wildlife 38, 219.

Davies G 1984. Flowers from fynbos - the need for a policy of resource management for the wildflower industry. Veld and Flora 70, 116-118.

De Kock A E 1985. Verslag oor Fynbosbioom Projek: argentynse mier opname. Final report, CSIR, Pretoria.

Donovan B J 1980. Interactions between native and introduced bees in New Zealand. New Zealand Journalof Ecology 3, 104-116.

Gess F W 1968. Insects found on proteas. Journal of the Botanical Society of South Africa 28, 29-33.

Greig J C 1984. The law of the jungle. African Wildlife 38, 135-139.

Hall A V and Veldhuis H A 1985. South African Red Data Book: Plants - fynbos and karoo biomes. South African National Scientific Programmes Report No 117. CSIR, Pretoria. 144 pp.

Herrmann J M 1984. The *Drosophila* fly in *Eucalyptus* flowers - who holds the answers to this riddle? South African Bee Journal 56, 5-8.

Howarth F G 1985. Impacts of alien land arthropodsand mollusks on native plants and animals in Hawaii. In: Stone C P and Scott J M (editors) Hawaii's terrestrial ecosystems: preservation and management. University of Hawaii, Honululu. pp 377-402.

Jongens-Roberts S M and Mitchell D T 1986. The distribution of dry mass and phosphorus in an evergreen fynbos shrub species, *Leucospermum parile* (Salisb ex J Knight) Sweet (Proteaceae), at different stages of development. New Phytologist 103, 669-683.

Line S 1965. Preventing wasp raids on beehives. New Zealand Journal of Agriculture 110, 161.

Loope L L, Medeiros A C and Cole F R 1986. Effects of Argentine ants on the endemic biota of subalpine shrubland, Haleakala National Park, Hawaii. Paper delivered at the Conference on Science in the National Parks, held in Colorado 1986, and to be published in the proceedings.

Middelmann W J 1984a. The story of SAPPEX. Veld and Flora 70, 107-109.

Middelmann W J 1984B. *Protea holosericea* and the flower-picking industry. African Wildlife 38, 216-217.

Moll E J and Gubb A A 1981. Aspects of the ecology of *Staavia dodii* in the south western Cape of South Africa. In: Synge H (editor) The biological aspects of rare plant conservation. Wiley, Chichester. pp 343-353.

Moll E J, Campbell B M, Cowling R M, Bossi L, Jarman M L and Boucher C 1984. A description of major vegetation categories in and adjacent the fynbos biome. National Scientific Programmes Report No 83. CSIR, Pretoria. 29 pp.

Paton J 1986. The role that insects play in the pollination of *Protea neriifolia* and *Protea eximea* (Proteaceae). Unpublished Honours project, University of Cape Town, Cape Town.

Rebelo A G (in press). Bird feeding at *Satyrium odorum*. Sand. Flowers. Ostrich.

Rebelo A G and Holmes P M (in preparation). The commercial exploitation of *Brunia albiflora* (Bruniaceae) in South Africa.

Smith M R 1936. Distribution of the Argentinian ant in the United States and suggestions for its control or eradication. United States Department of Agriculture Circular 387.

Smithers R H N 1983. The mammals of the southern African subregion. University of Pretoria, Pretoria.

Sugden E A 1985. Pollinators of *Astragalus monoensis* Barmby (Fabaceae): New host records; potential impact of sheep grazing. Great Basin Naturalist 45, 299-312.

Van Wilgen B W and Lamb A J 1986. The flower picking industry in relation to mountain catchment management in the fynbos. Acta Horticulturae 185, 181-187.

Whitehead V B and Prins A J 1975. The European wasp, *Vespula germanica* (F.)., in the Cape Province, Journal of the Entomological Society of southern Africa 38, 39-47.

CHAPTER 10 BIBLIOGRAPHY OF POLLINATION BIOLOGY RELATING TO THE CAPE FLORA

A G Rebelo

Little research has been undertaken on pollination biology in the Cape flora to date. The size of this bibliography has been inflated greatly by the addition of reports of peripheral interest to pollination biology. Perhaps the most conspicuous element noticed in compiling the bibliography is the lack of contributions from amateur naturalists. The absence of a strong naturalist component in the region, and methods of rectifying this shortage, requires investigation. Perhaps this synthesis will stimulate some amateur involvement in pollination biology.

INTRODUCTION

In addition to reports dealing directly with research on pollination, this bibliography includes two categories of reports marginally related to pollination biology in the Cape flora:

- reports on pollination biology outside the Cape flora, on genera that are important in the Cape flora; and
- those concerning floral morphology, phenology, insect and bird behaviour, floras and taxonomical accounts, which although not dealing with pollination biology, provide valuable information for pollination biologists.

In both categories, only the most informative reports have been included in the bibliography. For example, whereas many modern taxonomical treatises deal with plant breeding systems, hybridization, and pollination (and are thus included), this trend is a recent one, and many other treatises lack even a reliable description of flowering phenology.

An analysis of the keyword index reveals the paucity of research undertaken in the Cape flora. Phenology and ornithology together form the subject of over half the entries in the bibliography, with floral morphology, entomophily (mainly bees), visitor behaviour, plant breeding systems and seed set comprising the next level of information available. Notable for their lack of entries are research in gene flow, incompatability, pollen viability and pollen movement; despite these issues comprising the core of research needed for the conservation and horticultural utilization of the very rich Cape flora.

Similarly the representation of reports on different families is not proportional to the species richness of these families. Included in the plant taxonomic index are all plant families in the Cape flora with either more than 10 genera or more than 50 species (genera and species are listed in parentheses after the family name in the keyword index, respectively). Table 10.1 reveals that of these families, 14 have no recorded entries. However, two poorly represented families (Moraceae and Strelitziaceae) have a much larger literature than expected. Overall coverage of the plant families suggests that research has been undertaken on the visually dominant component of the fynbos vegetation within the Cape flora (ie the Proteaceae, Orchidaceae, Ericaceae and Fabaceae). The lack of studies in the field of anemophily is reflected by the general absence of studies in the Cyperaceae, Poaceae and Restionaceae.

In addition the major research within pollination biology in the Cape flora appears to have been done by researchers residing outside South Africa, fewer than ten of whom have contributed a substantial proportion of the available literature on pollination biology for the region.

It appears that pollination studies in the Cape flora are only beginning to get underway. Despite the early natural history works of Marloth, amateur naturalists have not yet begun contributing to the literature on pollination biology. With the input of foreign expertise, the study of pollination biology in the Cape flora may expand to its rightful place as one of the cornerstones to our understanding of the high species richness of the region, thus enabling an improved conservation of the flora. Furthermore it should contribute to the horticultural appreciation and utilization of the flora, so stimulating research by both amateurs and professionals.

TABLE 10.1 The major plant families of the Cape flora, and the extent of their published literature in the bibliography

Number of genera	Family	Number of entries
107	Asteraceae	10
61	Mesembryanthemaceae	0
61	Poaceae	3
39	Iridaceae	14
38	Fabaceae	21
35	Scrophulariaceae	5
29	Asclepiadaceae	10
28	Orchidaceae	24
26	Cyperaceae	0
24	Apiaceae	0
22	Ericaceae	22
20	Hyacinthaceae	3
19	Restionaceae	0
16	Campanulaceae	3
15	Amaryllidaceae	3
15	Rubiaceae	0
14	Euphorbiaceae	1
14	Proteaceae	88
13	Aizoaceae	0
12	Acanthaceae	0
12	Asphodelaceae	16

Number of species	Family	Number of entries
986	Asteraceae	10
672	Ericaceae	22
660	Mesembryanthemaceae	0
644	Fabaceae	21
612	Iridaceae	14
320	Proteaceae	88
310	Restionaceae	0
310	Scrophulariaceae	5
259	Rutaceae	2
222	Campanulaceae	3
206	Orchidaceae	24
203	Cyperaceae	0
181	Poaceae	3
172	Asphodelaceae	16
154	Hyacinthaceae	3
139	Polygalaceae	0
136	Rhamnaceae	0
133	Geraniaceae	4
129	Oxalidaceae	5
125	Asclepiadeaceae	10
124	Crassulaceae	1
122	Thymeliaceae	2
114	Rosaceae	0
109	Aizoaceae	0
100	Apiaceae	0

1. Adamson E J 1960. Some aspects of seed fertility in the genus Protea. Unpublished second year project, Botany Department, University of Cape Town. PROTEACEAE, SEED SET

2. Adamson R J and Salter T N 1950. Flora of the Cape Peninsula. Juta, Cape Town. FLORA, PHENOLOGY

3. Anderson R H 1985. Pollination of apples and pears. Elgin Cooperative Fruitgrowers, Elgin. APICULTURE, APPLIED, BEHAVIOUR, ENTOMOPHILY: HYMENOPTERA, SEED SET

4. Anderson R H, Buys B and Johannsmeier M F 1983. Beekeeping in South Africa. Department of Agricultural Technical Services Bulletin 394. APICULTURE, APPLIED, BEHAVIOUR, BREEDING, ENTOMOPHILY: HYMENOPTERA, FORAGING ECOLOGY, PHENOLOGY,

5. Armstrong J A 1979. Biotic pollination mechanisms in the Australian flora: a review. New Zealand Journal of Botany 17, 467-508. ENTOMOPHILY, ORNITHOPHILY, REVIEW

6. Baijnath H and Ramcharun S 1983. Aspects of pollination and floral development in Ficus capensis Thunb. (Moraceae). Bothalia 14, 883-888. ANTHESIS, BEHAVIOUR, BREEDING SYSTEMS, ENTOMOPHILY: AGAONIDAE, MORACEAE, MORPHOLOGY

7. Baker H A and Oliver E G H 1967. Ericas in southern Africa. Purnell, Cape Town. ERICACEAE, PHENOLOGY

8. Baker H G 1973. Evolutionary relationships between flowering plants and animals in American and African tropical forests. In: Meggers B J, Ayensu E S and Duckworth C D (editors) Tropical forest ecosystems in Africa and South America: a comparative review. Smithsonian Institute Press, Washington DC. pp 145-149. ENTOMOPHILY, EVOLUTION, REVIEW

9. Baker I and Baker H G 1979. Chemical constituents of the nectars of two Erythrina species and their hybrid. Annals of the Missouri Botanic Gardens 66, 446-450. FABACEAE, NECTAR CONSTITUTION

10. Ball J B 1970. The pollination of aloes. The dusky and malachite sunbirds. Aloe 4, 18-19. ASPHODELACEAE, ORNITHOPHILY

11. Banks D J 1975. Activity, feeding and distribution of Promerops cafer in relation to habitat. Unpublished Zoology Honours Project, University of Cape Town. BEHAVIOUR, ORNITHOPHILY, PROTEACEAE

12. Bannister P 1978. Flowering and shoot extension in heath plants of different geographical origin. Journal of Ecology 66, 117-131. ERICACEAE, PHENOLOGY

13. Barber M E 1869. On the structure and fertilization of Liparis bowkeri. Journal of the Linnean Society of Botany 10, 455-458. MORPHOLOGY, ORCHIDACEAE, SEED SET

14. Bates D M 1969. Systematics of the South African genus Anisodontea Presl (Malvaceae). Gentes Herbarium 10, 215-383. ANTHESIS, BREEDING SYSTEM, MALVACEAE, SEED SET

15. Beattie A J 1974. Floral evolution in Viola. Annals of the Missouri Botanic Gardens 61, 781-793. BEHAVIOUR, ENTOMOPHILY, EVOLUTION, MORPHOLOGY, VIOLACEAE

16. Beattie A J 1976. Plant dispersion, pollination and gene flow in Viola. Oecologia 25, 291-300. BEHAVIOUR, BREEDING SYSTEMS, ENTOMOPHILY: HYMENOPTERA, ENTOMOPHILY: LEPIDOPTERA, GENE FLOW, PHENOLOGY, VIOLACEAE

17. Beattie A J 1978. Plant-animal interactions affecting gene flow in Viola. In: Richards A J (editor) The pollination of flowers by insects. Academic Press, London. pp 151-164 and 23 plates. BREEDING SYSTEMS, ENTOMOPHILY, GENE FLOW, POLLEN MOVEMENT, VIOLACEAE

18. Bigalke R C 1979. Aspects of vertebrate life in fynbos, South Africa. In: Specht R L (editor) Ecosystems of the world. Volume 9a. Heathlands and related shrublands: descriptive studies. Elsevier, Amsterdam. pp 81-95. ORNITHOPHILY

19. Blackwell W H and Powell M J 1981. A preliminary note on pollination in the Chenopodiaceae. Annals of the Missouri Botanic Gardens 68, 524-526. ANEMOPHILY, CHENOPODIACEAE, ENTOMOPHILY

20. Bolus H 1918. The orchids of the Cape Peninsula. 2nd edition, Darter Brothers and Company, Cape Town. FLORA, ORCHIDACEAE

21. Bond P and Goldblatt P 1984. Plants of the Cape Flora, a descriptive catalogue. Journal of South African Botany, Supplementary Volume 13. FLORA, PHENOLOGY

22. Bond W J 1980. Periodicity in fynbos of the non-seasonal rainfall belt. Journal of South African Botany 46, 343-354. PHENOLOGY

23. Bornmann C H 1972. *Welwitschia mirabilis*: paradox of the Namib desert. Endeavour 31, 95-98. GYMNOSPERMAE

24. Boucher C 1981. Autecological and population studies of *Orothamnus zeyheri* in the Cape of South Africa. In: Synge H (ed) The biological aspects of rare plant conservation. Wiley, Chichester. pp 343-353. DEMOGRAPHY, PHENOLOGY, PROTEACEAE, SEED SET

25. Bowers K A 1975. The pollination ecology of *Solanum rostratum* (Solanaceae). American Journal of Botany 62, 633-638. SOLANACEAE

26. Bradshaw A D 1959. Population differentiation in *Agrostis tenuis* Sibth. I. Morphological differentiation. New Phytologist 58, 208-227. GENE FLOW, BREEDING SYSTEMS

27. Brauns H 1926. A contribution to the knowledge of the genus *Allodape*, St. Farg & Serv. Order Hymenoptera: Section Apidae (Anthophiea). Annals of the South African Museum 23, 417-433. ENTOMOPHILY: HYMENOPTERA

28. Brederode J M (undated). The fauna of *Protea neriifolia* with relation to the Cape Sugarbird *Promerops cafer*. Unpublished Zoology II Project, University of Cape Town. ENTOMOPHILY: COLEOPTERA, ORNITHOPHILY, PROTEACEAE

29. Brits G J 1977. Manipulation of flowering time in *Leucospermum cordifolium* with ethephon. Agroplantae 9, 127-130. APPLIED, PHENOLOGY, PROTEACEAE

30. Brits G J 1980. The development of Proteaceae as commercial cut-flowers in South Africa: breeding. Department of Agriculture and Fisheries. Progress Report (A)T-Rp 149/5, 1979/80. APPLIED, BREEDING SYSTEMS, HYBRIDIZATION, PROTEACEAE

31. Brits G J 1980. The protea family: breeding studies on Proteaceae. Published Lecture Number 11. University of Cape Town extra-mural lecture course, October 1980. APPLIED, HYBRIDIZATION, PROTEACEAE

32. Brits G J 1986. Extension of harvesting period in *Leucospermum* by means of manual and chemical pruning methods. Acta Horticulturae 185, 237-240. APPLIED, PHENOLOGY, PROTEACEAE

33. Brits G J, Jacobs G and Steenkamp J C 1986. Farming in South Africa. Flowers and ornamental shrubs B 15. The pruning of proteas for cut flower production. Horticultural Research Institute, Pretoria. ANTHESIS, APPLIED, PHENOLOGY, PROTEACEAE

34. Brits G J, Jacobs G and Vogts M M 1983. Domestication of fynbos Proteaceae as a floricultural crop. Bothalia 14, 642-646. APPLIED, HYBRIDIZATION, PHENOLOGY, PROTEACEAE

35. Broekhuysen G J 1959. The biology of the Cape Sugarbird *Promerops cafer* (L.). Ostrich Supplement Number 3, 180-221. BEHAVIOUR, BREEDING

36. Broekhuysen G J 1963. The breeding biology of the orange-breasted sunbird *Anthobaphes violacea* (Linnaeus). Ostrich 34, 187-234. BEHAVIOUR, BREEDING, FORAGING ECOLOGY

37. Brunhuber B S 1964. An investigation into the mechanisms of orientation connected with feeding in the Protea Beetle *Trichostetha fascicularis* (Linn). Unpublished Zoology Honours Project, University of Cape Town. BEHAVIOUR, ENTOMOPHILY: COLEOPTERA, FORAGING ECOLOGY, PROTEACEAE

38. Burger A 1973. The chemical composition and abundance of nectar in *Protea repens* Linneaus from a selected habitat. Unpublished report, Zoology Department, University of Cape Town. NECTAR CONSTITUTION, NECTAR SECRETION, PROTEACEAE

39. Burger A E, Siegfried W R and Frost P G H 1976. Nest-site selection in the Cape sugarbird. Zoologica Africana 11, 127-158. BREEDING

40. Burl V 1967. Studies of the pollens of the south western Cape montane marsh floras. Unpublished 3rd Year Botany Project, University of Cape Town. PALYNOLOGY

41. Buys B 1975. A survey of honeybee pests in South Africa. Proceedings of the 1st Congress of the Entomological Society of South Africa. pp 185-189. APICULTURE, APPLIED

42. Buys B 1984. *Drosophila flavohita*, a minor nectar competitor with honeybees in the western Cape. South African Bee Journal 129. APPLIED, ENTOMOPHILY: DIPTERA

43. Callow R S and Parker J S 1979. Breeding behaviour and population differentiation in the hexaploid grass *Koeleria vallesians* (Honk.) Bentol. New Phytologist 83, 537-547. BREEDING SYSTEMS, POACEAE

44. Cantwell G E 1974. The African Brazilian bee problem. American Bee Journal 114, 368-372. ALIENS

45. Carolin R 1961. Pollination of the Proteaceae. Australian Museums Magazine 371-374. ANTHESIS, MORPHOLOGY, PROTEACEAE

46. Carr J D 1976. The South African acacias. Conservation Press, Johannesburg. FABACEAE, PHENOLOGY

47. Cheke R A 1971. Feeding ecology and significance of interspecific territoriality of African montane sunbirds (Nectariniidae). Revue de Zoologie et de BoTonique Africaines 84, 50-64. BREEDING, FORAGING ECOLOGY, NECTAR CONSTITUTION, ORNITHOPHILY

48. Claassens A T M and Dickson C G C 1974. The early stages of *Aloeides thyre* (L.) (Lep. Lycaenidae) with notes on ant associations, distribution and general ecology of the species. Entomologists Record and Journal of Variation 86, 253-258. ENTOMOPHILY: LEPIDOPTERA, LIFE CYCLES

49. Claassens A J M and Dickson C G C 1980. The butterflies of the Table Mountain Range. Struik, Cape Town. ENTOMOPHILY: LEPIDOPTERA, LIFE CYCLES

50. Clarke G C and Dickson C G C 1971. Life histories of the South African Lycaenid butterflies. Purnell, Cape Town. ENTOMOPHILY: LEPIDOPTERA, LIFE CYCLES

51. Clifford H T 1962. Insect pollinators of *Plantago lanceolata* L. Nature 193, 196. ENTOMOPHILY, PLANTAGINACEAE

52. Coetzee J H 1986. Insects a hazard to the Protea industry. Acta Horticulturae 185, 209-216. APPLIED, ENTOMOPHILY, PROTEACEAE

53. Coetzee J H and Giliomee J H 1985. Insects in association with the inflorescence of *Protea repens* (L.) (Proteaceae) and their role in pollination. Journal of the Entomological Society of South Africa 48, 303-314. ENTOMOPHILY: COLEOPTERA, ORNITHOPHILY, PROTEACEAE, SEED SET

54. Coetzee J H and Latsky L M 1986. Faunal list of *Protea repens* (L.) L. Acta Horticulturae 185, 241-246. ENTOMOPHILY, PROTEACEAE

55. Coetzee J H, Rust D C J and Latsky L M 1986. *Acari* (mites) on proteas. Acta Horticulturae 185, 247-251. ENTOMOPHILY: ACARINA, PROTEACEAE

56. Cohen C 1937. Some aspects of the reproduction of *Stoebe vulgaris* and certain local grass and weed seeds. South African Journal of Science 33, 351-354. ASTERACEAE, POACEAE

57. Collins B G 1983. Seasonal variations in the energetics of territorial Cape sugarbirds. Ostrich 54, 121-125. ENERGETICS, FORAGING ECOLOGY, NECTAR SECRETION, PROTEACEAE

58. Collins B G 1983. Pollination in *Mimetes hirtus* (Proteaceae) by Cape sugarbirds and orange-breasted sunbirds. Journal of South African Botany 49, 125-142. ANTHESIS, FORAGINGECOLOGY, NECTAR SECRETION, ORNITHOPHILY, POLLENMOVEMENT, POLLEN VIABILITY, PROTEACEAE, SEED SET

59. Collins B G 1983. A first approximation of the energetics of Cape sugarbirds (*Promerops cafer*) and orange-breasted sunbirds (*Nectarinia violacea*). South African Journal of Zoology 18, 363-369. BEHAVIOUR, ENERGETICS, ERICACEAE,FORAGING ECOLOGY, NECTAR SECRETION, PROTEACEAE

60. Collins B G 1984. Australian nectarivorous bird systems: do they differ from those in other countries. BEHAVIOUR, ENERGETICS, FORAGING ECOLOGY, ORNITHOPHILY

61. Collins B G and Rebelo A G (in press). Pollination biology in the Proteaceae of Australia and southern Africa. Australian Journal of Ecology. ANTHESIS, BEHAVIOUR, BREEDING SYSTEMS, ENERGETICS, ENTOMOPHILY, FORAGING ECOLOGY, MORPHOLOGY, MORPHOMETRICS, NECTAR CONSTITUTION, NECTAR SECRETION, ORNITHOPHILY, PHENOLOGY, PROTEACEAE, POLLEN MOVEMENT, POLLEN VIABILITY, REVIEW, SEED SET,THEROPHILY

62. Cooke M J 1984. The European Wasp - a new alien invader in South Africa. African Wildlife 38, 219. ALIENS

63. Corry T H 1884. On the structure and development of the gynostegium, and mode of fertilization in *Asclepias cornuti*. Transactions of the Linnean Society of London 2, 173-207. ANTHESIS, ASCLEPIADACEAE, MORPHOLOGY

64. Cottrell C B 1978. Aspects of the biogeography of southern African butterflies. Zambesia Supplement 1978. ENTOMOPHILY: LEPIDOPTERA, LIFE CYCLES

65. Cottrell C B 1985. The absence of coevolutionary associations with Capensis floral element plants in the larval/plant relationships of south western Cape butterflies. In: Vrba E S (editor) Species and speciation. Transvaal Museum Monograph 4, 115-124. ENTOMOPHILY: LEPIDOPTERA, LIFE CYCLES

66. Cowling R M 1978. Nectar composition and production in *Protea* L. Unpublished Botany Honours Thesis, University of Cape Town. ENERGY UTILIZATION, NECTAR CONSTITUTION, PROTEACEAE

67. Cowling R M and Lamont B 1986. Population ecology of Western Australian *Banksia* species: implications for the wildflower industry. Acta Horticulturae 185: 217-228. APPLIED, ENERGY UTILIZATION, PROTEACEAE

68. Cowling R M and Mitchell D T 1981. Sugar composition, total nitrogen and accumulation of C-14 assimilates in floral nectaries of *Protea* species. Journal of South African Botany 47, 743-750. ENERGY UTILIZATION, NECTAR CONSTITUTION, PROTEACEAE

69. Crepet W L 1984. Advanced (constant) insect pollination mechanisms: pattern of evolution and implications vis-a-vis angiosperm diversity. Annals of the Missouri Botanic Gardens 71, 601-630. ENTOMOPHILY, EVOLUTION, REVIEW

70. Dahlgren R 1968. Studies on Peneaceae. Part 2. The genera *Brachysiphon*, *Sonderothamnus* and *Saltera*. Opera Botanica 18. ORNITHOPHILY, PENEACEAE

71. Dahlgren R, Nielsen B J, Goldblatt P and Rourke J P 1979. Further notes on Retziaceae: its chemical contents and affinities. Annals of the Missouri Botanic Gardens 66, 545-556. MORPHOLOGY, ORNITHOPHILY, PALYNOLOGY, RETZIACEAE

72. Day J M, Siegfried W R, Louw G N and Jarman M L 1979. Fynbos ecology: a preliminary synthesis. South African National Scientific Programmes Report No 40. CSIR, Pretoria. 166 pp. REVIEW

73. De Meillon B and Wirth W W 1979. Subsaharan Ceratopoginidae (Diptera) IV. *Rhinohelea*, a new subgenus of Forcipomyia from the south west Cape Province, South Africa. Annals of the Natal Museum 23, 881-886. ERICACEAE, ENTOMOPHILY: DIPTERA

74. Delpiere G R and du Plessis N M 1973. The winter-growing gladioli of South Africa. Tafelburg, Cape Town. IRIDACEAE, PHENOLOGY,

75. Devlin B and Stephenson A G 1984. Factors that influence the duration of the staminate and pistillate phases of *Lobelia cardinalis* flowers. Botanical Gazette 145, 323-328. ANTHESIS, BREEDING SYSTEMS, CAMPANULACEAE, MORPHOLOGY, SEED SET

76. Devlin B and Stephenson A G 1985. Sex differential floral longevity, nectar secretion, and pollinator foraging in a protandrous species. American Journal of Botany 72, 303-310. ANTHESIS, BEHAVIOUR, BREEDING SYSTEMS, CAMPANULACEAE, MORPHOLOGY,NECTAR SECRETION

77. Dickson C G C and Kroon D M 1978. Pennington's butterflies of southern Africa. Donker, Johannesburg. ENTOMOPHILY: LEPIDOPTERA, LIFE CYCLES

78. Downing B H and Gibbs Russel G E 1981. Phytogeographic and biotic relationships of a savanna in southern Africa. Analysis of an Angiosperm check-list from Acacia woodland in Zululand. Journal of South African Botany 47, 721-725. ENTOMOPHILY, ORCHIDACEAE

79. Dulberger R 1981. The floral biology of *Cassia didymobotrya* and *C auriculata* (Caesalpiniaceae). American Journal of Botany 68, 1350-1360. FABACEAE

80. Dulberger R and Ornduff R 1980. Floral morphology and reproductive biology of four species of *Cyanella* (Tecophilaeaceae). New Phytologist 86, 45-54. MORPHOLOGY, TECOPHILAEACEAE

81. Du Preez H L H and Walters M C 1975. The influence of pollination by African honeybees (*Apis mellifera* adansonii) on large white kidney bean (*Phaseolus multiflorus*) production in the Transvaal highveld. Phytophylectica 7, 53-58. APPLIED, ENTOMOPHILY: HYMENOPTERA, FABACEAE, FORAGING ECOLOGY, SEED SET

82. Durand B J 1981. A study of the short-term responses of fire in the Kogelberg State Forest, South Africa. Unpublished MSc Thesis, University of Cape Town. PHENOLOGY

83. Duthie A V 1916. Note on apparent apogamy in *Pterygodium newdigatae*. Transactions of the Royal Society of southern Africa 5, 583-598. BREEDING SYSTEMS, ORCHIDACEAE

84. Ehrenberg C G 1829. De antheris et polline *Asclepiadearum*. Linnaea 4, 94-97. ASCLEPIADACEAE, PALYNOLOGY

85. Eisikowitch D and Nahari N 1982. The discrimination of *Malavaviscus arboreus* flowers by the sunbird, *Nectarinia osea*. Acta Botanica Neerlandica 31, 55-58. BEHAVIOUR, MALVACEAE, ORNITHOPHILY

86. Ellis W M 1973. The breeding system and variation in populations of *Poa annua* L. Evolution 27, 656-662. BREEDING SYSTEM, HYBRIDIZATION, INCOMPATIBILITY, POACEAE

87. Erickson V L, Armitage A, Carlson W H and Miranda R M 1980. The effect of cumulative phytosynthetically active radiation on the growth and flowering of the seeding Geranium, *Pelargonium X hortorum* Bailey. Horticultural Science 15, 815-817. ENERGY UTILIZATION, GERANIACEAE, PHENOLOGY

88. Evans M S 1894. The fertilization of flowers with some illustrations from the Natal flora. (Lecture), pp 26. Durban. FLORA

89. Evans M S 1895. The fertilization of *Loranthus kraussianus* and *L dregei*. Nature 51, 235-236. LORANTHACEAE, SEED SET

90. Faegri K 1965. Reflections on the development of pollination systems in African Proteaceae. Journal of South African Botany 31, 133-136. ENTOMOPHILY: COLEOPTERA, MORPHOLOGY, ORNITHOPHILY, PROTEACEAE

91. Falkenhagen E R 1986. Reliability of measurement of open pollinated progeny tests of *Pinus elliottii* in South Africa. South African Forestry Journal 136, 39-42. APPLIED, GYMNOSPERMAE

92. Feehan J 1985. Explosive flower opening in ornithophily: a study of pollination mechanismsin some central African Loranthaceae. Botanical Journal of the Linnean Society 90, 129-144. ANTHESIS, EVOLUTION, LORANTHACEAE, MORPHOLOGY, ORNITHOPHILY

93. Feinsinger P, Linhart Y B, Swarm L A and Wolfe J A 1979. Aspects of the pollination biology of three *Erythrina* species on Trinidad and Tobago. Annals of the Missouri Botanic Gardens 66, 450-471. BREEDING SYSTEMS, FABACEAE, NECTAR SECRETION, ORNITHOPHILY, PHENOLOGY, POLLEN MOVEMENT

94. Ferguson I K and Skvarla J J 1982. Pollen morphology in relation to pollinators in Papilionoideae (Leguminosae). Botanical Journal of the Linnean Society 84, 183-193. FABACEAE, PALYNOLOGY, REVIEW

95. Ferreira D I 1986. The influence of temperature on the respiration rate and growing of *Protea neriifolia* R.Br. inflorescences. Acta Horticulurae 185, 121-130. APPLIED, ENERGY UTILIZATION, PROTEACEAE

96. Fourie K J 1968. Sugarbirds feeding on Eucalyptus flowers. Ostrich 39, 270. ALIENS,MYRTACEAE

97. Fries R E 1909. Über Kleistogamie bei *Argyrolobium andrewsianum* Steudel. Arkiv for Botanik 8, 14. BREEDING SYSTEM, FABACEAE,

98. Frost S K and Frost P G H 1980. Territoriality and changes in resource use by sunbirds at *Leonotis leonurus* (Labiatae). Oecologia 45, 109-116. BEHAVIOUR, ENERGETICS, FORAGING ECOLOGY, LABIATAE, MORPHOLOGY, NECTAR SECRETION, ORNITHOPHILY

99. Frost S K and Frost P G H 1981. Sunbird pollination of *Strelitzia nicolai*. Oecologia 49, 379-384. ANTHESIS, BREEDING SYSTEMS, MORPHOLOGY, NECTAR SECRETION, ORNITHOPHILY, STRELITZIACEAE

100. Anonymous (undated) Fruit and Fruit Technology Research Institute. *Protea* insects in cut flowers. Information Bulletin 28. APPLIED, ENTOMOPHILY: COLEOPTERA, PROTEACEAE

101. Galil J and Eisokowitch D 1968. On the pollination ecology of *Ficus sycomorus* in East Africa. Ecology 49, 259-269. ENTOMOPHILY: AGAONIDAE, MORACEAE

102. Galil J and Eisokowitch D 1968. Flowering and fruit types of *Ficus sycomorus* in Israel. New Phytologist 67, 74-758. ENTOMOPHILY, AGAONIDAE, MORACEAE

103. Galil J and Eisikowitch D 1969. Further studies on the pollination ecology of *Ficus sycomorus* L. (Hymenoptera, Chalcidoidea, Agaonidae). Tijdschrif Entomology 112, 1-13. ENTOMOPHILY: AGAONIDAE, MORACEAE

104. Galil J and Eisikowitch D 1974. Further studies on pollination ecology in *Ficus sycomorus*. II. Pocket filling and emptying by *Ceratosolen arabicus* Mayr. New Phytologist 73, 515-528. BEHAVIOUR, ENTOMOPHILY: AGAONIDAE, MORACEAE

105. Galil J and Neenan G 1977. Pollen transfer and pollination in the common fig (*Ficus caprica* L.) New Phytologist 79, 163-171. BEHAVIOUR, ENTOMOPHILY: AGAONIDAE, MORACEAE, POLLEN MOVEMENT

106. Galpin E 1984. The fertilization of flowers by birds. Referred to in: Botanische Jahrbuecher I. S. 271. ORNITHOPHILY

107. Garside S 1918. Pollen presentation in *Cryptostemma calendulaceum* R. Br. Annals of the Bolus Herbarium 2, 149-152. ANTHESIS, ASTERACEAE, ENTOMOPHILY: HYMENOPTERA, MORPHOLOGY

108. Garside S 1922. The pollination of Satyrium bicallosum Thunb. Annals of the Bolus Herbarium 2, 147-154. ENTOMOPHILY: DIPTERA, ENTOMOPHILY: LEPIDOPTERA, MORPHOLOGY, ORCHIDACEAE

109. Gawith E 1983. The autecology and conservation of *Watsonia maura* Thunb. (Iridacea). Unpublished honours project, Botany Department, University of Cape Town. DEMOGRAPHY, IRIDACEAE, PHENOLOGY

110. Gess F W 1968. Insects found on proteas. Journal of the Botanical Society of South Africa 28, 29-33. BEHAVIOUR, ENTOMOPHILY: COLEOPTERA, LIFE CYCLES, PROTEACEAE

111. Giliomee J H 1986. Hunting for insect pollinators on fynbos flowers. Veld and Flora 72, 6-7. ENTOMOPHILY

112. Gill F B 1978. Proximate costs of competition for nectar. American Zoology 18, 753-763. BEHAVIOUR, ENERGETICS, FORAGING ECOLOGY, NECTAR SECRETION, ORNITHOPHILY

113. Gill F B and Conway C A 1979. Floral biology of *Leonotis nepetifolia* (L) R.Br. (Labiatae). Proceedings of the Natural Sciences Museum of Philadelphia 131, 244-256. ANTHESIS, DEMOGRAPHY, FORAGING ECOLOGY, LABIATAE, MORPHOLOGY, NECTAR SECRETION, ORNITHOPHILY

114. Gill F B and Wolf L L 1975. Economics of feeding territoriality in the golden-winged sunbird. Ecology 56, 333-345. BEHAVIOUR, ENERGETICS, FORAGING ECOLOGY, LABIATAE, NECTAR SECRETION, ORNITHOPHILY

115. Gill F B and Wolf L L 1975. Foraging strategies and energetics of East African sunbirds at mistletoe flowers. American Naturalist 109, 491-510. BEHAVIOUR, ENERGETICS, FORAGING ECOLOGY, LORANTHACEAE, NECTAR SECRETION, ORNITHOPHILY

116. Gill F B and Wolf L L 1977. Nonrandom foragingby sunbirds in a patchy environment. Ecology 58, 1284-1296. FORAGING ECOLOGY, LABIATAE, NECTAR SECRETION, ORNITHOPHILY

117. Gill F B and Wolf L L 1978. Comparative foraging efficiencies of some montane sunbirds in Kenya. Condor 80, 391-400. ENERGETICS, FORAGING ECOLOGY, LABIATAE, MORPHOMETRICS, NECTAR SECRETION, ORNITHOPHILY

118. Gill F B and Wolf L L 1979. Nectar loss by golden-winged sunbirds to competitors. Auk 96, 448-461. ENERGETICS, FORAGING ECOLOGY, LABIATAE, NECTAR SECRETION, ORNITHOPHILY

119. Godschalk S K B 1983. The reproductive phenology of three mistletoe species in the Loskop Dam Nature Reserve, South Africa. South African Journal of Botany 2, 9-14. LORANTHACEAE, ORNITHOPHILY, PHENOLOGY, VISCACEAE

120. Goldblatt P 1972. A revision of the genus *Lapeirousia* Possret and *Anomatheca* Ker. in the winter rainfall region of South Africa. Contributions to the Bolus Herbarium 4. IRIDACEAE, PHENOLOGY

121. Goldblatt P 1981. Systematics and biology of *Homeria* (Iridaceae). Annals of the Missouri Botanic Gardens 68, 413-503. BREEDING SYSTEMS, ENTOMOPHILY: DIPTERA, ENTOMOPHILY: HYMENOPTERA, HYBRIDIZATION, IRIDACEAE, PHENOLOGY

122. Goldblatt P 1984. A revision of *Hesperantha* (Iridaceae) in the winter rainfall area of southern Africa. Journal of South African Botany 50, 15-141. ANTHESIS, BREEDING SYSTEMS, ENTOMOPHILY: LEPIDOPTERA, HYBRIDIZATION, IRIDACEAE, PHENOLOGY

123. Goldblatt P 1985. Systematics of the southern Africa genus *Geissorhiza* (Iridaceae). Annals of the Missouri Botanic Gardens 72, 277-447. ENTOMOPHILY: HYMENOPTERA, IRIDACEAE, MORPHOLOGY

124. Grey-Wilson C 1980. *Impatiens* of Africa. Balkema, Rotterdam. BREEDING SYSTEMS, ENTOMOPHILY: HYMENOPTERA, ENTOMOPHILY: LEPIDOPTERA, MORPHOLOGY

125. Guillarmod A J, Jueb R A and Skead C J 1979. Field studies of six southern African species of *Erythrina*. Annals of the Missouri Botanic Gardens 66, 521-527. FABACEAE, MORPHOLOGY, ORNITHOPHILY, SEED SET

126. Guth C J and Weller S G 1986. Pollination, fertilization and ovule abortion in *Oxalis magnifica*. American Journal of Botany 73, 246-253. POLLEN MOVEMENT, SEEDSET

127. Hagerup O 1950. Thrips pollination in *Calluna*. Kongelige Danske Videnskabernes Selskab Biologiske Meddelelser 18, 4. ANEMOPHILY, ENTOMOPHILY: HYMENOPTERA, ENTOMOPHILY: LEPIDOPTERA, ENTOMOPHILY: THRIPS, ERICACEAE

128. Hagerup O and Hagerup E 1953. Thrips pollination of *Erica tetralix*. New Phytologist 52, 1-7. BREEDING SYSTEMS, ENTOMOPHILY: THRIPS, ERICACEAE

129. Hall A V 1965. Studies of the South African species of *Eulophia*. Journal of South African Botany, Supplementary Volume 5. ORCHIDACEAE, PHENOLOGY

130. Hall A V 1982. A revision of the South African species of *Satyrium*. Contributions to the Bolus Herbarium 10. ORCHIDACEAE, PHENOLOGY

131. Hall A V and Veldhuis A A 1985. South African Red Data Book: Plants - fynbos and karoo biomes. South African National Scientific Programmes Report No 117. CSIR, Pretoria. 144 pp. DEMOGRAPHY, REVIEW, PHENOLOGY

132. Hamrick J L and Allard R W 1972. Microgeographical variation in allozyme frequencies in *Avena barbata*. GENE FLOW

133. Henning S F 1983. Biological groups within the Lycaenidae (Lepidoptera). Journal of the Entomological Society of southern Africa 46, 65-85. ENTOMOPHILY: LEPIDOPTERA

134. Henning S F 1984. Life history and behaviour of the rare myrmecophious lycaenid Erikssonia acraeina Trimen (Lepidoptera: Lycaenidae). Journal of the Entomological Society of southern Africa 47, 337-342. ENTOMOPHILY: LEPIDOPTERA, LIFE CYCLES

135. Hernandez H M 1981. The reproductive ecology of Nicotiana glauca, a cosmopolitan weed. Bulletin of the Society of Botany of Mexico 41, 47-74. ORNITHOPHILY, SOLANACEAE, SEED SET

136. Hernandez H M and Toledo V M 1979. The role of nectar pollinators in the reproduction of Erythrina leptorhiza. Annals of the Missouri Botanic Gardens 66, 512-520. BREEDING SYSTEM, FABACEAE, MORPHOLOGY, NECTAR CONSTITUTION, ORNITHOLOGY, PHENOLOGY, SEED SET

137. Herrmann J M 1983. Insect pollination of some Erica species in the south western Cape. Unpublished Agricultural Honours project, University of Stellenbosch. ENTOMOPHILY: HYMENOPTERA, ERICACEAE, MORPHOLOGY, ORNITHOPHILY

138. Herrmann J M 1983. Fruit flies and the eucalypt nectar flow. South African Bee Journal 55, 27-33. ALIENS, ENTOMOPHILY: DIPTERA, MYRTACEAE, NECTAR SECRETION

139. Herrmann J M 1984. The Drosophila fly in Eucalyptus flowers - who holds the answer to this riddle? South African Bee Journal 56, 5-8. ALIENS, BEHAVIOUR, ENTOMOPHILLY: DIPTERA, ENTOMOPHILY: HYMENOPTERA, LIFE CYCLES, MYRTACEAE, PHENOLOGY

140. Herrmann J M 1985. Insect pollination of some Erica species in the south western Cape. Veld and Flora 7, 57-59. ENTOMOPHILY: HYMENOPTERA, ERICACEAE, MORPHOLOGY, ORNITHOPHILY

141. Hesse A J 1934. Some insects associated with the plant Gnidia laxa. Annals of the South African Museum 30, 1-44. THYMELAEACEAE

142. Hill A W 1913. The flora mechanism of the genus Sebaea. Annals of Botany 27, 479-489. GENTIANACEAE, MORPHOLOGY

143. Hodgson L M 1976. Some aspects of flowering and reproductive behaviour in Eucalyptus grandis (Hill) Maiden at J.D.M. Keet Forest Research Station (formerly Zomerkomst Forest Research Station). 1. Flowering, controlled pollination methods, pollination and receptivity. South African Forestry Journal 97, 18-28. ANTHESIS, BREEDING SYSTEMS, ENTOMOPHILY, MYRTACEAE, ORNITHOPHILY, PHENOLOGY, SEED SET

144. Horn W 1962. Breeding research on South African plants. II. Fertility of Proteaceae. Journal of South African Botany 28, 259-268. PROTEACEAE, SEED SET

145. Horn W 1962. Breeding research on South African plants: III. Intra- and inter-specific compatibility in Ixia L., Sparaxis Ker, Watsonia Mill. and Zantedeschia Spreng. Journal of South African Botany 28, 269-277. ARACEAE, HYBRIDIZATION, IRIDACEAE, SEED SET

146. Hutchinson J 1946. A botanist in southern Africa. Gawthorn, London. ASTERACEAE, ENTOMOPHILY: COLEOPTERA, MIMICRY

147. Ingram C 1967. The phenomenal behaviour of a South African Gladiolus. Journal of the Royal Horticultural Society 92, 396-398. ANTHESIS, IRIDACEAE, MORPHOLOGY

148. Iwarsson M 1979. Pollen from bills of African sunbirds (Nectariniidae). Botanika Notiser 132, 349-355. ORNITHOPHILY, PALYNOLOGY

149. Jacobs G 1980. Aspects of flower initiation and development of pincussion Leucospermum cv. Red Sunset. Crop Production 9, 175-177. APPLIED, PHENOLOGY, PROTEACEAE

150. Jacobs G 1983. Flower initiation and development in Leucospermum cv Red Sunset. Journal of the American Society of Horticultural Science 108, 32-35. APPLIED, PHENOLOGY, PROTEACEA

151. Jacobs G and Honeyborne G E 1978. Delaying the flowering time of Leucospermum cv Golden Star by deheading. Agroplantae 10, 13-15. APPLIED, PHENOLOGY, PROTEACEAE

152. Jacobs G and Honeyborne G E 1979. The relationship between heat unit accumulation and the flowering date of *Leucospermum* cv. Golden Star. Agroplantae 11, 83-85. APPLIED, PHENOLOGY, PROTEACEAE

153. Jacobs G and Minnaar H R 1980. Light intensity and flower development of *Leucospermum cordifolium*. Horticultural Science 15, 644-645. APPLIED, PHENOLOGY, PROTEACEAE

154. Jacobs G, Napier D N and Malan D G 1986. Prospects of delaying flowering time of *Leucospermum*. Acta Horticulturae 185, 61-66. APPLIED, PHENOLOGY, PROTEACEAE

155. Jacobsen N H G and du Plessis E 1976. Observations on the ecology and biology of the Cape fruit bat *Rousettus aegyptiacus laechi* in the eastern Transvaal. South African Journal of Science 72, 270-273. CHIROPTEROPHILY

156. Jeppe B 1974. South African *Aloes* (2nd edition). Purnell, Cape Town. ASPHODELACEAE, PHENOLOGY

157. Johnson L A S and Briggs B G 1975. On the Proteaceae - the evolution and classification of a southern family. Journal of the Linnean Society of Botany 70, 83-182. BREEDING SYSTEMS, ENTOMOPHILY: COLEOPTERA, MORPHOLOGY, NECTAR SECRETION, ORNITHOPHILY, PALYNOLOGY, PROTEACEAE

158. Jongens-Roberts S M and Mitchell D T 1983. The distribution of dry mass and phosphorus in an evergreen fynbos shrub species, *Leucospermum parile* (Salisb. ex J. Knight) Sweet (Proteaceae), at different stages of development. New Phytologist 103, 669-683. APPLIED, ENERGY UTILIZATION, PROTEACEAE

159. Jorgensen H 1919. The pollination of *Asclepias cornuti* Decne. Dansk Botanisk Arkiv 2, 10: 1-6. ASCLEPIADACEAE, ENTOMOPHILY, SEED SET

160. Kronestedt E and Bystedt P A 1981. Thread-like formation in the anthers of *Strelitzia reginae*. Nordic Journal of Botany 1, 523-529. MORPHOLOGY, STRELITZIACEAE

161. Kronestedt E and Robards A 1985. Nectar secretion by the flower of *Strelitzia reginae*. Royal Microscopy Society 20, BM 20-21. NECTAR SECRETION, STRELITZIACEAE

162. Kronestedt E and Walles B 1983. Wall growth and separation of thread-forming cells in *Strelitzia reginae*. Journal of Ultrastructural Research 85, 110. MORPHOLOGY, STRELITZIACEAE

163. Kronestedt E and Waller B 1984. Secretery cells of the transmitting tissue in the pistil of *Strelitzia reginae*. Journal of Ultrastructural Research 88, 302-304. MORPHOLOGY, STRELITZIACEAE

164. Kronestedt E and Walles B 1986. Anatomy of the *Strelitzia reginae* flower (strelitziaceae). Nordic Journal of Botany 6, 307-320. MORPHOLOGY, STRELITZIACEAE

165. Kronestedt E, Walles B and Alkemar I 1985. The transmitting tract and pollen tube growth in *Strelitzia reginae*. Journal of Ultrastructural Research 91, 262. INCOMPATIBILITY, STRELITZIACEAE

166. Kronestedt E, Walles B and Alkemar I 1986. Structural studies of pollen tube growth in the pistil of *Strelitzia reginae*. Protoplasma 131, 224-232. MORPHOLOGY, NECTAR SECRETION, PALYNOLOGY, POLLEN MOVEMENT, STRELITZIACEAE

167. Kruger F J 1979. Seasonal growth and flowering rhythms: South African heathlands. In: Specht R L (editor) Ecosystems of the world. Volume 9a. Heathlands and related shrublands: descriptive studies. Elsevier, Amsterdam. pp 1-4. PHENOLOGY

168. Kugler H 1970. Blutenökologie (2nd edition). Fischer Verlag, Stuttgart. REVIEW

169. Kugler H 1973. Zur bestäubung von *Scaevola plumieri* (L) Vahl und *Ipomoea pes-caprae* Sweet, swei tropischer Strandpflanzen. Flora 162, 381-391. ENTOMOPHILY, GOODENIACEAE, MORPHOLOGY

170. Kugler H 1977. Zur Bestäubung mediterraner Frühjahrsblüher. Flora 166, 43-64. BREEDING SYSTEMS, ENTOMOPHILY: HYMENOPTERA, MORPHOLOGY, PHENOLOGY

171. Kugler H 1980. Zur Bestaubung von *Lantana camara* L. Flora 169, 524-529. ALIENS, ENTOMOPHILY, VERBENACEAE

172. Kummerow J 1983. Comparative phenology of mediterranean-type communities. In: Kruger F J, Mitchell D T and Jarvis J U M (editors) Mediterranean-type ecosystems: the role of nutrients. Springer Verlag, Berlin. pp 300-317. PHENOLOGY

173. Lachaise D 1977. Niche separation of African *Lissocephala* within the *Ficus* drosophilid community. Oecologia 31, 201-204. MORACEAE, EVOLUTION

174. Lachaise D and Tsacas L 1982. Breeding-sites in tropical African Drosophilids. In: Ashburner M, Carson H L and Thompson J N (editors) The genetics and biology of Drosophila Volume 3. Academic Press, New York. MORACEAE, EVOLUTION

175. Lachaise D, Tsacas L and Couturier G 1982. The Drosophilidae associated with tropical African figs. Evolution 36, 141-151. MORACEAE, EVOLUTION

176. Lack A 1977. Genets feeding on nectar from *Maranthes polyandra* in northern Ghana. East African Wildlife Journal 15, 233-234. BEHAVIOUR, THEROPHILY

177. Lamont B 1985. The comparative reproductive biology of three *Leucospermum* species (Proteaceae) in relation to fire responses and breeding systems. Australian Journal of Botany 33, 139-145. BREEDING SYSTEMS, NECTAR SECRETION, PHENOLOGY, PROTEACEAE, SEED SET

178. Lamont B B, Collins B G and Cowling R M 1985. Reproductive biology of the Proteaceae in Australia and South Africa. Proceedings of the Ecological Society of Australia 14, 213-224. BREEDING SYSTEMS, ENTOMOPHILY, ORNITHOPHILY, PHENOLOGY, PROTEACEAE, SEED SET

179. Lewis G J 1959. The genus *Babiana*. Journal of South African Botany Supplementary Volume 3. HYBRIDIZATION, IRIDACEAE, PHENOLOGY

180. Linder H P 1981. Taxonomic studies on the Disinae. III. A revision of the *Disa* Berg excluding section *Micranthe* Linde. Contributions to the Bolus Herbarium 9. ENTOMOPHILY: LEPIDOPTERA, MORPHOLOGY, NECTAR SECRETION, ORCHIDACEAE, PHENOLOGY

181. Linder H P 1985. Gene flow, speciation and species diversity patterns in a species rich area: the Cape flora. In: Vrba E J (editor) Species and speciation. Transvaal Museum Monograph 4. pp 53-57. ANEMOPHILY, ENTOMOPHILY, EVOLUTION, GENE FLOW, ORNITHOPHILY, THEROPHILY

182. Lloyd J W 1981. Taxonomy, distribution and autecology of *Leucadendron macowani*, on endangered species. Unpublished Undergraduate Thesis, Botany Department, University of Cape Town. DEMOGRAPHY, PHENOLOGY, PROTEACEAE

183. Loock E E M 1948. *Eucalyptus* species suitable for the production of honey (in South Africa). Journal of the South African Forestry Association 16, 67-71. APPLIED, MYRTACEAE, PHENOLOGY

184. Lotsky J P and Goddijn W A 1928. Voyages of exploration to judge the bearing of hybridisation upon evolution. 1. South Africa. Genetica 10, 1-315. HYBRIDIZATION

185. Louw G N and Nicolson S W 1982. Thermal, energetic and nutritional considerations in the foraging and reproduction of the Carpenter Bee *Xylocopa capitata*. Journal of the Entomological Society of southern Africa 46, 227-240. BEHAVIOUR, BREEDING, ENERGETICS, ENTOMOPHILY: HYMENOPTERA, FABACEAE, FORAGING ECOLOGY, NECTAR SECRETION, PALYNOLOGY

186. Low A B and Lamont B 1986. Nutrient allocation in winter rainfall proteaceous heathlands in relation to nutrient losses through wildflower picking and fire. Acta Horticulturae 185, 89-101. APPLIED, ENERGY UTILIZATION, PROTEACEAE

187. Low A B and Scott L B 1983. Flowering plants of the Cape Flats Nature Reserve. University of the Western Cape, Bellville. FLORA, PHENOLOGY

188. Lowry T K and Crawford D J 1986. Allotype variation in a dioecious tree Brachylaena rotundata (Compositae). American Journal of Botany 73, 774. ASTERACEAE, BREEDING SYSTEMS, ENTOMOPHILY

189. Majumdar S K and Riley H P 1967. Chromosome alteration in relation to speciation in Haworthia. Advances in the Frontiers of Plant Science 18, 63. ASPHODELACEAE, BREEDING SYSTEMS, EVOLUTION

190. Majumdar S K and Riley H P 1970. Pollen conditions in Haworthia species and hybrids. American Journal of Botany 57, 742. ASPHODELACEAE, HYBRIDIZATION, PALYNOLOGY

191. Majumbar S K and Riley H P 1973. Chromosome numbers, pollen fertility and pollen size in Haworthia species and hybrids. Canadian Journal of Botany 51, 1753. ASPHODELACEAE, HYBRIDIZATION, PALYNOLOGY, POLLEN VIABILITY

192. Markotter E I 1936. Die lewensgeskiedenis van sekere geslagte van Amaryllidaceae. Annals of the University of Stellenbosch 14, Series A(2), 1-84. AMARYLLIDACEAE, PHENOLOGY

193. Marloth R 1896. The fertilization of Disa uniflora Berg. by insects. Transactions of the South African Philisophical Society 7, 93-95. ENTOMOPHILY: LEPIDOPTERA, ORCHIDACEAE, SEED SET

194. Marloth R 1901. Die Ornithophilie in der Flora Südafrikas. Berichte de Deutschen Botanischen Gesellschaft 19: 177. ORNITHOPHILY, REVIEW

195. Marloth R B 1903. Some recent observations on the biology of Roridula. Annals of Botany 17, 151-157. RORIDULACEAE

196. Marloth R 1907. Notes on the morphology and biology of Hydnora africana Thunb. Transactions of the South African Philosophical Society 16, 465-468. HYDNORACEAE

197. Marloth R 1908. Some observations on entomophilous flowers. Report of the South African Association for the Advancement of Science. ENTOMOPHILY

198. Marloth R 1908. Some observations on entomophilous flowers. South African Journal of Science 4, 110-113. ENTOMOPHILY

199. Marloth R 1909. A diplostigmatic plant, Sebaea exacoides (L.) Schinz (Belmontia cordata L.). Transactions of the Royal Society of South Africa 1, 311-314. GERANIACEAE, MORPHOLOGY

200. Marloth R 1913, 1925, 1932. The flora of South Africa. Darters, Cape Town. FLORA

201. Marloth R 1914. Note on the entomophilous nature of Encephalartos. Transactions of the Royal Society of South Africa 4, 69-71. ENTOMOPHILY: COLEOPTERA, ZAMIACEAE

202. Marloth R 1920. Notes on the function of the staminal and staminodal glands in the flowers of Adenandra. Annals of the Bolus Herbarium 3, 38-39. ENTOMOPHILY, MORPHOLOGY, RUTACEAE

203. Marshak A 1934. Chromosomes and compatability in the Aloinae. American Journal of Botany 21, 592-596. ASPHODELACEAE, PHENOLOGY

204. Marshall A G 1983. Bats, flowers and fruit: evolutionary relationships in the old world. Biological Journal of the Linnean Society 20, 115-135. CHIROPTEROPHILY, EVOLUTION, REVIEW

205. Mason H J 1972. Western Cape Sandveld flowers. Struik, Cape Town. FLORA, PHENOLOGY

206. Mathews M R 1966. A study of pollen morphology and pollen biology in South African Thymeliaceae. Unpublished 3rd year Botany Project, University of Cape Town. ANEMOPHILY, PALYNOLOGY, THYMELIACEAE

207. Merwe P van der 1977. Die morfologie en voortplanting van *Orothamnus zeyheri* (Proteaceae). In: Cape Department of Nature and Environmental Conservation Research reports: Plants. pp 1-209. ENTOMOPHILY: COLEOPTERA, PROTEACEAE, SEED SET

208. Meynhardt J T (editor) 1974. Farming in South Africa. Series: flowers, Ornamental shrubs and trees. B. Proteas. B.2. Propagation of proteas. Horticultural Research Institute, Pretoria. APPLIED, PROTEACEAE

209. Meynhardt J T (editor) 1974. Farming in South Africa. Series: flowers, ornamental shrubs and trees, B. Proteas. B.5. Picking and handling. Horticultural Research Institute, Pretoria. APPLIED, PROTEACEAE

210. Michel F B, Cour P, Quet L and Marty J P 1976. Quantitative and qualitative comparison of pollen calendars for plain and mountain species. Clinical Allergy 6, 383-393. APPLIED, PHENOLOGY, POLLEN MOVEMENT

211. Michener C D 1970. Nest sites of stem and twig inhabiting African bees (Hymenoptera: Apoidea). Journal of the Entomological Society of southern Africa 33, 1-22. BREEDING

212. Michener C D 1979. Biogeography of the bees. Annals of the Missouri Botanic Gardens 66, 277-347. BREEDING, ENTOMOPHILY: HYMENOPTERA, REVIEW

213. Middelmann W J 1984. *Protea holosericea* and the flowerpicking industry. African Wildlife 38, 216-217. APPLIED, PROTEACEAE

214. Midgley J J and Vlok J H J 1986. Flowering patterns in Cape Proteaceae. Acta Horticulturae 185, 273-276. PHENOLOGY, PROTEACEAE

215. Milewski A V 1983. A comparison of ecosystems in Mediterranean Australia and southern Africa: Nutrient-poor sites at the Barrens and the Caledon coast. Annual Review of Ecology and Systematics 14, 57-76. REVIEW

216. Milton S J and Hall A V 1981. Reproductive biology of Australian acacias in the south western Cape Province, South Africa. Transactions of the Royal Society of South Africa 44, 465-487. ALIENS, BREEDING SYSTEMS, FABACEAE, SEED SET

217. Moffet A A 1932. Studies on the formation of multinuclear giant pollen grains in *Kniphofia*. Journal of Genetics 25, 315-337. ASPHODELACEAE, PALYNOLOGY

218. Moldenke A R 1979. Pollination ecology as an assay for ecosystemic organization convergent evolution in Chile and California, USA Phytologia 42, 415-454. REVIEW

219. Moll E J and Gubb A A 1981. Aspects of the ecology of *Staavia dodii* in the south western Cape of South Africa. In: Synge H (editor) The biological aspects of rare plant conservation. Wiley, Chichester. pp 331-342. DEMOGRAPHY, PENEACEAE, PHENOLOGY

220. Morton E S 1979. Effective pollination of *Erythrina fusca* by the Orchard Oriole (*Icterus spurius*): Coevolved behavioural manipulation? Annals of the Missouri Botanic Gardens 66, 482-489. BEHAVIOUR, FABACEAE, NECTAR CONSTITUTION, ORNITHOPHILY

221. Mostert D P 1974. The biology of *Promerops cafer* with special reference to the role of the nectar and satellite insect fauna of *Protea repens* in the reproductive cycle. Unpublished MSc Thesis, University of Stellenbosch. BEHAVIOUR, ENTOMOPHILY, FORAGING ECOLOGY, NECTAR CONSTITUTION, NECTAR SECRETION, ORNITHOPHILY, PROTEACEAE

222. Mostert D P, Siegfried W R and Louw G N 1980. *Protea* nectar and satellite fauna in relation to the food requirements and pollinating role of the Cape sugarbird. South African Journal of Science 76, 409-412. BEHAVIOUR, ENTOMOPHILY, FORAGING ECOLOGY, NECTAR CONSTITUTION, NECTAR SECRETION, ORNITHOPHILY, PROTEACEAE

223. Mulcahy D 1965. Heterostyly within *Nivenia* (Iridaceae). Brittonia 17, 349-351. BREEDING SYSTEMS, IRIDACEAE, MORPHOLOGY

224. Myburgh A C and Rust D J 1975. A survey of pests of the Proteaceae in the western and southern Cape Province. Journal of the Entomological Society of southern Africa 38, 55-60. APPLIED, PROTEACEAE

225. Myburgh A C, Rust D J and Starke L C 1973. Pests of protea cut flowers. Journal of the Entomological Society of southern Africa 36, 251-255. APPLIED, ENTOMOPHILY: COLEOPTERA, PROTEACEAE

226. Myburgh A C, Starke L C and Rust D J 1974. Destructive insects in the seed heads of *Protea barbigera*. Meisner (Proteaceae). Journal of the Entomological Society of southern Africa 37, 23-29. APPLIED, ENTOMOPHILY: COLEOPTERA, PROTEACEAE

227. Napier D N, Malan D G, Jacobs G and Bernitz J W 1986. Improving stem length and flower quality of *Leucospermum* with growth regulators. Acta Horticulturae 185, 67-74. APPLIED, PROTEACEAE

228. New T R 1979. Phenology and relative abundance of Coleoptera on some Australian acacias. Australian Journal of Zoology 27, 9-16. ALIENS, ENTOMOPHILY: COLEOPTERA, PHENOLOGY

229. Nicholls M S 1985. The evolutionary breakdown of distyly in *Linum tenuifolium* (Linaceae). Plant Systematics and Ecology 150, 291-301. BREEDING SYSTEMS, INCOMPATIBILITY, LINACEAE, MORPHOLOGY, PHENOLOGY, SEED SET

230. Nicholls M S 1985. Pollen flow, population composition, and the adaptive significance of distyly in *Linum tenuifolium* L. (Linaceae). Biological Journal of the Linnean Society 25, 235-242. BREEDING SYSTEMS, LINACEAE, POLLEN MOVEMENT

231. Nicholls M S 1986. Population composition, gender specialization and the adaptive significance of distyly in *Linum perenne* (Linaceae). New Phytologist 102, 209-217. BREEDING SYSTEMS, DEMOGRAPHY, LINACEAE, MORPHOLOGY

232. Nicholson S A 1981. The flight of the Carpenter bee. South African Journal of Science 77, 152. ENTOMOPHILY: HYMENOPTERA

233. Nicholson S W and Louw G N 1980. Preflight thermogenesis, conductance and thermoregulationin the *Protea* beetle, *Trichostetha fascicularis* (Scarabaeidae: Cetoniinae). South African Journal of Science 76, 124-126. ENERGETICS

234. Nicolson S W and Louw G N 1982. Simultaneous measurement of evaporative waterloss, oxygen consumption and thoracic temperature during flight in a Carpenter Bee. Journal of Experimental Zoology 222, 287-296. ENERGETICS, ENTOMOPHILY: HYMENOPTERA, FABACEAE

235. Niven C 1968. Mass feeding of the malachite sunbird *Nectarinia famosa*. Ostrich 39: 40. FORAGING ECOLOGY, ORNITHOLOGY

236. Nordenstam B 1982. A monograph of the genus *Ornithoglossom* (Liliaceae). Opera Botanica 674, 1-51. COLCHIDACEAE, PHENOLOGY

237. Oatley T B 1964. The probing of *Aloe* flowers by birds. Lammergeyer 3, 2-8. ASPHODELACEAE, ORNITHOPHILY

238. Oatley T B and Skead D M 1972. Nectar feedingby South African birds. Lammergeyer 15, 65-74. ASPHODELACEAE, FABACEAE, ORNITHOPHILY

239. Oliver E G H 1976. Studies in the Ericoideae. I. The genera Eremia and Eremiella. Bothalia 12, 29-48. ANEMOPHILY, ERICACEAE, PHENOLOGY

240. Oliver E G H 1976. Studies in the Ericoideae. II. The new genus Stokoeanthus. Bothalia 12, 49-52. ANEMOPHILY, ERICACEAE, PHENOLOGY

241. Oliver E G H 1980. Studies in the Ericoideae. III. The genus Grisebachia. Bothalia 13, 65-93. ENTOMOPHILY: HYMENOPTERA, ERICACEAE, PALYNOLOGY, PHENOLOGY

242. Olivier M C 1966. Die plantegroei en flora van die Worcesterse veld reservaat. Unpublished DSc Thesis, University of Stellenbosch. FLORA

243. Olson S L and Ames P L 1984. Promerops as a thrush, and its implications for the evolution of nectarivory in birds. Ostrich 56, 213-218. EVOLUTION, ORNITHOPHILY

244. Ornduff R 1966. The origin of dioecism from heterostyly in Nymphoides (Menyanthaceae). Evolution 20, 309-314. EVOLUTION, GENTIANACEAE, MORPHOLOGY

245. Ornduff R 1972. The breakdown of trimorphic incompatibility in Oxalis section corniculatae. Evolution 26, 52-65. BREEDING SYSTEMS, EVOLUTION, MORPHOLOGY, PALYNOLOGY, OXALIDACEAE, SEED SET

246. Ornduff R 1974. Heterostyly in South African flowering plants: a conspectus. Journal of South African Botany 40, 169. HAEMODORACEAE, MORPHOLOGY, TECOPHILIACEAE

247. Ornduff R 1983. Studies on the reproductive system of Nivenia corymbosa (Iridaceae), an apparently androdioecious species. Annals of the Missouri Botanic Gardens 70, 146-148. BREEDING SYSTEMS, ENTOMOPHILY, IRIDACEAE

248. Ornduff R 1985. Reproductive ecology and chromosome numbers of native and exotic races of Oxalis pes caprae L. and their bearing on the genesis of a noxious weed. Abstract II AETFAT: 8. BREEDING SYSTEMS, OXALIDACEAE, SEED SET

249. Ornduff R and Dulberger R 1978. Floral enantiomorphy and the reproductive system of Wachendorfia paniculata (Haemodoraceae). New Phytologist 80, 427-434. BREEDING SYSTEMS, HAEMODORACEAE, MORPHOLOGY, PHENOLOGY, SEED SET

250. Palser B P and Murth Y S 1967. Studies of floral morphology in the Ericales. VIII. Organography and vascular anatomy in Erica. Bulletin of the Torrey Botanical Club 94, 243-320. ERICACEAE, MORPHOLOGY

251. Parisi M 1985. The demography of Audouinia capitata (Bruniaceae). Unpublished Honours project, Botany Department, University of Cape Town. NECTAR SECRETION, BRUNIACEAE, PHENOLOGY

252. Pasteels J M and Pasteels J J 1975. Etudie au microscope electroniquea balayage des scopas collectrices de pollen chez les Fideliidae (Hymenoptera, Apoidea). Archives de biologie (Bruxelles) 86, 453-466. ENTOMOPHILY: HYMENOPTERA, PALYNOLOGY

253. Paton J 1986. The role that insects play in the pollination of Protea neriifolia and Protea eximea (Proteaceae). Unpublished Honours project, Zoology Department, University of Cape Town. BEHAVIOUR, ENTOMOPHILY, POLLEN MOVEMENT, PROTEACEAE

254. Pearson H H W 1906. Notes on the South African cycads. Transactions of the South African Philosophical Society 16, 341-353. ZAMIACEAE

255. Pemadosa M A and Lovell P 1974. Factors controlling the flowering time of some dune annuals. Journal of Ecology 52, 869-880. PHENOLOGY

256. Percival M 1965. Floral biology. Pergammon, Oxford. REVIEW

257. Pettet A 1977. Seasonal changes in nectar-feeding by birds at Zaria, Nigeria. Ibis 119, 291-308. MIGRATION, ORNITHOPHILY, PHENOLOGY

258. Phillips J 1926. *Virgilia capensis*: a contribution to its ecology and silviculture. South African Journal of Science 23, 435-454. FABACEAE

259. Philp J and Sherry S P 1946. The degree of natural crossing in green wattle (*Acacia decurrens* Willd) and its bearing on wattle breeding. Journal of the South African Forestry Association 14, 1-28. ALIENS, BREEDING SYSTEMS, FABACEAE

260. Pierce S M 1984. A synthesis of plant phenology in the fynbos biome. South African National Scientific Programmes Report No 88. CSIR, Pretoria. 57 pp. PHENOLOGY, REVIEW

261. Pierce S M and Cowling R M 1984. Phenology of fynbos, renosterveld and subtropical thicket in the south eastern Cape. South African Journal of Botany 3, 17-21. PHENOLOGY

262. Pijl L van der 1954. *Xylocopa* and flowers in the tropics. I-III. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen Series C Biological and Medical Sciences 57, 413-423, 541-562. BEHAVIOUR, ENTOMOPHILY: HYMENOPTERA

263. Pijl L van der 1972. Functional considerations and observation on the flowers of some Labiatae. Blumea 20, 93-103. LABIATAE, MORPHOLOGY

264. Pillans N S 1947. A revision of the Bruniaceae. Journal of South African Botany 8, 121-206. BRUNIACEAE, PHENOLOGY

265. Pooley A C 1968. A short note on the diet of the vervet monkey *Cercopithecus aethiops* in Zululand. Lammergeyer 9, 29-31. THEROPHILY

266. Porsch O 1924. Zukunftsaufgaben der Vogelblumenforschung auf Grund neuesten Tatbestandes. Natuurwissenschaft und Medizin 47, 993-1000. ORNITHOPHILY

267. Porsch O 1924. Vogelblumenstudien I. Jarb. Wiss. Bot. 63, 553-706. ORNITHOPHILY

268. Porsch O 1926. Vogelblütige Orchideen I. Biologia Generalis 2, 107-136. ORCHIDACEAE, ORNITHOPHILY

269. Porsch O 1926. Kritische Quellenstudien über Blumenkesuch durch Vogel. I. Biologia Generalis 2, 217-240. ORNITHOPHILY

270. Porsch O 1927. Kritische Quellenstudien über Blumenkesuch durch Vogel. II. Biologia Generalis 3, 171-206. ORNITHOPHILY

271. Porsch O 1927. Kritische Quellenstudien über Blumenkesuch durch Vogel. III. Biologia Generalis 3, 475-548. ORNITHOPHILY

272. Porsch O 1929. Kritische Quellenstudien über Blumenkesuch durch Vogel. IV. Biologia Generalis 5, 157-210. ORNITHOPHILY

273. Porsch O 1929. Die Bedrohung der Lebensgemeinscaft Blumen und Vogel. Bol. Fac. Stint. Cern. 3, 193-207. ORHITHOPHILY

274. Porsch O 1929. Vogelblumenstudien. II. Jarb. Wiss. Bot. 70, 181-277. ORNITHOPHILY

275. Porsch O 1930. Kritische Quellenstudien über Blumenkesuch durch Vogel. V. Biologia Generalis 6, 133-246. ORNITHOPHILY

276. Porsch O 1931. Grellrot als Vogelblumenfarbe. Biologia Generalis 1, 647-674. ORNITHOPHILY

277. Porsch O 1934. Säugetiere als Blumenausbeuter und die Frage der Säugetierblume. I. Biologia Generalis 10, 657-685. THEROPHILY

278. Porsch O 1935. Säugetiere als Blumenausbeuter und die Frage der Säugetierblume. II. Biologia Generalis 11, 171-188. THEROPHILY

279. Porsch O 1936. Säugetiere als Blumenausbeuter und die Frage der Säugetierblume. III. Biologia Generalis 12, 1-21. THEROPHILY

280. Prendergast H D V 1983. Competition for nectar between sunbirds and butterflies. Malimbus 5, 51-53. ENTOMOPHILY: LEPIDOPTERA, MALVACEAE, ORNITHOPHILY

281. Prentice H C 1984. Enzyme polymorphism, morphometric variation and population structure in a restricted endemic, *Silene diclinis* (Caryophyllaceae). Biological Journal of the Linnean Society 22, 125-143. GENE FLOW, BREEDING SYSTEMS

282. Pretorius J 1986. Correct terminology for *Protea* inflorescences. Acta Horticulturae 185, 277-280. MORPHOLOGY, PROTEACEAE

283. Prins A J 1982. Morphological and biological notes on six South African blow-flies (Diptera, Calliphoridae) and their immature stages. Annals of the South African Museum 90, 201-217. ENTOMOPHILY: DIPTERA, LIFE CYCLES

284. Raamsdonk L W D van 1985. Crossing and selfing experiments in the *Ornithogalum umbellatum/angustifolium* complex. Plant Systematics and Evolution 150, 175-190. BREEDING SYSTEMS, HYBRIDIZATION, INCOMPATIBILITY, HYACINTHACEAE

285. Raitt L M 1984. An analysis of the flora and floral phenology of a disturbed area of the Cape Flats. Unpublished paper from Proceedings of the 5th National Weeds Conference, Stellenbosch, South Africa. 10 pp. PHENOLOGY

286. Raitt L M 1985. Why are Namaqualand's flowers so attractive? African Wildlife 31, 135-143. ENTOMOPHILY, PHENOLOGY

287. Rattray G 1913. Notes on the pollination of some South African cycads. Transactions of the Royal Society of South Africa 3, 259-270. ENTOMOPHILY, ZAMIACEAE

288. Reader R J 1975. Competitive relationships of some bog ericads for major insect pollinators. Canadian Journal of Botany 53, 1300-1305. ENTOMOPHILY: HYMENOPTERA, ERICACEAE, PHENOLOGY, SEED SET

289. Reader R J 1982. Variation in the flowering date of transplanted ericaceous shrubs in relation to their flowering season. Journal of Biogeograhy 9, 397-410. ERICACEAE, PHENOLOGY

290. Reader R J 1983. Using heat sum models to account for geographical variation in the floral phenology of two ericaceous shrubs. Journal of Biology 10, 47-64. ERICACEAE, PHENOLOGY

291. Reader R J 1984. Comparison of the annual flowering schedules for Scottish heathland and mediterranean-type shrublands. Oikos 43, 1-8. ERICACEAE, PHENOLOGY, REVIEW

292. Rebelo A G 1983. Birds, blossoms and beauty. Veld and Flora 69, 24-25. ERICACEAE, ORNITHOPHILY, PROTEACEAE

293. Rebelo A G 1985. Might mites pollinate Proteas? South African Journal of Science 81, 694. ENTOMOPHILY: ACARINA, PROTEACEAE

294. Rebelo A G 1987. Mass emigration of kelp flies (Coelopidae). Journal of the Entomological Society of southern Africa 50, 257-258. ENTOMOPHILY: DIPTERA, MIGRATION

295. Rebelo A G (in press). Bird feeding at *Satyrium odorum* Sond. flowers. Ostrich NECTAR SECRETION, ORCHIDACEAE, ORNITHOPHILY

296. Rebelo A G (in press). Sugarbird *Promerops cafer* visitation to *Oldenburgia grandis* (Thunb.) Baillon (Asteraceae). Ostrich. ASTERACEAE, ORNITHOPHILY

297. Rebelo A G and Rourke J P 1985. Pollination, seed dynamics and longevity in Proteaceae: ecological determinants and horticultural problems. Protea News 3, 11. BREEDING SYSTEMS, ENTOMOPHILY, ORNITHOPHILY, PROTEACEAE, SEED SET

298. Rebelo A G and Rourke J P 1986. Seed germination and seed set in southern African Proteaceae: ecological determinants and horticultural problems. Acta Horticulturae 185, 75-88. APPLIED, BREEDING SYSTEMS, PROTEACEAE, SEED SET

299. Rebelo A G and Siegfried W R 1985. Colour and size of flowers in relation to pollination of Erica species. Oecologia 65, 584-590. ANEMOPHILY, BREEDING SYSTEMS, ENTOMOPHILY, ERICACEAE, MORPHOLOGY, ORNITHOPHILY, PHENOLOGY

300. Rebelo A G, Siegfried W R and Crowe A A 1984. Avian pollinators and the pollination syndromes of selected mountain fynbos plants. South Africa Journal of Botany 3, 285-296. ERICACEAE, EVOLUTION, MIGRATION, MORPHOLOGY, ORNITHOPHILY, PHENOLOGY, PROTEACEAE

301. Rebelo A G, Siegfried W R and Oliver E G H 1985. Pollination syndromes of *Erica* species in the south western Cape. South African Journal of Botany 51, 270-280. ANEMOPHILY, ENTOMOPHILY, ERICACEAE, MORPHOLOGY, ORNITHOPHILY

302. Rebelo A G and Walboom J C (in preparation). The red light hypothesis: is rendezvous attraction equivalent to sexual attraction in beetles? BEHAVIOUR, ENTOMOPHILY: COLEOPTERA, PROTEACEAE

303. Reddi E U B and Reddi C S 1984. Pollination ecology of *Euphorbia geniculata* (Euphorbiaceae). Journal of the Bombay Natural History Society 81, 571-582. EUPHORBIACEAE

304. Regal P J 1982. Pollination by wind and animals: Ecology of geographic patterns. Annual Review of Ecology and Systematics 13, 497-524. ANEMOPHILY, ENTOMOPHILY, REVIEW

305. Reynolds G W 1982. The aloes of South Africa. Balkema, Cape Town. ASPHODELACEAE, MORPHOLOGY, PHENOLOGY

306. Robertson H G 1980. Pollination of selected *Erica* species in the Cape fynbos. Unpublished Zoology Honours project, University of Cape Town. BEHAVIOUR, ENTOMOPHILY: HYMENOPTERA, ERICACEAE, NECTAR SECRETION, ORNITHOPHILY, POLLEN MOVEMENT

307. Robertson C 1886. Notes on the mode of pollination of *Asclepias.* Botanical Gazette 11, 262-269. ASCLEPIADACEAE, ENTOMOPHILY

308. Robertson C 1887. Insect relations of certain Ascelpiads. Botanical Gazette 11, 207-216. ASCLEPIADACEAE, ENTOMOPHILY

309. Rooyen M W van, Grobbelaar N and Theron G K 1979. Phenology of the vegetation in the Hester Malan Nature Reserve in the Namaqualand Broken Veld. Journal of South African Botany 45, 279-293. PHENOLOGY

310. Roubik D W 1978. Competitive interactions between Neotropical pollinators and Africanized honey bees. Science 201, 1020-1032. ALIENS, BEHAVIOUR, FORAGING ECOLOGY

311. Rourke J R 1978. *Leucospermum winteri.* The flowering plants of Africa 45, 1781. ENTOMOPHILY: DIPTERA, PROTEACEAE

312. Rourke J P 1972. Taxonomic studies on *Leucospermum* R.Br. Journal of South African Botany, Supplementary Volume 8, 1-194. ENTOMOPHILY: COLEOPTERA, MORPHOLOGY, ORNITHOPHILY, PHENOLOGY, PROTEACEAE

313. Rourke J P 1976. A revision of *Diastella.* (Proteaceae). Journal of South African Botany 42, 185-210. MORPHOLOGY, PHENOLOGY, PROTEACEAE

314. Rourke J P 1969. Taxonomic studies on *Sorocephalus* R.Br. and *Spatalla* Salisb. Journal of South African Botany, Supplementary Volume 7. MORPHOLOGY, PHENOLOGY, PROTEACEAE

315. Rourke J P 1980. Rodents as pollinators of dwarf Proteas. Veld and Flora 66, 55-56. PROTEACEAE, THEROPHILY

316. Rourke J P 1980. The proteas of southern Africa. Purnell, Cape Town. HYBRIDIZATION, PHENOLOGY, PROTEACEAE

317. Rourke J P 1983. A remarkable new *Leucospermum* (Proteaceae) from the southern Cape. Journal of South African Botany 49, 213-219. PHENOLOGY, PROTEACEAE, THEROPHILY

318. Rourke J P 1984. A revision of the genus *Mimetes* Salisb. (Proteaceae). Journal of South African Botany 50, 171-236. EVOLUTION, MORPHOLOGY, ORNITHOPHILY, PHENOLOGY, PROTEACEAE

319. Rourke J P 1984. *Vexatorella* Rourke, a new genus of the Proteaceae from southern Africa. Journal of South African Botany 50, 373-391. ENTOMOPHILY, MORPHOLOGY, PHENOLOGY, PROTEACEAE

320. Rourke J P and Wiens D 1977. Convergent floral evolution in South African and Australian Proteaceae and its possible bearing on pollination by nonflying mammals. Annals of the Missouri Botanic Gardens 64, 1-17. EVOLUTION, HYBRIDIZATION, ORNITHOPHILY, PROTEACEAE, THEROPHILY

321. Rowan M K 1968. The foods of South African birds. Ostrich Supplement 8, 343-356. ORNITHOPHILY

322. Ryan P 1982. Aspects of ecology of *Mimetes fimbriifolius*. Unpublished Botany Project, University of Cape Town. DEMOGRAPHY, ORNITHOPHILY, PROTEACEAE

323. Ryke P A J 1954. Two new predatory mites (Acarina: Phytoseiinae) from proteas in the western Province. Journal of the Entomological Society of South Africa 17, 241-245. ENTOMOPHILY: ACARINA, PROTEACEAE

324. Ryke P A J 1964. *Acarina* associated with *Protea* flowers in the Cape Province. Journal of the Entomological Society of South Africa 26, 337-354. ENTOMOPHILY: ACARINA, PROTEACEAE

325. Rozen J G 1970. Biology, immature stages and phylogenetic relationships of fidelline bees, with description of a new species of *Neofidelia* (Hymenoptera, Apoidea). "REFERENCE ???". ENTOMOPHILY: HYMENOPTERA, LIFE CYCLES

326. Rozen J G 1974. The biology of two African melittid bees (Hymenoptera, Apoidea). New York Entomological Society 82, 6-13. ENTOMOPHILY: HYMENOPTERA, LIFE CYCLES

327. Rycroft H B 1950. A quantitative ecological study of the vegetation of Biesievlei, Jonkershoek. Unpublished PhD Thesis, University of Cape Town. FLORA

328. S E J 1935. Pollination of the little water-uintjie. Cape Naturalist 1, 51. APONOGETONACEAE, ENTOMOPHILY

329. Salter T M 1936. Some notes of hybridisation of Ericaceae in the Klaver valley at Simonstown. Journal of South African Botany 2, 129-139. ERICACEAE, HYBRIDIZATION

330. Salter T M 1944. The genus *Oxalis* in South Africa. Journal of South African Botany, Supplement 1. OXALIDACEAE, PHENOLOGY

331. Schemske D W 1976. Pollinator specificity in *Lantana camara* in *L trifolia* (Verbenaceae). Biotropica 8, 260-264. ENTOMOPHILY: LEPIDOPTERA, MORPHOLOGY, MORPHOMETRICS, VERBENACEAE

332. Schemske D W 1984. Population structure and local selection in *Impatiens pallida* (Balsaminaceae), a selfing annual. Evolution 38, 187-832. BALSAMINACEAE, BREEDING SYSTEMS

333. Schmidt R K 1964. The Lesser double-collared sunbird (*Cinnyris chalybeus* (L.)) in the south western Cape. Ostrich 35, 86-94. BEHAVIOUR, BREEDING, MIGRATION

334. Schmitt J 1980. Pollinator foraging behaviour and gene dispersal in *Senecio* (Compositae). Evolution 34, 934-943. ASTERACEAE, BEHAVIOUR, ENTOMOPHILY: HYMENOPTERA, ENTOMOPHILY: LEPIDOPTERA, GENE FLOW

335. Schmitt J 1983. Flowering plant density and pollinator visitation in *Senecio*. Oecologia 60, 60-97. ASTERACEAE, BEHAVIOUR, ENTOMOPHILY: HYMENOPTERA, ENTOMOPHILY: LEPIDOPTERA, LIFE CYCLES, NECTAR SECRETION, PHENOLOGY, SEED SET

336. Sclater P L 1900. Birds of the Cape Peninsula. Bulletin of the British Ornithological Club 10, 32. ORNITHOPHILY, PROTEACEAE

337. Scott C L 1985. The genus *Haworthia* (Liliaceae). A taxonomic revision. Aloe Books, Johannesburg. ASPHODELACEAE, HYBRIDIZATION, PHENOLOGY

338. Scott R 1903. On the movements of the flowers of *Sparmannia africana* and their demonstration by means of the kinematograph. Annals of Botany 17, 761-777. ANTHESIS, MORPHOLOGY, TILIACEAE

339. Scott Elliot G F 1890. Note on the fertilization of *Musa*, *Strelitzia reginae* and *Ravenala madagascariensis*. Annals of Botany 4, 265-280. ORNITHOPHILY, STRELITZIACEAE

340. Scott Elliot G F 1890. Ornithophilous flowers in South Africa. Annals of Botany 4, 265-280. ORNITHOPHILY

341. Scott Elliot G F 1891. Notes on the fertilization of South African and Madagascar flowering plants. Annals of Botany 5, 333-405. ENTOMOPHILY, ORNITHOPHILY

342. Seiler H W and Rebelo A G 1987. A sexual difference in the Cape sugarbird's role as a pollinator of *Protea lepidocarpodendron*? Ostrich 58, 53-55. BEHAVIOUR, ORNITHOPHILY, PROTEACEAE

343. Shelbourne C J A and Dank R S 1963. Controlled pollination work with *Eucalyptus grandis*: selfing, crossing and hybridizing with *Eucalyptus tereticornis*. Research Pamphlet of the Northern Rhodesia Government Forestry Department. ALIENS, BREEDING SYSTEMS, HYBRIDIZATION, MYRTACEAE

344. Siegfried W R 1982. Trophic structure of some communities of fynbos birds. In: Moll E J (editor) Proceedings of a Symposium on Coastal Lowlands of the Western Cape. University of the Western Cape, Bellville. pp 31-51. ORNITHOPHILY

345. Siegfried W R 1983. Trophic structure of some communities of fynbos birds. Journal of South African Botany 49, 1-43. MIGRATION, ORNITHOPHILY, PHENOLOGY

346. Siegfried W R and Crowe T M 1983. Distribution and species diversity of birds and plants in fynbos vegetation of Mediterranean-climate Zone, South Africa. In: Kruger F J, Mitchell D T and Jarvis J U M (editors) Mediterranean-type ecosystems, the role of nutrients. Springer Verlag, Berlin. pp 403-416. ORNITHOPHILY

347. Siegfried W R, Rebelo A G and Prys-Jones R P 1985. Stem thickness of *Erica* plants in relation to avian pollination. Oikos 45, 153-155. ERICACEAE, ENTOMOPHILY, MORPHOLOGY, ORNITHOPHILY

348. Skaife S H 1952. The yellow-banded carpenter bee, *Mesotrichia caffra* Linn., and its symbiotic mite, *Dinogamasus braunsi* Vitzthun. Journal of the Entomological Society of South Africa 15, 63. ENTOMOPHILY: HYMENOPTERA

349. Skead C J 1963. Sunbirds and strelitzias. Bokmakierie 14, 24-26. ORNITHOPHILY, STRELITZIACEAE

350. Skead C J 1967. The sunbirds of southern Africa. Balkema, Cape Town. ORNITHOPHILY, REVIEW

351. Skead C J 1975. Weaverbird pollination of *Strelitzia reginae*. Ostrich 46, 183-185. ORNITHOPHILY, STRELITZIACEAE

352. Skovsted A 1944. Some hybridization experiments in the tribe Hibisceae. Comptes Rendus des Travaux du Laboratoire Carlsberg Serie Physiologique 24, 1-3. HYBRIDIZATION, MALVACEAE

353. Small J 1915. Preliminary observations on the pollination mechanism of Arctotis aspera, Linn. New Phytologist 15, 216. ASTERACEAE, ENTOMOPHILY

354. Snijman D 1984. A revision of the genus Haemanthus L. (Amaryllidaceae). Journal of South African Botany, Supplementary Volume 12. AMARYLLIDACEAE, ENTOMOPHILY, HYBRIDIZATION, PHENOLOGY

355. Snijman D 1985. A new species of Tenicroa (Liliaceae-Scilleae) from Namaqualand. South African Journal of Botany 51, 284-286. HYACINTHIDAE, MORPHOLOGY

356. Specht R L, Rogers R W and Hopkins A J M 1981. Seasonal growth and flowering rhythms: Australian heathlands. In: Specht R L (editor) Ecosystems of the world. Volume 9B. Heathlands and related shrublands. Analytic studies. Elsevier, Amsterdam. pp 5-13. PHENOLOGY

357. Steiner K E 1979. Passerina pollination of Erythrina megistophylla Diels (Fabaceae). Annals of the Missouri Botanic Gardens 66, 450-502. BEHAVIOUR, FABACEAE, NECTAR CONSTITUTION, NECTAR SECRETION, ORNITHOPHILY, PHENOLOGY

358. Stewart J, Linder H P, Schelpe E A and Hall A V 1982. Wild orchids of South Africa. MacMillan, Johannesburg. ENTOMOPHILY: LEPIDOPTERA, ORCHIDACEAE, PHENOLOGY

359. Stiles F G 1978. Ecological and evolutionary implications of bird pollination. American Zoology 18, 715-727. EVOLUTION, ORNITHOPHILY, REVIEW

360. Stirton C H 1976. Thuranthos: notes on generic status, morphology, phenology and pollination biology. Bothalia 12, 161-165. ANTHESIS, ENTOMOPHILY: LEPIDOPTERA, HYACINTHACEAE, PHENOLOGY

361. Stirton C H 1977. A note on the flowers of Halleria lucida. Bothalia 12, 223-224. ANTHESIS, BREEDING SYSTEMS, ORNITHOPHILY, SCROPHULARIACEAE

362. Stirton C H 1977. Broad spectrum pollination of Plectranthus neochilus. Bothalia 12, 229-230. ENTOMOPHILY: DIPTERA, ENTOMOPHILY: HYMENOPTERA, LABIATAE

363. Stirton C H 1977. The pollination of Canavalia virosa by Xylocopid and Megachilid bees. Bothalia 12, 225-227. BEHAVIOUR, ENTOMOPHILY: HYMENOPTERA, FABACEAE

364. Stirton C H 1983. Nocturnal petal movements in the Asteraceae. Bothalia 14, 1003-1006. ANTHESIS, ASTERACEAE

365. Strasburger E 1901. Einige Bemerkungen zue Pollenbildung bei Asclepais. Berichte der Deutschen Botanischen Gesellschaft 19, 450-461. ASCLEPIADACEAE, ENTOMOPHILY

366. Strid A K 1972. Revision of the genus Adenandra (Rutaceae). Opera Botanica 32. ANTHESIS, ENTOMOPHILY, HYBRIDIZATION, RUTACEAE

367. Stucky J M 1985. Pollination systems of sympatric Ipomaea hederacea and I purpurea and the significance of interspecific pollen flow. American Journal of Botany 72, 32-43. BREEDING SYSTEMS, CONVOLVULACEAE, POLLEN MOVEMENT, SEED SET

368. Sussman R W and Raven P H 1978. Pollination by lemurs and marsupials: an archaiac coevolutionary system. Science 200, 731-736. REVIEW, THEROPHILY

369. Taylor N L, Quesenberry K H and Anderson M K 1979. Genetic system relationships in Trifolium. Economic Botanist 33, 431-441. BREEDING SYSTEMS, FABACEAE, MORPHOLOGY

370. Thonner F 1908. Die Blütenpflanzen Afrikas. Berlin. REVIEW

371. Thulin M 1975. The genus Wahlenbergia S. Lat. (Campanulaceae) in tropical Africa and Madagascar. Symbolae Botanicae Upsalienses 21, 1. BREEDING SYSTEMS, CAMPANULACEAE, ENTOMOPHILY: HYMENOPTERA, INCOMPATIBILITY

372. Tölken H R 1977. A revision of the genus Crassula in southern Africa. Contributions to the Bolus Herbarium 8. CRASSULACEAE, MORPHOLOGY, PHENOLOGY

373. Torr S M 1973. The fauna associated with Proteas. Unpublished Zoology third year project, University of Cape Town. ANTHESIS, ENTOMOPHILY: COLEOPTERA, ORNITHOPHILY, PHENOLOGY, PROTEACEAE

374. Tribe G D 1983. What is the Cape Bee? South African Bee Journal 55, 77-87. ENTOMOPHILY: HYMENOPTERA

375. Trimen R 1864. On the fertilization of Disa grandiflora. Journal of the Linnean Society of Botany 7, 144-147. ENTOMOPHILY: LEPIDOPTERA, ORCHIDACEAE

376. Trimen R 1865. On the structure of Bonatea speciosa, Linn species, with reference to its fertilization. Journal of the Linnean Society of Botany 9, 156-160. MORPHOLOGY, ORCHIDACEAE

377. Tsacas L and Lachaise D 1979. African radiation of Lissocephala related to Ficus diptera (Drosophilidae). Annals of the Society of Entomology of France 15, 589-603. EVOLUTION, MORACEAE

378. Valdeyron G and Lloyd D G 1979. Sex differences and flowering phenologies in the common fig, Ficus carica L. Evolution 33, 573-685. ENTOMOPHILY: AGAONIDAE, MORACEAE, PHENOLOGY

379. Van Wilgen B W and Lamb A J 1986. The flower picking industry in relation to mountain catchment management in the fynobs. Acta Horticulturae 185, 181-187. APPLIED

380. Visser C 1966. Anatomie van stingels van Protea repens en Leucadendron adscendens. Journal of South African Botany. MORPHOLOGY, PROTEACEAE

381. Visser J 1981. South African parasitic flowering plants. Juta, Cape Town. ENTOMOPHILY, ORNITHOPHILY, PHENOLOGY

382. Vogel S 1954. Blutenbiologische Typen als Elemente der Sippengliederung: Dargestellt annhard der flora Südafrikas. Gustav Fischer: Jena. REVIEW

383. Vogel S 1955. Über den Blütendimorhismums einiger Südafrikanischer Pflanzen. Österr. Bot. Z. 102, 486-500. MORPHOLOGY

384. Vogel S 1959. Organographie der Blüten kapländischer Ophrydeen mit Bemerken zum Koaptationsproblem. I. Disinae und Satyriinae. Abhandlurgen der Akademie der Wissenschaften der DDR Abterlung - Naturwissenschaften 7, 265-402. MORPHOLOGY, ORCHIDACEAE

385. Vogel S 1959. Organographie der Blüten kapländischer Ophrydeen mit Bemerken zum Koaptationsproblem. II. Disperidinae - Über Beziehungssystem und Koaptation der Ophrydeenblüten. Abhandlurgen der Akademie der Wissenschaften der DDR Abterlung - Naturwissenschaften Kl. 7, 403-532. MORPHOLOGY, ORCHIDACEAE

386. Vogel S 1961. Die Bestäubung der Kesselfallenblüten von Ceropygia. Beitraege zur biologie der Pflanzer 36, 159-237. ASCLEPIACACEAE, ENTOMOPHILY: DIPTERA

387. Vogel S 1974. Ölblumen und Ölsammelnde Bienen. Trop. Subtrop. Pflanzenwelt 7, 283-547. ENTOMOPHILY: HYMENOPTERA, OIL

388. Vogel S 1981. Bestaubungskonzepte der Monokotylen und ihr Ausdruk im System. Berichte der Deutschen Botanischen Gessellschaft 94: 663-675.

389. Vogel S 1984. The Diascia flower and its bee- and oil-based symbiosis in southern Africa. Acta Botanica Neerlandica 33: 509-518. BEHAVIOUR, ENTOMOPHILY: HYMENOPTERA, OIL, SCROPHULARIACEAE

390. Vogel S and Michener C D 1985. Long bee legs and oil-producing floral spurs and a new *Rediviva* (Hymeroptera, Mellittidae; Scrophularinaceae). Journal of the Kansas Entomological Society 58, 359-364. BEHAVIOUR, ENTOMOPHILY: HYMENOPTERA, OIL, SCROPHULARIACEAE

391. Vogts M M 1971. Geografie en geografiese variasie van *Protea cynaroides*. Unpublished PhD Thesis, University of Stellenbosch. MORPHOLOGY, PHENOLOGY, PROTEACEAE

392. Vogts M M (editor) 1977. Farming in South Africa. Series: flowers, ornamental shrubs and trees. B. proteas. B.8. The bearded proteas: *Protea magnifica*, (*P barbigera*) *Protea grandiceps* and *Protea neriifolia*. Horticultural Research Institute, Pretoria. APPLIED, PHENOLOGY, PROTEACEAE

393. Vogts M M (editor) 1977. Farming in South Africa. Series: flowers, ornamental shrubs and trees. B. Proteas. B.9. *Protea cynaroides* (L.) L. intensive cut-flower cultivation: Part 1. giant or king protea. Horticultural Research Institute, Pretoria. APPLIED, PHENOLOGY, PROTEACEAE

394. Vogts M M (editor) 1977. Farming in South Africa. Series: flowers, ornamental shrubs and trees, B. Proteas. B.10. *Protea cynaroides* (L.) L. intensive cut-flower cultivation: Part II. giant or king protea. Horticultural Research Institute, Pretoria. APPLIED, PHENOLOGY, PROTEACEAE

395. Vogts M 1982. South Africa's Proteaceae, know them and grow them. Struik, Cape Town. APPLIED, ORNITHOPHILY, PHENOLOGY, PROTEACEAE

396. Volkens G 1899. Über die Bestäubung einiger Loranthaceen und Proteaceen. Festchr. f. Schwendener, 251-270. LORANTHACEAE, ORNITHOPHILY, PROTEACEAE

397. Vos M P de 1972. The genus *Romulea* in South Africa. Journal of South African Botany, Supplementary Volume 9. HYBRIDIZATION, IRIDACEAE, MORPHOLOGY, PHENOLOGY

398. Walt J J A van der 1977. Pelargoniums of southern Africa. Purrnell, Cape Town. GERANIACEAE, PHENOLOGY

399. Walt J J A van der and Vorster P J 1981. Pelargoniums of southern Africa. Juta, Kenwyn. GERANIACEAE, PHENOLOGY

400. Wanndorp H E 1974. *Calotropis gigantea* (Asclepidacee) and *Xylocopa tenuscapa* (Hymenoptera, Apoidea). Svensh Botanisk Tidskrift 68, 25-32. ASCLEPIACACEAE, ENTOMOPHILY: HYMENOPTERA

401. Watmough R H 1974. Biology and behaviour of carpenter bees. Journal of the Entomological Society of southern Africa 3, 261-281. BEHAVIOUR, ENTOMOPHILY: HYMENOPTERA, LIFE CYCLES

402. Weale J P M 1869. Notes on the structure and fertilization of the genus *Bonatea* with a special description of a species *B darwinii* found at Bedford, South Africa. Journal of the Linnean Society 10, 470-476. ENTOMOPHILY, ORCHIDACEAE

403. Weale J P M 1871. Notes on a species of *Disperis* found on the Kagaberg, South Africa. Journal of the Linnean Society of Botany 13, 42-45. ORCHIDACEAE

404. Weale J P M 1871. Some observations on the fertilization of *Disa macrantha*. Journal of the Linnean Society of Botany 13, 45-47. ENTOMOPHILY, ORCHIDACEAE

405. Weale J P M 1871. Notes on some species of *Habenaria* found in South Africa. Journal of the Linnean Society of Botany 13, 47-48. ORCHIDACEAE

406. Weale J P M 1871. Observations on the mode in which certain species of Asclepiadeae are fertilized. Journal of the Linnean Society of Botany 13, 48-58. ENTOMOPHILY, ASCLEPIADACEAE

407. Weberling F 1983. Fundamental features of modern inflorescence morphology. Bothalia Kl, 917-922. MORPHOLOGY

408. Weisser P and Weisser J 1975. Notes on aloes and hummingbirds in central Chile. Excelsa 5, 100-103. BEHAVIOUR, MORPHOLOGY, ORNITHOPHILY

409\. Weller S G 1981. Pollination biology of heteromorphic populations of *Oxalis alpina* (Rose) Knuth (Oxalidaceae) in south-eastern Arizona. Botanical Journal of the Linnean Society 83, 189-198. BREEDING SYSTEMS, OXALIDACEAE

410\. Weller S G 1981. Fecundity in populations of *Oxalis alpina*. Evolution 35, 197-200. BREEDING SYSTEMS, OXALIDACEAE, SEED SET

411\. Werth E 1900. Nektarinidenblumen in Ostrafrika. Verhandlungen des Botanischen Vereins der Provinz Brandenburg 42, 222-260. ORNITHOPHILY

412\. Werth E 1915. Kurzer Öberblick über die Gesamtfrage der Ornitholophilie. Botanische Jahrbuecher fuer Systematik Pflanzengeschichte und Planzengeographie 53, 1-313. ORNITHOPHILY

413\. Werth E 1923. Über die Bestäubung von Viscum und Loranthus. Berichte der Deutschen Botanischen Gesellschaft 41, 151-164. LORANTHACEAE, ORNITHOPHILY

414\. Werth E 1942. Über einige umstrittene oder weniger bekannte Bestäubungseintichtungen tropischer Blumen. Berichte der Deutschen Botanischen Gesellschaft 40, 473.

415\. Wharton R A 1980. Insects and arachnids associated with *Zygophyllum simplex* (Zygophyllaceae) in the Namib Desert. Madoqua 12, 131-139. ENTOMOPHILY, PHENOLOGY, ZYGOPHYLLACEAE

416\. Wharton R A, Tilson J W and Tilson R L 1980. Asynchrony in a wild population of *Ficus sycomorus* L. South African Journal of Science 76, 478-480. DEMOGRAPHY, ENTOMOPHILY: AGOANIDAE, MORACEAE, PHENOLOGY

417\. Whitehead D R 1968. Wind pollination in the Angiosperms: evolutionary and environmental considerations. Evolution 23, 28-35. ANEMOPHILY, REVIEW

418\. Whitehead V B 1984. Distribution, biology and flower relationships of fideliid bees of southern Africa (*Hymenoptera*, *Apoidea*, Fideliidae). South African Journal of Zoology 19, 97-90. BEHAVIOUR, BREEDING, ENTOMOPHILY: HYMENOPTERA, LIFE CYCLE

419\. Whitehead V B and Prins A J 1975. The European Wasp, *Vespula germanica* (F.), in the Cape Province. Journal of the Entomological Society of southern Africa 38, 39-47. ALIENS, APPLIED, ENTOMOPHILY: HYMENOPTERA, LIFE CYCLE, MORPHOMETRICS

420\. Whitehead V B, Schelpe E A C L E and Anthony N C 1984. The bee, *Rediviva longimanus* Michener (Apoidea: Melittidae) collecting pollen and oil from *Diascia longicornis* (Thunb.) Druce (Scrophulariaceae). South African Journal of Science 80, 286. BEHAVIOUR, ENTOMOPHILY: HYMENOPTERA, OIL, SCROPHULARIACEAE

421\. Whitehead V B and Steiner K 1985. Oil-collecting bees in South Africa. African Wildlife 31, 144-146. BEHAVIOUR, ENTOMOPHILY: HYMENOPTERA, LIFE CYCLES, OIL, SCROPHULARIACEAE

422\. Wiebes J J 1981. Towards strategy concepts in flower ecology as exemplified by the fig-wasp symbiosis. Acta Botanica Neerlendica 30, 493-495. ENTOMOPHILY: AGAONIDAE, EVOLUTION, MORACEAE

423\. Wiens D 1978. Mimicry in plants. Evolutionary Biology 11, 365-403. ASTERACEAE, MIMICRY, ORCHIDACEAE, REVIEW

424\. Wiens D and Rourke J P 1978. Rodent pollination in southern Africa *Protea* species. Nature 276, 71-73. BEHAVIOUR, MORPHOLOGY, PROTEACEAE, THEROPHILY

425. Wiens D and Rourke J P, Casper B B, Rickart E A, Lapine T R, Peterson C J and Channing A 1983. Nonflying mammal pollination of southern African proteas: a non-coevolved system. Annals of the Missouri Botanic Gardens 70, 1-31. ANTHESIS, BEHAVIOUR, BREEDING SYSTEMS, ENERGETICS, EVOLUTION, MORPHOLOGY, NECTAR CONSTITUTION, NECTAR SECRETION, ORNITHOPHILY, POLLEN MOVEMENT, POLLEN VIABILITY, PROTEACEAE, SEED SET, THEROPHILY

426. Williams I J M 1972. A revision of the genus *Leucadendron*. Contributions to the Bolus Herbarium 3, 1-425. ANEMOPHILY, ENTOMOPHILY, NECTAR SECRETION, PHENOLOGY, PROTEACEAE

427. Williamson G 1976. Orchids of south central Africa: some interesting miniature terrestrials. Orchid Review 376-380. BREEDING SYSTEMS, ENTOMOPHILY: DIPTERA, ORCHIDACEAE

428. Williamson G 1984. Observations of a mechanism by which self-pollination may occur in *Eulophia* (Orchidaceae). Journal of South African Botany 50, 417-423. BREEDING SYSTEMS, ORCHIDACEAE

429. Willson M F and Rathcke B J 1974. Adaptive design of the floral display in *Asclepics syriaca* L. American Midland Naturalist 92, 47-57. ASCLEPIADACEAE, MORPHOLOGY, SEED SET

430. Wilson J H 1886. On the adaptation of *Albuca corymbosa* and *Albuca juncifolia* to insect fertilization. Transactions of the Proceedings of the Botanical Society of Edinburgh 16, 365-370. ASPHODELACEAE, ENTOMOPHILY, MORPHOLOGY

431. Wilson J H 1887. The dimorphism of the flowers of *Wachendorfia paniculata*. Transactions of the Proceedings of the Botanical Society of Edinburgh 17, 73-77. HAEMODORACEAE, MORPHOLOGY

432. Wilson J H 1891. Observations on the fertilization and hybridization of some species of *Albuca*. Botanische Jahrbuecher fuer Systematik Pflanzengeschichte und Planzengeographie 3, 232-258. ASPHODELACEAE, ENTOMOPHILY

433. Wilson J H 1893. On the prolongation of the flowering period of *Tritonia* (Montbretia) *wilsoni*. Transactions of the Proceedings of the Botanical Society of Edinburgh 19, 166-167. APPLIED, IRIDACEAE, PHENOLOGY

434. Winterbottom J M 1962. Breeding season of long-tailed sugarbird *Promerops cafer* (L). Ostrich 33, 77. BREEDING, ORNITHOPHILY

435. Winterbottom J M 1964. Notes on the comparative ecology of the long-tailed sugarbird and the orange-breasted sunbird. Ostrich 35, 239-240. BREEDING, ERICACEAE, ORNITHOPHILY, PROTEACEAE

436. Winterbottom J M 1971. Seasonal changes in the passerine avifauna of the Cape macchia. Ostrich 42, 291-293. ORNITHOPHILY

437. Winterbottom J M 1978. Birds. In: Werger M J A (editor) Biogeography and ecology of southern Africa. W Junk, The Hague. pp 949-979. ORNITHOPHILY

438. Wolf L L 1975. Energy intake and expenditures in a nectar-feeding sunbird. Ecology 56, 92-104. ASPHODELACEAE, BEHAVIOUR, ENERGETICS, FORAGING ECOLOGY, NECTAR SECRETION, ORNITHOPHILY

439. Wolf L L 1978. Aggressive social organization in nectarivorous birds. American Zoology 18, 765-778. ENERGETICS, FORAGING ECOLOGY, ORNITHOPHILY

440. Wolf L L and Gill F B 1980. Resource gradients and community organization of nectarivorous birds. Acta 17 Congress International 2, 1105-1113. FORAGING ECOLOGY, ORNITHOPHILY

441. Wolf L L and Hainsworth F R 1985. Economics of foraging strategies in sunbirds and hummingbirds. In: Aspey W P and Lustick S I (editors) Behavioural energetics, the cost of survival in vertebrates. Ohio State University Press, Columbia. pp 223-264. BEHAVIOUR, ENERGETICS, FORAGING ECOLOGY, ORNITHOPHILY

442. Wolf L L, Hainsworth F R and Gill F B 1975. Foraging efficiencies in time budgets in nectar-feeding birds. Ecology 56, 117-127. BEHAVIOUR, ENERGETICS, FORAGING ECOLOGY, NECTAR SECRETION, ORNITHOPHILY

443. Wolf L L and Wolf J S 1976. Mating system and reproductive biology of malachite sunbirds. Condor 78, 27-39. ASPHODELACEAE, BEHAVIOUR, BREEDING, DEMOGRAPHY, ORNITHOPHILY

444. Wooller R D 1982. Feeding interactions between sunbirds and sugarbirds. Ostrich 53, 114-115. BEHAVIOUR, ORNITHOPHILY, PROTEACEAE

445. Wolley-Dod A H 1886. Time of flowering of Cape bulbs. Garden Chronicle Series 2, 25: 210. PHENOLOGY

446. Woycicky Z 1927. Grains de pollen, tubes polliniques et spermatogenese chez *Haemanthus katharinae* Bulletin de l'academie Polonaise des Sciences Serie des Sciences biolegiques 1926, 177-188. AMARYLLIDACEAE, PALYNOLOGY

447. Young D A 1972. The reproductive biology of *Rhus integrifolia* and *Rhus ocata* (Anacardiaceae). Evolution 26, 405-414. ANACARDIACEAE, BREEDING SYSTEM, ENTOMOPHILY: HYMENOPTERA, HYBRIDIZATION, MORPHOLOGY, SEED SET

448. Wyk S van 1983. 'n Monographiese studie van die genus *Virgilia* Poir. Unpublished MSc Thesis, University of Stellenbosch. MORPHOLOGY, FABACEAE

449. Zinderen Bakker E M van 1953. South African pollen grains and spores. Part 1, 1-88. Balkema, Cape Town. PALYNOLOGY

CONCLUSIONS

Pollination in the Cape flora is poorly studied. Community studies of outbreeding and compatibility levels are almost nonexistant. Little is known about insect pollinators. No research has been undertaken on wind pollination or gene flow in the Cape flora. Human impacts, whether by picking, introducing alien species, increasing grazing or modifying habitats by ubanization and agriculture, on pollination in the Cape flora are unknown.

Nevertheless a great potential exists in the Cape flora. Pollination is a key component to the high species diversity of plants and insects (especially bees) in the Cape flora. The close proximity of 'nutrient-rich' and 'nutrient-poor' soils, high and low rainfall, and high and low altitudes makes the Cape flora an ideal testing ground for exploring theories of community organization and population biology.

The future direction of pollination studies in the Cape flora are clear. Research themes considered to be of critical importance in the Cape flora are outlined in Appendix 1. Research in the pollination biology of the Cape flora should concentrate on the interplay between the fragmented plant populations, the behavorial specificity of pollinators and the incompatibility systems of plants, all of which contributed to the evolution and maintenance of the high plant species richness in plant communities on 'nutrient-poor' substrata.

Paramount in initiating a study of pollination biology in the Cape flora is an education of the layman for the creation of a multiracial amateur naturalist class, and the involvement of international pollination biologists in studies in the Cape flora.

In addition, the conservation of representative vegetation communities within the Cape flora is essential.

SUBJECT KEYWORD INDEX

ALIENS
44, 62, 96, 138, 139, 171, 216, 228, 259, 310, 343, 419.

ANEMOPHILY
19, 127, 181, 206, 239, 240, 299, 301, 304, 417, 426.

ANTHESIS
14, 33, 45, 58, 61, 63, 75, 76, 92, 99, 107, 113, 122, 143, 147, 338, 360, 361, 364, 366.

APICULTURE
3, 4, 41.

APPLIED
3, 4, 29, 30, 31, 32, 33, 34, 41, 42, 52, 67, 81, 91, 95, 100, 149, 150, 151, 152, 153, 154, 158, 183, 186, 208, 209, 210, 213, 224, 225, 226, 227, 298, 379, 392, 393, 394, 395, 419, 433.

BEHAVIOUR (OF FLOWER VISITORS)
3, 4, 6, 11, 15, 16, 35, 36, 37, 59, 60, 61, 76, 85, 98, 104, 105, 110, 112, 114, 115, 139, 176, 185, 220, 221, 222, 253, 262, 302, 306, 310, 333, 334, 335, 342, 357, 363, 389, 390, 401, 408, 418, 420, 421, 424, 438, 441, 442, 443, 444.

BREEDING (OF FLOWER VISITORS)
4, 35, 36, 39, 47, 185, 211, 212, 333, 418, 434, 435, 443.

BREEDING SYSTEMS (OF PLANTS)
6, 14, 16, 17, 26, 30, 43, 61, 75, 76, 83, 86, 93, 97, 99, 121, 122, 124, 128, 136, 143, 157, 170, 177, 178, 188, 189, 216, 223, 229, 230, 231, 245, 247, 248, 249, 259, 281, 284, 297, 298, 299, 409, 410.

CHIROPTEROPHILY
155, 204.

DEMOGRAPHY
24, 109, 113, 131, 182, 219, 231, 322, 416, 443.

ENERGY UTILIZATION (OF PLANTS)
66, 67, 68, 82, 95, 158, 186.

ENERGETICS (OF VISITORS)
57, 59, 60, 61, 98, 112, 114, 115, 117, 118, 185, 233, 234, 425, 438, 439, 441.

ENTOMOPHILY (GENERAL)
5, 8, 15, 17, 19, 51, 52, 54, 61, 69, 78, 113, 143, 159, 169, 171, 178, 181, 188, 197, 198, 201, 202, 221, 222, 247, 253, 286, 287, 297, 299, 301, 304, 307, 308, 319, 328, 341, 347, 353, 354, 365, 366, 381, 402, 404, 406, 415, 426, 430, 432.

ENTOMOPHILY: ACARINA
55, 293, 323, 324.

SUBJECT KEYWORD INDEX
(continued)

ENTOMOPHILY: AGAONIDAE
6, 101, 102, 103, 104, 105, 378, 416, 422.

ENTOMOPHILY: COLEOPTERA
28, 37, 53, 90, 100, 110, 146, 157, 201, 207, 225, 226, 228, 302, 312, 373.

ENTOMOPHILY: DIPTERA
42, 73, 108, 121, 138, 139, 283, 294, 311, 362, 386, 427.

ENTOMOPHILY: HYMENOPTERA
3, 4 , 16, 27, 81, 107, 121, 123, 124, 127, 137, 139, 140, 170, 185, 212, 232, 234, 241, 252, 262, 288, 306, 325, 326, 334, 335, 348, 362, 363, 371, 374, 387, 389, 390, 400, 401, 418, 419, 420, 421, 447.

ENTOMOPHILY: LEPIDOPTERA
16, 48, 49, 50, 64, 65, 77, 108, 122, 124, 127, 133, 134, 180, 193, 280, 331, 334, 335, 358, 360, 375.

ENTOMOPHILY: THRIPS
127, 128.

EVOLUTION
8, 15, 69, 92, 173, 174, 175, 181, 189, 204, 243, 244, 245, 300, 318, 320, 359, 377, 422, 425.

FLORA
2, 20, 21, 88, 187, 200, 242, 327.

FORAGING ECOLOGY
4, 36, 47, 57, 58, 59, 60, 61, 81, 98, 112, 113, 114, 115, 116, 117, 118, 185, 221, 222, 235, 310, 438, 439, 440, 441, 442.

GENE FLOW
16, 17, 26, 132, 181, 281, 334.

HYBRIDIZATION
30, 31, 34, 86, 121, 122, 145, 179, 184, 190, 191, 284, 316, 320, 329, 337, 343, 352, 354, 366, 447.

INCOMPATIBILITY
86, 165, 229, 284, 371.

LIFE CYCLES (AND PHENOLOGY OF INSECTS)
48, 49, 50, 64, 65, 77, 110, 134, 139, 283, 325, 326, 335, 401, 418, 419, 421.

MIGRATION (SEASONAL MOVEMENT OF FLOWER VISITORS)
258, 294, 300, 333, 345.

MIMICRY
146, 423.

SUBJECT KEYWORD INDEX
(continued)

MORPHOLOGY (OF BLOSSOMS)
6, 13, 15, 45, 61, 63, 71, 75, 76, 80, 90, 92, 98, 99, 107, 108, 113, 114, 123, 124, 125, 136, 137, 140, 142, 147, 157, 162, 163, 164, 166, 169, 170, 180, 199, 202, 223, 229, 231, 244, 245, 246, 249, 250, 263, 282, 299, 300, 301, 305, 312, 313, 314, 318, 319, 331, 338, 347, 355, 369, 372, 376, 380, 383, 384, 385, 391, 407, 408, 424, 425, 429, 430, 431, 447, 448.

MORPHOMETRICS (OF FLOWER VISITORS)
61, 117, 331, 419.

NECTAR CONSTITUTION
9, 38, 47, 66, 68, 136, 220, 221, 222, 357, 425.

NECTAR SECRETION
38, 57, 58, 59, 61, 76, 93, 98, 99, 112, 113, 114, 115, 116, 117, 118, 138, 157, 161, 166, 176, 180, 185, 221, 222, 251, 295, 306, 335, 357, 425, 426, 438, 442.

OIL (REWARD)
389, 390, 420, 421.

ORNITHOPHILY
5, 10, 11, 18, 28, 47, 53, 58, 60, 61, 70, 71, 85, 90, 92, 93, 98, 99, 106, 112, 113, 114, 115, 116, 117, 118, 119, 125, 135, 136, 137, 140, 143, 148, 157, 178, 181, 194, 220, 221, 222, 235, 237, 245, 257, 266, 267, 268, 269, 270, 271, 272, 273, 274, 275, 276, 280, 292, 295, 296, 297, 299, 300, 301, 306, 312, 318, 320, 321, 322, 336, 339, 340, 341, 342, 344, 345, 346, 347, 349, 350, 351, 357, 359, 361, 373, 381, 395, 396, 408, 411, 412, 413, 425, 434, 435, 436, 437, 438, 439, 440, 441, 442, 443, 444.

PALYNOLOGY
40, 71, 84, 94, 148, 157, 166, 185, 190, 191, 206, 217, 241, 245, 252, 446, 449.

PHENOLOGY (OF PLANTS)
2, 4, 7, 12, 16, 21, 22, 24, 29, 32, 33, 34, 46, 61, 74, 82, 87, 93, 109, 119, 120, 121, 122, 129, 130, 131, 136, 139, 143, 149, 150, 151, 152, 153, 154, 156, 167, 170, 172, 177, 178, 179, 180, 182, 183, 187, 192, 203, 205, 210, 214, 219, 228, 229, 236, 239, 240, 241, 249, 251, 255, 257, 260, 261, 264, 285, 286, 288, 289, 290, 291, 299, 300, 305, 309, 312, 313, 314, 316, 317, 318, 319, 330, 335, 337, 345, 354, 356, 357, 358, 360, 372 373, 378, 381, 391, 392, 393, 394, 395, 397, 399, 415, 426, 433, 445.

POLLEN MOVEMENT
17, 58, 61, 93, 105, 126, 166, 210, 230, 253, 306, 367, 425.

POLLEN VIABILITY
58, 191, 425.

REVIEW
5, 8, 61, 69, 72, 94, 131, 168, 194, 204, 212, 215, 218, 256, 260, 291, 304, 350, 370.

SUBJECT KEYWORD INDEX
(continued)

SEED SET
1, 3, 13, 14, 24, 53, 58, 61, 75, 81, 89, 125, 126, 135, 136, 143, 144, 145, 159, 177, 178, 193, 207, 216, 229, 245, 248, 249, 288, 298, 335, 367, 410, 425, 429.

THEROPHILY
61, 176, 181, 265, 277, 278, 279, 315, 317, 320, 368, 424, 425.

PLANT TAXONOMICAL KEYWORD INDEX

(Arranged alphabetically by family. Numbers in parentheses are the number of genera and species per family, respectively).

ACANTHACEAE (12, 27) -

AIZOACEAE (13, 109) -

AMARYLLIDACEE (15,83) 192, 354, 446.

ANACARDIACEAE (4,28) 447.

APIACEAE (24, 100) -

APONOGETONACEAE (1, 4) 328.

ARACEAE (1, 1) 145.

ASCLEPIADACEAE (29, 125) 63, 84, 159, 307, 308, 365, 386, 400, 406, 429.

ASPHODELACEAE (12, 172) 10, 156, 189, 190, 191, 203, 217, 237, 238, 305, 337, 430, 432, 438, 443.

ASTERACEAE (109, 986) 56, 107, 146, 188, 296, 334, 335, 353, 364, 423.

BALSAMINACEAE (1, 1) 332.

BRASSICACEAE (10,70) -

BRUNIACEAE (12, 75) 251, 264.

CAMPANULACEAE (16, 222) 75, 76, 371.

CHENOPODIACEAE (9,21) 19.

COLCHICACEAE (6, 30) 236.

CONVOLVULACEAE (5, 16) 367.

CRASSULACEAE (5, 124) 372.

CYPERACEAE (26, 203) -

PLANT TAXONOMICAL KEYWORD INDEX
(continued)

ERICACEAE (22, 672) 7, 12, 59, 73, 127, 128, 137, 140, 239, 241, 250, 288, 289, 291, 292, 299, 301, 306, 329, 347, 435.

EUPHORBIACEAE (14, 97) 303.

FABACEAE (38, 644) 9, 46, 79, 81, 93, 94, 97, 125, 136, 185, 216, 220, 234, 238, 258, 259, 357, 363, 369, 448.

GENTIANACEAE (5, 33) 142, 244.

GERANIACEAE (5, 133) 88, 199, 398, 399.

GOODENIACEAE (1,1) 169.

GYMNOSPERMAE (4, 13) 23, 91.

HAEMODORACEAE (3, 10) 246, 249, 431.

HYACINTHACEAE (20, 154) 284, 355, 360.

HYDNORACEAE (1, 1) 196.

IRIDACEAE (39, 612) 74, 109, 120, 121, 122, 123, 145, 147, 179, 223, 247, 397, 433.

LABIATAE (8, 42) 98, 113, 114, 116, 117, 118, 263, 362.

LINACEAE (1, 14) 229, 230, 231.

LORANTHACEAE (2, 2) 89, 92, 115, 119, 396, 413.

MALVACEAE (5, 26) 14, 85, 280, 352.

MESEMBRYANTHEMACEAE (61, 660) -

MORACEAE (1, 4) 6, 101, 102, 103, 104, 105, 173, 174, 175, 377, 378, 416, 422.

MYRTACEAE (2, 2) 96, 138, 139, 143, 183, 343.

ORCHIDACEAE (28, 206) 13, 20, 78, 83, 108, 129, 130, 180, 193, 268, 358, 375, 376, 384, 385, 402, 403, 404, 405, 423, 427, 428.

OXALIDACEAE (1, 129) 245, 248, 31, 409, 410.

PENEACEAE (7, 21) 70, 219.

PLANT TAXONOMICAL KEYWORD INDEX
(continued)

PLANTAGINACEAE (1, 3) 51.

POACEAE (61, 181) 43, 56, 86.

POLYGALACEAE (3, 139) -

PROTEACEAE (14, 320) 1, 11, 24, 28, 29, 30, 31, 32, 33, 34, 37, 38, 45, 52, 53, 54, 55, 57, 58, 59, 61, 66, 67, 68, 90, 95, 100, 110, 144, 149, 150, 152, 153, 154, 157, 158, 177, 178, 182, 186, 207, 208, 209, 213, 214, 221, 222, 224, 225, 226, 227, 253, 282, 292, 293, 297, 298, 300, 302, 311, 312, 313, 314, 315, 316, 317, 318, 319, 320, 322, 323, 324, 336, 342, 373, 380, 391, 392, 393, 394, 395, 396, 424, 425, 426, 435, 444.

RESTIONACEAE (19, 310) -

RETZIACEAE (1,1) 71.

RHAMNACEAE (4, 136) -

RORIDULACEAE (1,2) 195.

ROSACEAE (7, 114) -

RUBIACEAE (15, 54) -

RUTACEAE (14, 259) 202, 366.

SANTALACEAE (4, 88) -

SCROPHULARIACEAE (35, 310) 361, 389, 390, 420, 421.

SOLANACEAE (2, 19) 25, 135

STERCULIACEAE (2, 64) -

STRELITZIACEAE (1, 3) 99, 160, 161, 162, 163, 164, 165, 166, 339, 349, 351.

TECOPHILIACEAE (2, 6) 80, 246.

THYMELAEACEAE (5, 122) 141, 206.

TILIACEAE (2, 2) 338.

VERBENACEAE (1, 3) 171, 331.

PLANT TAXONOMICAL KEYWORD INDEX
(continued)

VIOLACEAE (2, 2) 15, 16, 17.

VISCACEAE (1, 6) 119.

ZAMIACEAE (1, 4) 201, 254, 287.

ZYGOPHYLLACEAE (3,17) 415.

APPENDIX 1: RESEARCH THEMES OF CRITICAL IMPORTANCE

A G Rebelo

Listed below are the research themes rated by the chapter authors as the most important issues in pollination biology requiring attention at present. The list was compiled as follows:

The authors of each chapter, based on their respective reviews, independently submitted a list of five key questions which they felt required urgent attention. After the ellimination of duplicate questions the list below was circulated to the authors who ranked them from most (1) to least important.

The research themes are presented below as originally submitted. The figures in parentheses are their mean score, the number of scores above 10, and the maximum and minimum scores out of the six ratings returned.

Although a bias towards insect-pollination was anticipated, this did not materialize. Research themes rated most important indicate a curious mix of theoretical (1) and natural history (2) approaches, underlying the need for nurturing naturalists in order to obtain the basic observations necessary for theoretical investigations of the Cape flora.

Interestingly, the study of 'the rates of gene flow within a plant species' rated far lower (9) than the study of 'rates of gene flow between populations of a plant species' (1). The large number of plant species comprising isolated populations probably explains this bias towards '1', and together with '2' and '3', suggest that the role of gene flow, pollination and incompatibility systems in the evolution and maintenance of the high species richness of the Cape flora is a paramount key question. How wind pollinated speices maintain such a high species richness (4) is simply baffling.

Conservation also features prominently in the top research themes: 1,2,5,7 and 10 deal with prime components in pollination aspects of conservation biology. However, the effects of aliens (16, 17) and commercial undertakings (15, 17) are rated rather low in importance among the top 22 themes.

1. Rates of gene flow between populations of plants of the major pollination syndromes. (7.0, 5, 1-11)

2. The degree of pollinator specificity in the major vegetation types, especially where seasonal or juvenile phases may require different habitats. (8.0, 5, 4-14)

3. Incompatability systems in major plant genera. (8.2, 4, 2-22)

4. Community level studies of wind pollination, related to climate, and plant demography and distribution. (8.2, 3, 2-15)

5. Minimum viable population sizes in plants. (8.8, 4, 1-21)

6. Community level studies of plant breeding systems. (9.2, 4, 3-17)

7. Community level studies of pollinator abundance and seasonality. (9.3, 4, 3-16)

8. Pollination biology of the major plant breeding systems. (9.5, 3, 1-19)

9. Rates of gene flow for the major pollination syndromes. (9.5, 3, 3-18)

10. The effects of insularization on pollinator movements and pollinator plant interactions in the different vegetation communities. (9.8, 3, 1-18)

11. Comparative studies of reproductive biology in genera exhibiting more than one pollination syndrome (eg *Erica*, *Leucadendron*, *Protea*). (10.2, 2, 3-15)

12. Why are some pollination syndromes more restricted in their distribution to nutrient-poor communities? (10.2, 2, 6-15)

13. Patterns of genetic diversity in the major plant breeding systems. (10.8, 3, 5-16)

14. A central slide reference collection or an illustrated slide index of pollen spores for the Cape flora is required. (11.0, 3, 1-21)

15. The effects of commercial picking on pollinator dynamics and plant seed set. (12.0, 2, 2-22)

16. What are the comparative energy and nutrient demands made on plants in catering for different pollen vectors. (12.7, 2, 4-20)

17. The effects of commercial apiaries and alien pollinators (eg *Vespula*) on indigenous pollinators and plants visited. (14.0, 2, 8-19)

18. Correlations between pollination syndromes and geologically preserved or inferable features are needed to interpret the fossil record in terms of pollination biology. (14.2, 3, 4-22)

19. Reproductive biology of the fire-adapted annuals and geophytes which flower only in the immediate post-fire environment. (15.7, 0, 12-18)

20. Comparative pollination in the families Asteraceae and Orchidaceae. (16.2, 1, 8-22)

21. Pollen calendars are required for aeropalynology and would contribute to an understanding of wind pollination. (16.3, 3, 7-21)

22. Why do rodent pollinated Proteaceae tend to occur in small populations? (17.5, 1, 7-22)

APPENDIX 2: WORK CURRENTLY UNDERWAY IN SOUTHERN AFRICA

TITLE: Sexual selection in Leucadendron.
RESEARCHER: Bond W J and Midgley J (Saasveld Forestry Research Centre)
STATUS: In progress.

We have attempted to explain vegetative dimorphism in Leucadendron in terms of sexual selection and interspecific variation in dimorphism in terms of different pollinators. We may extend this work to look further at pollination in Leucadendron.

TITLE: Flower-colour polymorphism in the George lily.
RESEARCHER: Bond W J and Vlok J (Saasveld Forestry Research Centre)
STATUS: In progress.

The genetic and pollination biology of flower-colour polymorphism in the George lily (Vallota / Cyrtanthus purpureus / speciosus / elatus (Amaryllidaceae)) is being investigated.

TITLE: Pollination of red petaloid monocots.
RESEARCHER: Bond W J and Vlok J (Saasveld Forestry Research Centre)
STATUS: In progress.

The behaviour of a butterfly Meneris tulbaghiae is being investigated in an attempt to explain the group of red petaloid monocots which flower in summer in fynbos.

TITLE: Quality of Protea pollination.
RESEARCHER: Bond W J and Vlok J (Saasveld Forestry Research Centre)
STATUS: Planned.

The consequences of different patterns of pollen-flow for seed quality in Proteaceae are unknown. The question posed is whether beetles and sugarbirds as pollinators have different effects on recruitment after seed set.

TITLE: Pollinator success in Protea
RESEARCHER: Breytenbach G J and Breytenbach W (Saasveld Forestry Research Centre)
STATUS: In progress.

The effect of bird versus insect versus control exclosure experiments on Protea lorifolia, P repens, P punctata, and P eximia were conducted. Several studies were done in which seed set of Proteaceae was assessed. These data indicate that pollination and/or resource allocation by plants vary.

TITLE: The role of animals in the reproductive biology of fynbos plants.
RESEARCHER: Breytenbach G J and Breytenbach W (Saasveld Forestry Research Centre)
STATUS: In progress.

Nothing is known about the role of insects as pollinating agents of fynbos plants in the southern Cape. The major objective of the project was to determine which insects are involved, what the pollen loads are, and what levels of fidelity exist between the pollinating agents and plant species involved. A pollen reference collection was made to compare pollen tranported by insects. Results will be available soon.

TITLE: *Gazania* - *Gorteria* beetle mimicry interactions.
RESEARCHER: De Winter B (Botanical Research Institute), Wiens D (University of Utah) and Rebelo A G (Percy FitzPatrick Institute of African Ornithology)
STATUS: In progress.

Initial attempts to find beetles which resemble the beetle-like structures found on the ligula of some of the ray flowers of the 'beetle daisy' (*Gorteria* species) common in the immediate vicinity of Springbok, proved unsuccessful. Searches further afield in related but distinct taxa also did not yield either the kind of beetle expected, or strong beetle *Gorteria* - *Gazania* interactions. Predation by beetles, although present, seemed less pronounced than in some of the other associated members of the Asteraceae. Pollinators of both *Gazania* and *Gorteria* are mainly flies. The study is being continued with emphasis on unravelling the complicated taxonomy of the *Gorteria* taxa which only became evident during the study.

TITLE: Reproductive biology of *Leonotis*.
RESEARCHER: Getliffe Norris F (University of Natal)
STATUS: In progress.

A field study of bird pollination including analysis of flowering sequence, pollen and stigma details, nectar quantity and quality and seed output is underway.

TITLE: Reproductive biology of *Syncolostemon macranthus*.
RESEARCHER: Getliffe Norris F (University of Natal)
STATUS: In progress.

A field study of pollination including analysis of flowering sequence, pollen and stigma details, nectar quantity and quality and seed output is underway.

TITLE: Reproductive biology of Acanthaceae
RESEARCHER: Getliffe Norris F (University of Natal)
STATUS: Planned.

A field study of pollination including analysis of flowering sequence, pollen and stigma details, nectar quantity and quality and seed output is planned.

TITLE: The feeding ecology of nectarivorous birds in the Natal Drakensberg.
RESEARCHER: Daniels C (University of Natal)
STATUS: In progress.

The feeding ecology of nectarivorous birds in the Natal Drakensberg was investigated. The project will be written up during 1987.

TITLE: Pollination biology of the Iridaceae.
RESEARCHER: Goldblatt P (Missouri Botanical Garden)
STATUS: In progress.

Observations are being made on pollinators/visitors to flowers of Iridaceae, together with a small collection of bees and flies caught on *Homeria*, *Moraea* and *Nivenia* species. The insects are being ethanol-washed for pollen to confirm and identify the grains carried. The insects, mostly bees, will also be identified by available experts. This project is being done with the collaboration of P Bernhardt (St Louis University) and J Manning (University of Natal), and includes making crosses in both distylous and homostylous species to determine compatability relationships (self, intra- and inter-morph). The results of crosses are determined by measuring pollen tube growth. Observations of sunbird pollination are also being compiled - mainly at *Watsonia* species. The large, red to orange flowered *Watsonia* species appear to be bird-pollinated. Nectar volumes and concentrations in *Watsonia* and *Nivenia* are being measured, and I Baker (Berkeley University) has done some nectar analyses. All these studies relate to the researcher's systematic studies in the Iridaceae.

TITLE: Genetic diversity and gene flow in Bruniaceae.
RESEARCHER: Hall A V (Bolus Herbarium, University of Cape Town) and Paterson F W (Cape Technikon)
STATUS: In progress.

Methods for the assessment of genetic diversity by isozyme analysis are being refined in a pilot study on the rare plant *Audouinia capitata* (Bruniaceae). If suitably distinctive genetic markers can be found it may be possible to estimate the species' apparently rare gene flow between populations.

TITLE: Reproductive biology of forest trees in relation to stand dynamics.
RESEARCHER: Koen J (Saasveld Forestry Research Centre)
STATUS: In progress.

The importance of the different pollination strategies of the woody vegetation will be looked at and the following two questions will be addressed:
How does irregular flowering affect potential pollinators?
What is the ratio of flowers to mature fruit? This will indicate pollination success.

TITLE: Pollination of *Welwitschia*: wind or insects?
RESEARCHER: Marsh B (Desert Ecological Research Unit)
STATUS: In progress.

The pollination biology of *Welwitschia* is being studied.

TITLE: Pollen fall-out in and around Cape Town.
RESEARCHER: Meadows M (Department of Environmental and Geographical Science, University of Cape Town)
STATUS: Planned to commence in July 1987.

The aim of this project is to establish the quantity of pollen in the atmosphere in Cape Town and to examine the variation on a daily basis with meteorological conditions. An active pollen sampler which collects pollen over a seven-day period is to be purchased and installed in Cape Town. It is hoped that the resultant data would be of use to hay fever sufferers.

TITLE: Contemporary pollen rain studies in southern Africa.
RESEARCHER: Meadows M (Department of Environmental and Geographical Science, University of Cape Town)
STATUS: In progress.

A series of simple pollen traps has been erected in a range of vegetation communities mainly in the mountain areas in and around the Karoo. The aim of this project is to gain insight into the relationship between contemporary vegetation and pollen rain and to use this information in gaining more knowledge of the vegetation changes that have taken place as seen through analysis of fossil pollen. Coupled with an analysis of the pollen content of surface samples, it is hoped to develop an understanding of differential pollen production, dispersal and preservation for a range of vegetation communities. Multiple discrimination analysis, a multivariate statistical technique, is used in the analysis of the data and enables more precise conclusions to be drawn about the vegetation-pollen relationships.

TITLE: Mass flowering in *Watsonia fourcadi*
RESEARCHER: Vlok J (Saasveld Forestry Research Centre)
STATUS: In progress

The effect of mass flowering on pollination efficiency in *Watsonia fourcadi* is being investigated.

TITLE: Oil collecting bees and their flowers
RESEARCHER: Whitehead V B (South African Museum, Cape Town) and Steiner K (Compton Herbarium, Kirstenbosch National Botanic Gardens)
STATUS: In progress.

Extensive work is being undertaken on the pollinators of *Diascia* and related genera in the western Cape and Namaqualand. To date, in a limited area of Namaqualand, 14 new species of oil-collecting bees have been discovered. Although there appears to be some geographic limits to their distribution, the species of oil-flowers utilized are determined by the accessibility of the oil-bearing areas in the flower and the length of the bees oil-collecting legs.

TITLE: Studies of floral morphology and pollinators in members of the Orchidaceae.
RESEARCHER: Whitehead V B (South African Museum, Cape Town) and Steiner K (Compton Herbarium, Kirstenbosch National Botanic Gardens)
STATUS: In progress.

Studies of the floral morphology and pollination of *Pterygodium*, *Corycium*, *Disperis*, *Evota*, *Ceratandra* and *Anochilus* (Orchidaceae) are being undertaken.

LIST OF CONTRIBUTORS

A Scholtz	S A Museum, P O Box 61, Cape Town 8000 (present address) Department of Archaeology, University of Stellenbosch, Stellenbosch 7600 (address at time of writing chapter)
K E Steiner	Compton Herbarium, National Botanic Gardens of South Africa, Private Bag X7, Claremont 7735
V B Whitehead	S A Museum, P O Box 61, Cape Town 8000
A G Rebelo	Percy FitzPatrick Institute for African Ornithology, University of Cape Town, Rondebosch 7700
G J Breytenbach	Saasveld Forestry Research Centre, Private Bag X6515, George 6530
D Koutnik	Huntington Botanic Gardens (present address) Bolus Herbarium, University of Cape Town, Rondebosch 7700 (address at time of writing chapter)
A V Hall	Bolus Herbarium, University of Cape Town, Rondebosch 7700
M L Jarman	FRD, CSIR, Botany Building, University of Cape Town, Rondebosch 7700
J H Giliomee	Department of Entomology, University of Stellenbosch, Stellenbosch 7600

RECENT TITLES IN THIS SERIES

110. The limnology of Hartbeespoort Dam. NIWR. September 1985. 269 pp.

111. Management of invasive alien plants in the fynbos biome. I A W Macdonald, M L Jarman and P Beeston (editors). October 1985. 140 pp.

112. *The SANCOR Marine Pollution Research Programme 1986-1990. October 1985. 16 pp.

113. Alien and translocated aquatic animals in southern Africa: a general introduction, checklist and bibliography. M N Bruton and S V Merron. October 1985. 71 pp.

114. A synthesis of field experiments concerning the grasslayer in the savanna regions of southern Africa. T G O'Connor. October 1985. 126 pp.

115. *South African marine pollution survey report 1979-1982. B D Gardner, A D Connell, G A Eagle, A G S Moldan, R J Watling. December 1985. 81 pp.

116. Basic needs in rural areas. A report on a seminar held in Cape Town on 19 February 1985. December 1985. 103 pp.

117. South African Red Data Book: Plants - fynbos and karoo biomes. A V Hall and H A Veldhuis. 1985. 144 pp.

118. Invasive alien plants in the terrestrial ecosystems of Natal, South Africa. I A W Macdonald and M L Jarman (editors). 1985. 88 pp.

119. Invasive alien organisms in South West Africa/Namibia. C J Brown, I A W Macdonald and S E Brown. 1985. 74 pp.

120. The impact of climate and weather on the activities of the building and construction industry in South Africa. G du Toit de Villiers (compiler). 1986. 40 pp.

121. Ecological research on South African rivers - a preliminary synthesis. J H O'Keeffe. 1986. 121 pp.

122. A description of the Karoo Biome Project. R M Cowling. 1986. 42 pp.

123. *SANCOR: Summary report on marine research 1985. 1986. 57 pp.

124. The karoo biome: a preliminary synthesis. Part I - Physical environment. R M Cowling, P W Roux and A J H Pieterse (editors). 1986. 114 pp.

125. South African Red Data Book - Terrestrial Mammals. R H N Smithers. 1986. 216 pp.

126. A bibliography of sandy beaches and sandy beach organisms on the African continent. R Bally. 1986. 179 pp.

127. Activities of the National Programmes for Ecosystem and Aquaculture Research, 1983-1985. E W Auret. 1986. 68 pp.

128. Historical sites at the Prince Edward Islands. J Cooper and G Avery. 1986. 80 pp.

129. Richards Bay effluent pipeline. D A Lord and N D Geldenhuys. 1986. 30 pp.

130. An assessment of the state of the estuaries of the Cape and Natal 1985/86. A E F Heydorn (editor). 1986. 39 pp.

131. The conservation of South African rivers. J H O'Keeffe (editor). 1986. 117 pp.

132. SIBEX - II: Report of the South African study in the sector (48-64°E) of the Southern Ocean. D G M Miller (editor). 1986. 47 pp.

133. The regional landscape: Nylsvley in perspective. P G H Frost. 1987. 30 pp.

134. South African Southern Ocean Research Programme. SASCAR. 1986. 58 pp.

135. Disturbance and the dynamics of fynbos communities. R M Cowling, C D Le Maitre, B McKenzie, R P Prys-Jones and B W van Wilgen (editors). 1987. 70 pp.

136. SANKON: Opsommingsverslag oor mariene navorsing. SANKOR. 1987. 45 pp.

137. South African Red Data Book - Fishes. P H Skelton. 1987. 199 pp.

138E Report of the Main Research Support Programme. September 1984-June 1987. 1987. 23 pp.

138A Verslag van die Hoofprogram vir Navorsingsondersteuning. September 1984-Junie 1987. 1987. 23 pp.

139. Marine research in Natal. A P Bowmaker, D van der Zee and H Ridder (editors). 1987. 184 pp.

140. Environmental impact assessment of the proposed emergency landing facility on Marion Island - 1987. G Heymann, T Erasmus, B J Huntley, A C Liebenberg, G de Retief, P R Condy and O A van der Westhuizen. 209 pp. (Available only from Department of Environment Affairs).

141. A preliminary synthesis of pollination biology in the Cape flora. A G Rebelo (editor). 1987. 257 pp.

*Out of print