PATTERN AND PROCESS IN SOUTH COAST DUNE FYNBOS : POPULATION, COMMUNITY AND LANDSCAPE LEVEL STUDIES

Shirley May Pierce

Thesis submitted in fulfilment of the requirements for the Degree of Doctor of Philosophy in the Department of Botany at the University of Cape Town, January 1990.

To my Father and Mother

ABSTRACT

The study aimed to explain vegetation dynamics in response to disturbance in a dune landscape comprising a mosaic and admixture of grassland, fynbos and thicket. A hierarchical approach directed investigations at the landscape, community and population levels, with emphasis on seed banks. The study concentrated on fynbos, the predominant vegetation type. At the landscape-level, pattern was attributed to successional processes rather than abiotic factors. Each vegetation was maintained under defined disturbance regimes of fire, grazing and bushcutting. In the absence of disturbance, succession proceeded from grassland, through fynbos, to thicket. The study contributed to existing theory on the effects of disturbance on seed bank size, and the relationship between seed bank composition and its above-ground vegetation. No single model for successional pathways and mechanisms was supported: these differed amongst vegetation types and within fynbos communities. After fire in fynbos, the initial floristic composition pathway was followed, but on a south-facing slope, pioneering herbs inhibited shrub seedlings. Life-histories of six, small-leaved, non-resprouting fynbos shrubs and their population dynamics in response to fire and bushcutting were studied. The distribution of the study species across the dune landscape could be explained mainly by their life-histories. Germination was cued to alternating diurnal temperatures. Therefore, fire acted as an indirect cue by removing the insulating effect of vegetation which dampens soil temperature fluctuations. Cafeteria experiments indicated that myrmecochory (ant dispersal) of small (2-4 mg), elaiosome-bearing seeds may not be as efficient as reported for larger-seeded species. Soil-stored seed banks of mature fynbos shrubs were small and not persistent relative to those in other fire-prone shrublands such as Calluna heath and chaparral. Although seed banks of mature shrubs showed no change in size over three years, other aspects of the seed biology (i.e. seed production, germinability, dormancy, predation and dispersal, decay in the soil) fluctuated widely. This variability in seed available for post-fire recruitment may explain the different proportions of species in different communities, and hold implications for shrub co-existence and diversity in Cape fynbos.

PREFACE

The eastern Cape is very special to me. If one travels eastwards from the western Cape, it is there that the first thorn trees of Africa appear. It is there where the temperate, tropical and arid floras of southern Africa meet. I have had the good fortune to work in the area - first as a field assistant, and later as a researcher, exploring the fascinating differences amongst these floras. But the coastal dunes of the south eastern Cape have particularly enchanted me. The dunes cover a narrow strip, only 8 km at their widest. They carry a diversity of habitats: from the "knoffelbuchu"-scented shrublands of the dune fynbos, to the cool, shaded glades of the mature thickets, to the stark simplicity and harshness of the shifting sand dunes. The sense of wilderness of the dunefields was heightened for me the day I was shown the fresh spoor of a leopard on the Brandewynkop dunes.

During a year in Australia, I was involved in population studies of Banksia (Proteaceae) species in response to fire. On my return home, I found that here, as in Australia, the more glamorous members of the Proteaceae, were given much attention, while the less conspicuous, small-leaved, small-seeded fynbos shrubs were neglected. Furthermore, a brief spell of working in a nursery made me aware of the dearth of horticultural knowledge regarding the propagation of fynbos shrubs.

In view of the tremendous pressures on the Cape coast by resort development, invasion by exotic species, and mismanagement leading to destabilization and blow-outs, I resolved to focus on the dune vegetation. I was familiar with dune communities from assisting in survey work as well as carrying out phenological research. The dune fynbos communities are also some of the simplest in terms of species richness, and, I presumed, easier to study. Dr F. J. Kruger, a leader in the Fynbos Biome Project, Foundation for Research Development (CSIR), had identified the need for studies on seed bank dynamics and in particular, the germination requirements of the small-leaved, non-resprouting species of the Cape fynbos. I therefore submitted a project proposal on the subject, and fortunately, the funding was granted. I was privileged to live in the field for a year before moving nearer to laboratory facilities. This time so close to the field proved invaluable for learning and observing at close hand the vagaries of my study species. I soon realized, as I grappled with the tiny seed of my study species, why the glamorous, large-seeded species had been so popular amongst botanists. Nonetheless, those days of field work on the high, wind-swept dunes of Brandewynkop, alone but for my dog, were some of my finest times.

Except for the first and last chapters, the thesis chapters are each in the form of a scientific paper, although they include more information than required for primary publications. This format has the advantage over the classical thesis of succinctness, although it has led to repetition in some sections, such as study site descriptions. For the sake of brevity, study species' descriptions were tabulated and in some chapters the same table has been used. In Chapter 5, I took the discussion far beyond the data in speculating about the evolution of myrmecochory in Cape fynbos.

Although the published paper in Appendix 1 was written mainly by R. M. Cowling, I shared equally in all aspects of this particular study, including field work, data analysis, paper preparation, and revision for publication. Regarding the data which I used and reanalysed in the ordination as clearly stated in Chapter 7, I had assisted in the original data collection in the field. Apart from these two instances, this thesis is entirely my own work.

ACKNOWLEDGEMENTS

I am most grateful to my supervisor, Professor Eugene Moll, for his steadfast support and faith in me. I am indebted to him for the free rein he gave me. Without his efforts this study would not have been possible.

My husband, Richard Cowling, is due special acknowledgement for his encouragement and enthusiasm. Our shared love of, and interest in, the eastern Cape dunes allowed invaluable discussions and debate, as well as his support in the field. His love and moral support made this study possible.

My gratitude extends to Niki Phillips for her insights and invaluable assistance in sorting seeds. Thanks are due to George Davis for his advice and support. The overwhelming generosity of my colleagues with their time, and their willingness to discuss and give guidance is gratefully acknowledged. Their assistance covered the full spectrum from trapping rodents to use of computers. I thank Pat Beeston, Lucia Bossi, William Bond, Johan Breytenbach, Bruce Campbell, Karen Esler, Craig Hilton-Taylor, Timm Hoffman, Graham Kerley, Richard Knight, Graham Levitt, Penny Mustart, Wendy Paisley, Natasha Romoff, Willie Stock, Jan Vlok, Alice Wiseman and Ed Witowski. Technical assistance is acknowledged after each chapter.

Access to field sites was kindly granted by Francis and Johan Linstrom of the farm, "Brandewynkop", and Mr O. Nauhaus of "Ongegunde Vryheid", and the Humansdorp Divisional Council for access to the Irma Booysen Floral Reserve. Gwen and Henry Brown are thanked for their warm hospitality on my return trips to Cape St Francis.

CONTENTS

CHAPTER 1

INTRODUCTION

INTRODUCTION

Rationale

The need for explanation and prediction of fynbos community structure and dynamics in response to disturbance, especially fire, was identified by Kruger (1983). Fire as a management tool in fynbos had been well established. The study of population level processes, with the emphasis on germination ecology was also identified as a major gap in the knowledge on Cape fynbos (Kruger 1983).

Many studies have been made on the Proteaceae, and some findings (e.g. Bond 1984; Bond & Slingsby 1983) have made a major impact on mediterranean ecosystem ecology (Cowling 1987). Much of fire management policy for Cape fynbos has been based on the responses of the conspicuous members of the Proteaceae. However, fynbos communities are dominated by small-leaved (leptophyll and smaller), non-resprouting shrubs. Population-level studies of these elements have until now been neglected. With regard to germination studies, most work has concentrated on the Proteaceae (e.g. Brits 1986; Brits & Van Niekerk 1986), with few studies on small-leaved species, all members of the Ericaceae (Small & Garner 1980; Small et al 1982, Van de Venter & Esterhuizen 1988).

The small-leaved shrubs which dominate in the fire-prone fynbos communities, are apparently reliant on soil-stored seeds for recruitment after fire. Studies on this shrub group were seen as essential for a gaining an understanding of the structure and function of vegetation, a prerequisite for the development of sound management programmes for maintaining diversity. This was a major goal of the Fynbos Biome Project, part of the National Programme for Ecosystem Research of the Council for Scientific and Industrial Research which funded this research (Kruger 1978).

The valuable insights gained from population studies, and in particular, on species with canopy-stored seed (Bond 1985; Bond, Vlok & Viviers 1984), as well as the work on the fire-prone Calluna heath by Mallik, Hobbs & Legg (1984) and on chaparral species by Keeley (1977) inspired this first investigation of the dynamics of the non-resprouting fynbos shrub species with reputed soil-stored seed.

Approach

This study aimed to explain vegetation pattern and structure by considering life-history attributes of species and the responses of their populations to disturbance. The study used an hierarchical approach: patterns at one level (e.g. community) were explained by studying processes at another level (e.g. population). Studies were aimed at different levels of organization, namely individual, population and community. A further objective was to use the information thus gleaned to explain landscape-level vegetation patterns. At all levels, the role of disturbance was considered, and therefore, succession was also studied. Because succession may be viewed as the individualistic result of the interaction of disturbance and predominant reproductive life-history attributes of plants, great emphasis was laid on seed dynamics (Glenn-Lewin 1980).

Selection of study site

The vegetation of the south eastern Cape coastal dunefields, which consists of a mosaic and admixture of grassland, fynbos and thicket, provides an excellent opportunity for studying pattern in vegetation. The investigation concentrated on the fynbos community, with detailed studies on the life-history attributes and interactions of six dominant fynbos shrubs (Table 1). The study approximated the "vital attributes" approach of Noble & Slatyer (1977) in which life-history attributes of important species in a community and their interactions over time after disturbance provide a basis for describing successional processes. The study emphasized individual properties and their interactions within the community at the scale of local populations. Explanations were also sought for the distributions of the individual species across the landscape. The importance of this research approach for mediterranean-type ecosystems has since been reiterated (Keeley 1989; Zedler & Zammit 1989).

Study site

The study site was set in South Coast Dune Fynbos (*sensu* Cowling 1984) for several reasons. It includes a very simple form of fynbos, with the small-leaved shrub element showing much lower alpha richness and beta diversity than in most other fynbos communities. It has a restricted distribution, occurring only on the narrow strip of Recent calcareous coastal dune sands of the southern and eastern coast of South Africa between Port Alfred and Mossel Bay (Fig. 1). It is a highly endangered vegetation type, threatened by coastal development, poor management by graziers, and severe encroachment by two Australian species of *Acacia*. Degradation can lead to remobilization of the dunes, and the formation of blow-outs (Tinley 1985).

Lastly, I had gained some familiarity with the vegetation, having assisted in an earlier survey of the region, and later having carried out phenological work in the region (Pierce & Cowling 1984).

The mosaic and admixture of fynbos, grassland and subtropical thicket comprising South Coast Dune Fynbos is depicted in Fig.2 and Plates 1-6. The grassland communities are maintained by continuous grazing, and often managed for grazing by frequent bushcutting or burning to eliminate fynbos species and promote the grass species. The fynbos communities are open to dense shrublands, 0.5-1 m tall, dominated by sclerophyllous shrubs and reed-like species of the Restionaceae. The calcareous sands of the dunes are higher in nitrogen than in the acid sands of most other Cape fynbos (Cowling 1984). Dune fynbos lacks members of the Proteaceae, and differs markedly from other Cape fynbos communities in including large-leaved, sclerophyllous subtropical thicket species which are resprouters, and dependent on seed dispersal by birds and wind for inter-fire recruitment.

The study area is set in the parallel wind-rift dunes (Tinley 1985) of the Humansdorp (34°02'S;24°47'E) region. One study site was near Cape St Francis, and the other near Oyster Bay on the farm Brandewynkop. The former site comprises gently sloping dunes, while the latter site has the largest and most spectacular wind-rift dunes in South Africa (Tinley 1985). Here the vegetated dunes are up to 12 km long and are 177 m at the highest point. The dune slopes are asymmetric, ca. 35° on the steep side, and 12°-25° on the gentle slope (see Fig. 2.). In some areas of the dunefields, there are remobilized driftsands.

In brief, the climate of the study area is mild, with a mean annual temperature of 17°C at Cape St Francis. Frost is rare, and highest temperatures are in autumn when "berg" or fohn-like winds raise temperatures to 40°C, usually prior to frontal rains. Annual rainfall ranges across the study area from east to west from ca. 500 to 900 mm yr^{-1}. Rain can fall at any time of year, although there are spring and autumn peaks. However, the summer/autumn season is effectively a period of drought. The pattern of a moisture surplus in winter and a deficit in summer is typical of a mediterranean type climate (Bond 1980). The summer/autumn period is the most fire-prone. Fire frequency varies from 10-20 years although extremes of 4-40 years are also possible.

Thesis structure and outline

Depending on the level of detail desired by the reader, the thesis may be read in different parts and sequences :

Level one: the most succinct summary is provided by the thesis abstract.
Level two: overall findings are listed in Conclusions (Chapter 8).
Level three : all results are synthesized in Chapter 7.
Level four : further detail is provided by chapter abstracts in this order : Chapters 2, 3, 4, 5, Appendix 1, Chapters 6, 7.
Level five: entire thesis reads in this order : Chapters 1, 2, 3, 4, 5, Appendix 1, Chapters 6, 7, 8.

The study begins in Chapter 2 with the detailed investigation of the germination requirements of the six fynbos study species (Table 1). The population responses of the study species to fire and bushcutting, as well as their occurrence in mature communites is dealt with in Chapter 3. In Chapter 4 the seed production of the six fynbos species, and their soil-stored seed banks , as well as seed banks of other fynbos community species was determined. The fate of the seed of the study species after release and prior to burial was investigated, and speculation regarding the high incidence of myrmecochory in the Cape was discussed in

Chapter 5. Appendix 1 described the succession monitored shortly after disturbances of fire and bushcutting in three different fynbos communities. The relationship of the size and composition between grassland, fynbos and thicket and their underlying seed banks was explored in relation to their respective disturbance regimes in Chapter 6. In Chapter 7, determinants of vegetation pattern at the landscape-level were investigated, and information on life-history attributes of the study species was used to explain their patterns of distribution in communities across the dune landscape. Finally, in Chapter 8 the major findings from the study were summarized, and recommendations and solutions given to problems encountered during the course of the project.

Table 1. Characteristics of the study species.

Species [a]	Family	No. spp.[b] in Cape flora	Distribution[b]	Shrub height (m)	Shrub longevity (yr)	Pollination	Dispersal	Seed prodn [d]	Seed mass (mg) ($x \pm SE$)
Agathosma apiculata	Rutaceae	135	Riversdale to Port Elizabeth	0.8	25	Insect	Ballistic and myrmecochory	May-Oct	4.6 ± 0.2 (n=38)
Agathosma stenopetala	Rutaceae	135	Humansdorp to Port Elizabeth	0.6	20	Insect	Ballistic and myrmecochory	Sep-Dec	2.1 ± 0.03 (n=50)
Felicia echinata	Asteraceae	83	Mossel Bay to Port Alfred	0.1	5	Insect	Wind	May-Sep	0.4 ± 0.03 (n=300)
Metalasia muricata	Asteraceae	50	Cape to Drakensberg	2.3	>30	Insect	Wind	May-Jul	0.6 ± 0.03 (n=50)
Muraltia squarrosa	Polygalaceae	115	Mossel Bay to Port Elizabeth	0.8	14	Insect/[c] self	Myrmecochory	All year	3.7 ± 0.1 (n=50)
Passerina vulgaris	Thymelaeaceae	18	Cape to Drakensberg	1.5	14	Wind	Unspecialized	Oct-Feb	1.3 ± 0.03 (n=47)

[a] Nomenclature after Bond & Goldblatt (1984).
[b] From Bond & Goldblatt (1984).
[c] Levyns (1954).
[d] Pierce & Cowling (1984) and this study.

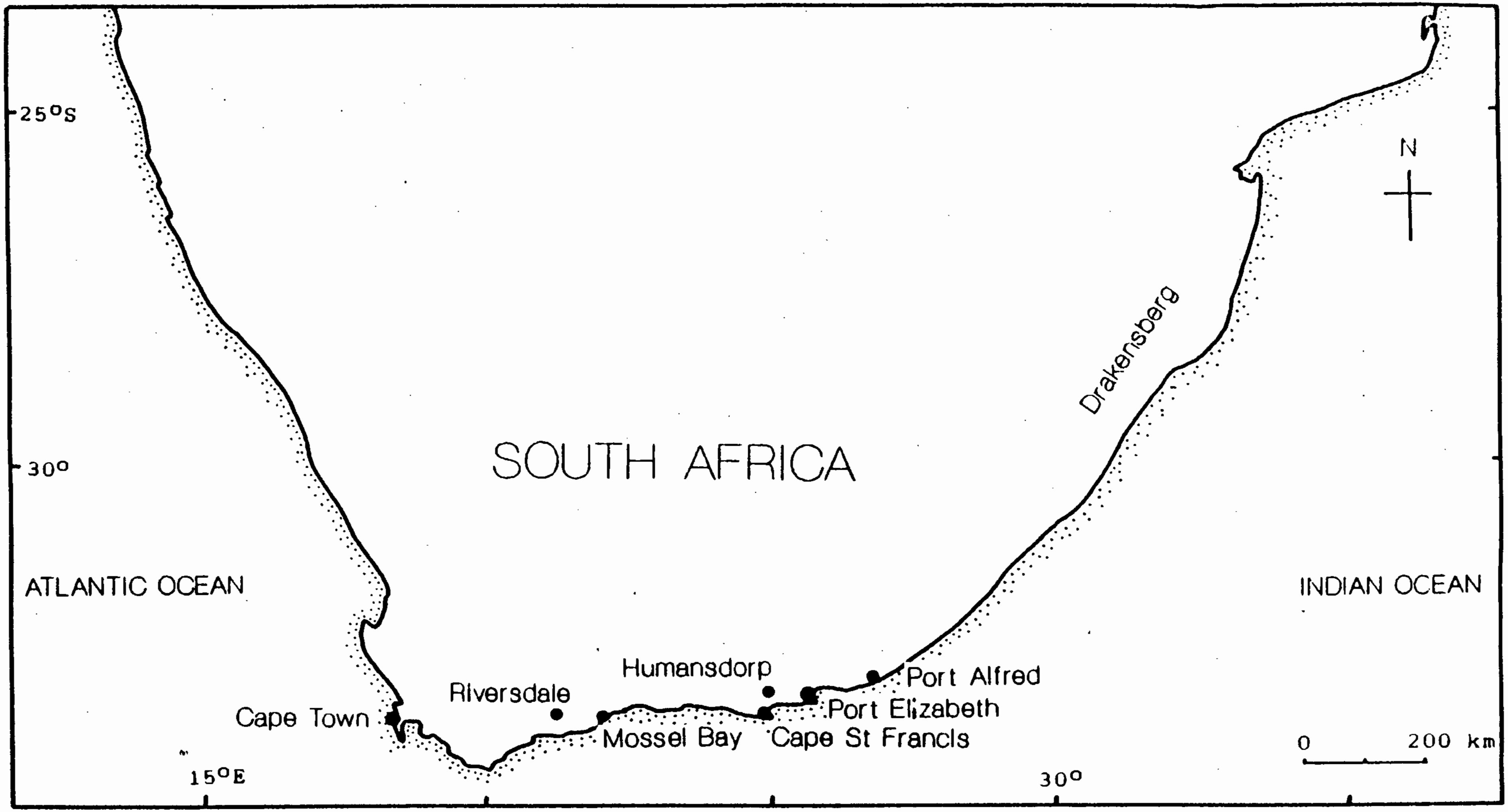


Fig. 1. Map of South Africa showing place names of distribution limits of study species (see Table 1). South Coast Dune Fynbos is distributed on the narrow coastal strip of Recent calcareous sands between Mossel Bay and Port Alfred.

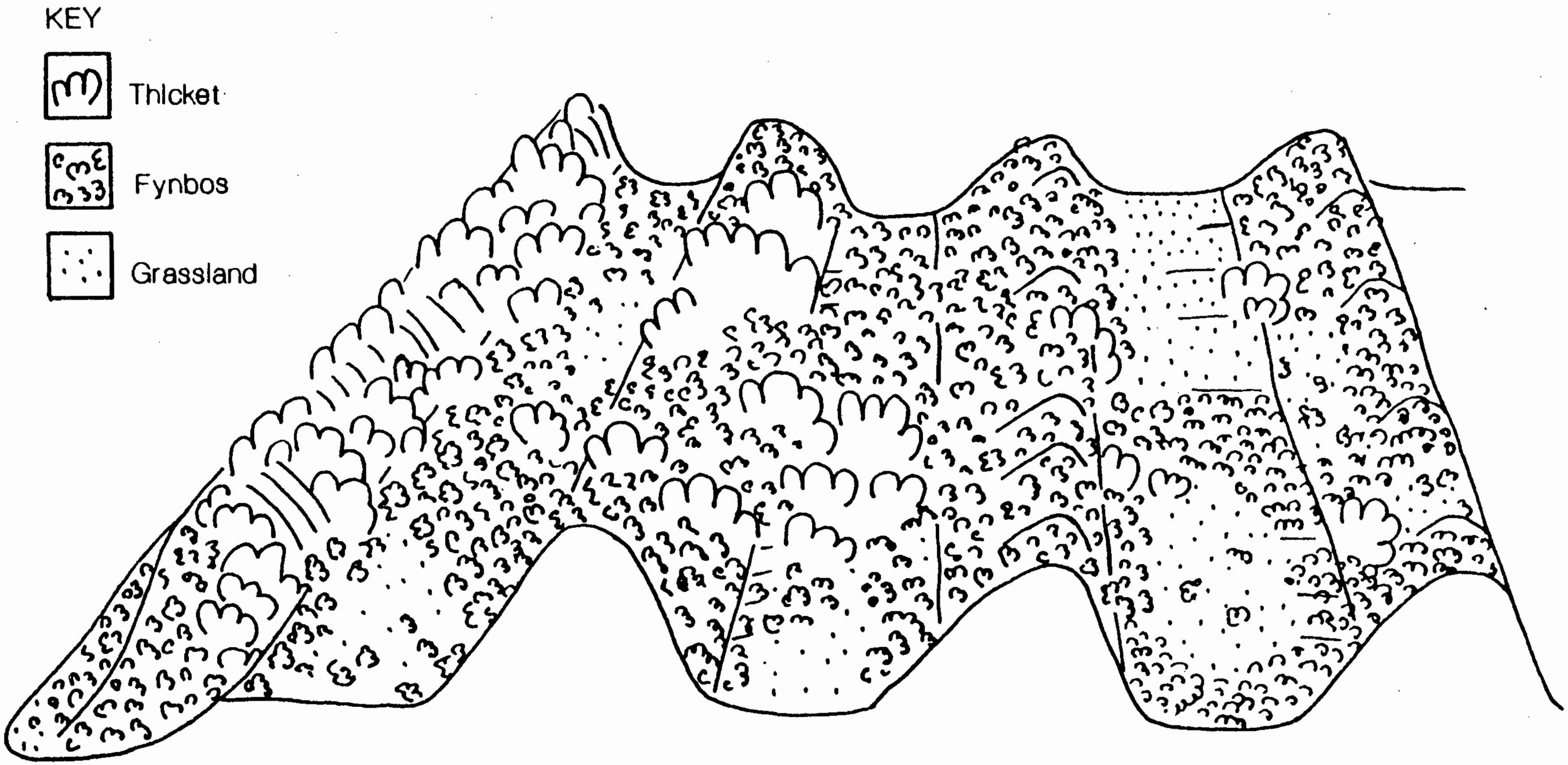
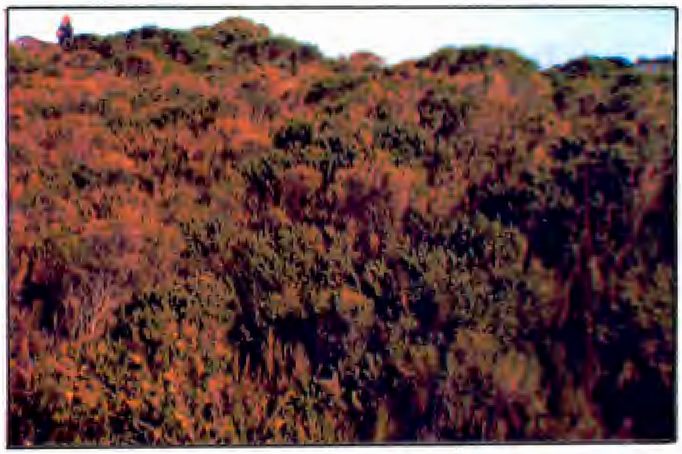


Fig. 2. Illustration of dune landscape indicating the mosaic and admixture of grassland, fynbos and thicket vegetation types. Dune are classified as parallel wind-rift dunes, which are wind-breached parabolic dunes with asymmetric slopes (see Tinley 1985).



REFERENCES

Bond, P. & Goldblatt, P. (1984). see p. 57.

Bond, W. J. (1980). Periodicity in fynbos of the non-seasonal rainfall belt. Journal of South African Botany, 46, 343-354.

Bond, W. J. (1984). Fire survival of Cape Proteaceae - influence of fire season and fire predators. Vegetatio, 56, 65-74.

Bond, W. J. (1985). Canopy-stored seed reserves (serotiny) in Cape Proteaceae. South African Journal of Botany, 51, 181-86.

Bond, W. J. & Slingsby, P. (1983). Seed dispersal by ants in shrublands of the Cape Province and its evolutionary implications. South African Journal of Science, 79, 231-33.

Bond, W. J., Vlok, J. & Viviers, M. (1984). Variation in seedling recruitmment of Cape Proteaceae after fire. Journal of Ecology, 72, 209-21.

Brits, G. J. (1986). Influence of fluctuating temperatures and H_2O_2 treatments on germination of *Leucospermum cordifolium* and *Serruria florida* (Proteaceae) seeds. *South African Journal of Botany*, *52*, 286-90.

Brits, G. J. & Van Niekerk, M. N. (1986). Effects of air temperature, oxygenating treatments and low storage temperature on seasonal germination response of *Leucospermum cordifolium* (Proteaceae) seeds. *South African Journal of Botany*, *52*, 207-11.

Cowling, R. M. (1984). A syntaxonomic and synecological study in the Humansdorp region of the Fynbos Biome. *Bothalia* *15*, 175-227.

Cowling, R. M. (1987). Introduction. Disturbance and the dynamics of fynbos biome communities. (Ed. by R. M. Cowling, D. C. Le Maitre, B. McKenzie, R. P. Prys Jones and B. W. van Wilgen), pp.1-5. *South African Scientific Programmes Report No. 135*. CSIR, Pretoria.

Glenn-Lewin, D. C. (1980). The individualistic nature of plant community development. *Vegetatio*, *43*, 141-146.

Keeley, J. E. (1977). Seed production, seed populations in soil, and seedling production after fire for two congeneric pairs of sprouting and non-sprouting chaparral shrubs. Ecology, 58, 820-29.

Keeley, S. C. (1989). The California chaparral. Paradigms Reexamined. Natural History Museum of Los Angeles County, Science Series No. 34. Los Angeles.

Kruger, F. J. (Ed.) (1978). A Description of the Fynbos Biome Project. South African Scientific Programmes Report No. 28. CSIR, Pretoria.

Kruger, F. J. (1983). Plant community diversity and dynamics in relation to fire. Mediterranean-type Ecosystems. The Role of Nutrients. (Ed. by F. J. Kruger, D. T. Mitchell and J. U. M. Jarvis), pp. 446-472. Springer-Verlag, New York.

Levyns, M.R. (1954). see p. 61.

Mallik A. U., Hobbs, R. J. & Legg, C. J. (1984). Seed dynamics in Calluna-Arctostaphylos heath in north-eastern Scotland. Journal of Ecology, 72, 855-871.

Noble, I. R. & Slatyer, R. O. (1977). Post fire succession of plants in Mediterranean ecosystems. Proceedings of the Symposium on the Environmental Consequences of Fire and Fuel Management in Mediterranean Ecosystems. (Ed. by H. A. Mooney and C. E. Conrad), pp. 27-36. USDA Forest Service General Technical Report WO-3, Washington, DC.

Pierce, S. M. & Cowling, R. M. (1984). Phenology of fynbos, renosterveld and subtropical thicket in the south eastern Cape. South African Journal of Botany, 3, 1-16.

Small, J. G. C. & Garner, C. J. (1980). Gibberellin and stratification required for the germination of Erica junonia, an endangered species. Zeitschrift fur Pflanzenphysiologie, 99, 179-182.

Small, J. G. C., Robbertse, P. J., Grobbelaar, N. & Badenhorst, C. M. (1982). The effect of time of application and sterilization method of gibberellic acid, and temperature on the seed germination of Erica junonia, an endangered species. South Afican Journal of Botany, 1, 139-141.

Tinley, K. L. (1985). Coastal Dunes of South Africa. *South African National Scientific Programmes Report No. 109*. CSIR, Pretoria.

Van der Venter, H. A. & Esterhuizen, A. D. (1988). The effect of factors associated with fire on seed germination of *Erica sessiliflora* and *E. hebecalyx* (Ericaceae). *South African Journal of Botany*, *54*, 301-304.

Zedler, P. H. & Zammit, C. A. (1989). A population-based critique of concepts of change in the chaparral. *The California Chaparral. Paradigms Reexamined*. (Ed.by S. C. Keeley, pp. 73-83). Natural History Museum of Los Angeles County, Science Series No. 34. Los Angeles.

CHAPTER 2

Germination ecology of six shrubs growing in fire-prone fynbos : response cued to alternating temperatures

ABSTRACT

In the Cape fynbos, recruitment of non-resprouting, non-serotinous shrubs from soil-stored seed banks occurs mainly after fire. This study aimed to test the hypothesis that germination is cued to fire. It also tested the hypothesis that each species would have different germination cues as a component of different regeneration niches. Dormancy and extended seed longevity were predicted for soil-stored seeds subject to fire frequencies of 10-20 years. Variation amongst crops, and response to seed ageing were also investigated. Seeds subjected to two heat treatments (80oC for 5 min and 100oC for 20 min and sown on dune soil heated at 100oC for 1 hour) and a charcoal extract, failed to enhance germination significantly. Instead, highest germination successes (80-100% in five species and 28% in the sixth), were achieved under alternating diurnal temperatures (20°/10°C) in light/dark for 10/14 h. Contrary to predictions, dune fynbos shrubs showed similar germination requirements. Charcoal treatment failed to break possible dark-induced dormancy, a trait predicted for soil-stored seeds in fire-prone environments. Stimulation by alternating temperatures implied an indirect fire cue, viz. the removal of insulating vegetation. Leachate solution inhibited germination in two out of the six species, suggesting allelopathic effects during inter-fire periods.

Only two species showed dormancy and three species showed declining germinability after three years. Comparisons showed the study species to be more similar to Californian coastal sage than to chaparral shrubs in having germination independent of fire, and low dormancy. In two species, proportions of empty seeds varied widely amongst populations and crops. Germination varied widely amongst similar aged seed from different crops. Also, different crops varied in their germination response to ageing. These data were used to simulate the synchronous germination of a seed bank comprising accumulations of crops. From this, recruitment of varying proportions of the different species would result after each disturbance event. This variability might promote coexistence of competitively equivalent species.

INTRODUCTION

Many fynbos shrub species recruit from soil-stored seed banks primarily after fire (Kruger 1984). For these species, it is reasonable to predict that their seeds have a well-developed dormancy, broken only by fire-related cues. It has been argued that inter-fire conditions do not favour germination (Kruger 1984; Brits 1986), while establishment between fires may be limited by granivory (Bond & Breytenbach 1985) and/or by herbivory of seedlings (Breytenbach 1984).

Detailed germination studies in fynbos have concentrated on the large-seeded members of the Proteaceae (reviewed by Van Staden & Brown 1977; Deall and Brown 1981; Brits 1986; Brits & Van Niekerk 1986). There has been much less interest in the small-leaved, small-seeded elements which comprise the major part of the approximately 8500 fynbos species of the Cape flora (Bond & Goldblatt 1984). Studies on this group have been few, especially those with ecological interpretations, and have concentrated on members of the genus _Erica_ (Small & Garner 1980; Small _et al_. 1982; Van de Venter & Esterhuizen 1988).

This study aimed to determine germination requirements of six small-leaved shrub species, all dominant species co-occurring in dune fynbos communities, and all members of important genera in the Cape fynbos (Table 1). The study tested the hypothesis that germination is fire-induced by subjecting seed to heat treatments and charcoal extract, or charate (sensu Keeley & Pizzorno 1986; Keeley 1987). Studies were made of germination responses to a range of laboratory treatments simulating natural environmental conditions for buried and unburied seed, including : varying conditions of temperature and light; plant leachates for possible allelopathy; filter paper and soil substrates; and acid, scarification and leaching treatments for a tardy species. Tests were made to determine if dark-inhibition could be overcome by a charate as a possible fire effect on soil-stored seed (Keeley 1987). Germination of different seed crops and of different ages up to three years old were analysed to determine implications for soil-stored seed banks.

The study also sought to test an aspect of Grubb's (1977) "regeneration niche" hypothesis. This proposes that competitively equivalent species can coexist if they differ in aspects of their regeneration niches (e.g. different germination requirements). The fire-prone fynbos shrublands of the Cape Floral Kingdom, like tropical forests, provide ideal subjects for understanding coexistence, as many physiognomically and presumably competitively equal species co-occur (Grubb 1986; Cowling 1987). Should the species have different germination requirements, long term coexistence could then be explained in terms of different recruitment in response to different environmental conditions.

METHODS

Site description

The study site was located on the coastal dunes at Cape St Francis in the south eastern Cape (34°02'S, 24°47'E). Details on the physiography, climate and soils and vegetation are given in Cowling (1984). The climate is mild (mean annual temperature of 17°C) and frost-free. Hottest temperatures are experienced in late autumn as a result of "berg" or fohn-like winds (Cowling 1984) and warm periods in mid winter are not uncommon. Late summer and autumn periods are the most fire-prone. Annual rainfall ranges from 500-900 mm. Although rain falls at any time of the year, there is a wet winter season with spring and autumn peaks. The driest months are December to February. A more detailed account of rainfall and temperature is given elsewhere (Chapter 3). The vegetation comprises a mixture and mosaic of fynbos and subtropical thicket. The study site was located in fynbos which is predominant in the dune landscape and has been subject to natural fires every 10-20 years. Dune fynbos is distinguished from other fynbos types in lacking Proteaceae and in the general occurrence of subtropical shrubs (e.g. Euclea, Maytenus, Rhus etc.).

Seed collection and germination treatments

Details of the selected species are given in Table 1. They will be referred to hereafter by their generic names except in the case of the two congeners, Agathosma apiculata and A. stenopetala. In many cases germination trials were severely limited by low seed numbers because sorting of the small seeds (Table 1; see also Fig.1 in Chapter 5) by means of forceps was very slow . Also, selection for presumably plump or viable seed was even slower in two species which had high proportions of empty seeds. This phenomenon was not initially recognized. Very low germination in Muraltia and Passerina in preliminary trials led to an investigation of seed quality by dissection and selection by weighing or flotation. In the other four species, seeds were selected by light pressure applied with forceps. The loss of plumpness during laboratory storage was negligible (Chapter 4). Seeds were variously collected by bagging, open-bagging to allow access to pollinators, or by shaking shrubs over collecting trays. Additional collections of Muraltia, called annual harvests, were collected from a population of shrubs open-bagged for a period of a year (see Seed production methods in Chapter 4). Seeds of each species were collected from the same populations each year (equivalent to a crop) between 1984-1989 and stored in the laboratory.

The germination trials were run between 1986 and 1989. Unless otherwise indicated , ten seeds per ten petri dishes were sown on three layers of S & S filter paper and treated with 4 ml of fungicide solution of benomyl (0.75 g l^{-1}) and maintained in a saturated state throughout the trial. Preliminary trials indicated that the fungicide had no inhibitory effect; germination improved in the absence of fungal infections. Fungal growth on seed of Muraltia in preliminary trials was avoided in all subsequent trials by prior removal of the elaiosomes. Trial conditions in the controlled environment chambers were : alternating light and dark (L/D) at 20°/10°C for 10/14 h for 130 days, unless otherwise indicated. Germination was defined as emergence of the radicle.

Seed ageing, crop variation and a simulated seedbank

Treatments were designed to determine independently the effects of seed age, and of different crops on germination success. In addition, germination data were used to simulate the synchronous response of a seedbank comprising seed from different crops and of different ages.

The effects of seed ageing were determined by germinating subsamples of the same seed crops each year for up to three consecutive years from 1985 to 1988. Trials were also run on miscellaneous harvests of different ages where subsamples were unavailable. Germination variation amongst different seed crops was determined by germinating seeds of different crops of the same age. To simulate the synchronous germination of a seedbank comprising different aged seeds from preceding crops , germination experiments were run on a sequence of different crops of seeds of successive ages

Varying light, temperature and other conditions

Temperature conditions included : continuous 10°C; continuous 20°C; or alternating 20°/10°C for 10/14 h. Varying light conditions included : continuous dark; alternating light and dark (L/D) for 10/14 h. Counts of trials under continuous dark conditions were made under safety green light. Conditions of 20°/10°C were selected to test the hypothesis that widely alternating temperature promotes highest germination in fynbos species (Brits 1986), as opposed to constant temperatures (10°C or 20°C). Varying light and dark regimes tested for effects of burial, which is relevant to seed stored in the soil. After 130 days, these experimental conditions were changed as follows.

Experimental petri dishes under conditions of L/D at 20°C; continuous dark at 10°C; and continuous dark at 20°C, were moved to new conditions of L/D at 20°/10°C. Petri dishes under conditions of dark at 10°/20°C were treated by adding, after 130 days, 3 ml of charate solution (see below) . This treatment aimed to test if dark inhibition could be overcome by charate (Keeley 1987).

A further trial tested for a higher temperature regime of alternating diurnal temperatures of a high regime of 30°/15°C (10/14 h, L/D) versus a control of a low regime of 20°/10°C. In trials where zero germination was recorded after 60 days, treatment conditions were altered from the higher to the lower temperature regime, and vice versa, and results were recorded after a further 60 days.

Simulated field effects

Seed germination in petri dishes was tested on two types of medium: three layers of filter paper versus sifted dune soil.

In order to simulate post-fire exposure of seeds to charcoal, a solution of "charate" was prepared according to the method of Keeley & Pizzorno (1986). Stems (10 mm diameter) of the selected species were charred with a propane torch, ground in a mill, and made up into an aqueous solution (125 g l^{-1}) which stood for 8 h and was then filtered (Whatman no.1). Three millitres were added to each treatment dish.

To simulate allelopathic effects, a leachate solution was prepared by spraying a bunch of branches (100 g of each of the six species) with 1.3 l distilled water over 24 h (see also Hobbs 1984). The excess was filtered and 3 ml applied to each dish.

Owing to the poor germination of *Passerina* in early trials, seeds were exposed to separate treatments of acid (conc. H_2SO_4 for 15 min.) (Everitt 1983) and mechanical scarification. To remove possible inhibiting substances, leaching treatments were carried out in which seeds were placed under flowing distilled water for 48 h at 500 ml h^{-1}

Heat effects on germination response were studied in two separate ways. Treatment choice was determined by the possible range of conditions that soil-stored seeds might experience during a fire (Humphreys & Craig 1981; Hobbs & Gimingham 1984; Van Wilgen 1985) :- treatment H1 = dry heating seeds at 80°c for 5 min; and treatment H2 = in addition to dry heating seeds for 20 min at 100°c, dry heating sieved dune soil medium for 1 h prior to placing in petri dishes. The control trials for H1 and H2 were C1 which used filter paper, while control C2 used unheated soil as a petri dish medium.

Data analysis

Percentage data were arc-transformed, and tested for differences by means of t-tests and one-way analysis of variance (see also Keeley (1987) and Pons (1989a)). Results were limited in some cases due to seed shortages as explained earlier.

RESULTS

Seed plumpness

In the selection of plump seed for germination trials, some observations on the different harvests ($n>30$) were noted. In *Passerina*, plumpness (i.e. number of plump seed expressed as a percentage of number of seeds per subsample) ranged from 4% to 93%, and varied between years. Results of 1985 harvests were : 4%, 38%, 90%, 90% and for 1987 : 22%, 62%, 68%, 80%, 93%. *Muraltia* seed plumpness varied from month to month: June 1986 = 27%; September 1987 = 24% and 11%; October 1986 = 1% and 5%; November 1985 = 14%. Annual harvests (ie seeds produced over the period of a year) also varied widely : 1985 = 5%

and 14%; 1986 = 18%; 1987 = 1%, 50% and 80%. For the other four species, these plump percentages varied less widely: e.g. Agathosma apiculata 81%, 87%; A. stenopetala 78%, 86%; Felicia 96%, 72%; Metalasia 88%, 61%.

Seed ageing

In both Muraltia and A. apiculata, germination success of seed of the current crop was significantly lower than one-year old seed from the same crop. This indicated dormancy during the first year (Table 2). Felicia showed a significant decline in germination response from fresh to one year old seed, although the latter was still high at 91%. Not all data were comparable as, in some cases, miscellaneous crops were used e.g.a trial with three year-old Felicia seed crop had a germination response of 1±1% (x±S.E.%, n=10x10). A similarly aged crop of Metalasia seed had a response of 7±3% (x±S.E.%, n=10x10). The other species showed no significant difference with age, indicating neither dormancy over a year, nor deterioration (Table 2).

Variation amongst generations

There were significant differences in the germination success of the same-aged seeds from different generations for A. apiculata, A. stenopetala, Metalasia and Muraltia (Table 3). There was no consistent trend for generation amongst the species. Although the 1987 crop was significantly higher than that of 1986 for the two *Agathosma* species, the reverse held true for *Metalasia* and *Muraltia*.

The comparison of synchronous germination of the simulated seedbank (different aged seeds from different crops) indicated significant differences in responses in all species except *Felicia* and *Passerina* (Table 4). For the two *Agathosma* species, percentage germination was higher in the one-year old crop than in the current seed. Similarly, current and one year old seed crops of *Metalasia* showed higher germination over two year old seed. However, in *Muraltia* seeds, highest germination success was recorded in the one year-old generation.

Light and temperature

Alternating (20°C/10°C) as opposed to constant (10°C or 20°C) temperatures produced the highest germination response for all species studied (Table 5). Only *Metalasia* showed a significantly higher response to alternating light. Significant differences in response were apparent between conditions at 10°C or 20°C relative to the alternating 10°/20°C treatment regardless of light conditions in *A. stenopetala* and *Felicia*. The statistical analyses of Table 5 did not, in all cases, indicate significant differences between alternating versus constant 10° or 20°C.

However, Fig. 1 indicated clearly a positive response in germination when the conditions of the petri dishes were changed from conditions of (a) dark at 10°; (b) L/D at 20°C; and (c) dark at 20°C to (d) L/D at 10°/20°C. The germination of *A. stenopetala* (0=current crop) in Fig. 1(a) was inexplicably low.

None of the species responded to the addition of charate after 130 days under conditions of continuous dark at 10°/20°C.

Treatments of diurnal alternating temperatures at a high regime of 30°/15°C compared to a control low regime of 20°/10°C resulted in significantly greater responses by *Muraltia* and *Passerina* (Table 6). Control trials of *Passerina* registering zeros reacted positively to a change to the higher temperatures. Conversely, the two *Agathosma* species had higher responses to the control, and the higher temperature test trials responded strongly to the change to the low regime (Table 6). Both *Felicia* and *Metalasia* had higher germination in the low regime.

Response to simulated field effects

Treatments of leachate (to determine allelopathic effects) and charate (to determine post-fire stimuli) produced no effect in current year's seed of *Muraltia*, *A. stenopetala* and *Felicia* (Table 7). However, the leachate showed a negative effect on one-year old seed of *A. apiculata*, and both treatments inhibited two year-old seed of *Muraltia* (Table 7.). Leachate appeared to stimulate current seed of *Metalasia*, but the charate had no effect.

Germination was not significantly different on sieved dune soil as opposed to filter paper as a medium in current year's seed of *A. stenopetala* and *Muraltia*, but had a negative effect on *Felicia* and *Metalasia* (Table 7.) However, current year's seed of *A. apiculata* germination on soil showed a significantly higher response, achieving maximum germination in all trials.

Seeds of *Passerina* were exposed to a different set of treatments in an attempt to break dormancy. These resulted in minimal response, with highest, but non-significant, results after leachate treatment and mechanical scarification (Table 7).

In all species, both heat treatments H1 and H2 resulted in non-significant differences from unheated controls (Table 8). Some inhibition was apparent in two year-old *Muraltia* seed and three year-old *Passerina* seed, but values were extremely low.

Summary of maximum germination response

Highest germination successes of the study species were summarized below. All species showed maximum germination success under conditions of alternating diurnal temperatures (10/14 h,L/D) after ca. 60 days; thereafter responses levelled off. Muraltia (autumn crop) was the only species to respond maximally (100%) to the high temperature regime (30°/15°C), although for the same crop, the low regime (20°/10°C) produced results not significantly different (Table 6). The other five species responded best to 20°/10°C. Felicia (current crop) reached 100% germination (Table 3), although very high successes (ca.90%) were not uncommon for one year-old seed and under different treatments. However, for this species, a high temperature regime was inhibitory (Table 6). Metalasia showed similarly unspecialized requirements, with responses in the 80's to a range of treatments, and an overall high of 82% (Table 3). However, this species showed some requirement for light (Table 5). Agathosma apiculata peaked at 80% success at the low temperature regime on soil (Table 7), but generally had a 50% response on filter paper. A. stenopetala had highest success (79%) with heat treatment, although results were not significantly different from unheated controls with 58% success (Table 8). In both these congeners, a positive response to alternating and low temperature regimes was obvious (Fig.1 and Table 6). Passerina showed highest germination of 28% in response to a leachate treatment, although this was not significantly different from responses to scarification (20%) nor the control (11%) (Table 7). This species showed a positive response to a change from the low to the high regime (Table 6).

Table 1. Characteristics of the study species.

Species [a]	Family	No.spp.[b] in Cape flora	Distribution[b]	Shrub height (m)	Shrub longevity (yr)	Pollination	Dispersal	Seed [d] prodn	Seed mass (mg) ($x \pm SE$)
Agathosma apiculata	Rutaceae	135	Riversdale to Port Elizabeth	0.8	25	Insect	Ballistic and myrmecochory	May-Oct	4.6 ± 0.2 (n=38)
Agathosma stenopetala	Rutaceae	135	Humansdorp to Port Elizabeth	0.6	20	Insect	Ballistic and myrmecochory	Sep-Dec	2.1 ± 0.03 (n=50)
Felicia echinata	Asteraceae	83	Mossel Bay to Port Alfred	0.1	5	Insect	Wind	May-Sep	0.4 ± 0.03 (n=300)
Metalasia muricata	Asteraceae	50	Cape to Drakensberg	2.3	>30	Insect	Wind	May-Jul	0.6 ± 0.03 (n=50)
Muraltia squarrosa	Polygalaceae	115	Mossel Bay to Port Elizabeth	0.8	14	Insect/[c] self	Myrmecochory	All year	3.7 ± 0.1 (n=50)
Passerina vulgaris	Thymelaeaceae	18	Cape to Drakensberg	1.5	14	Wind	Unspecialized	Oct-Feb	1.3 ± 0.03 (n=47)

[a] Nomenclature after Bond & Goldblatt (1984).
[b] From Bond & Goldblatt (1984).
[c] Levyns (1954).
[d] Pierce & Cowling (1984) and this study.

Table 2. Effects of ageing on the germination response of seeds of dune fynbos shrubs. Germination conditions were light/dark at 20°C/10°C for 10/14 h over 130 days. Data are mean percentage ± standard error; n=10 X 10 seed unless otherwise indicated[a].

	Crop	Seed[b] age (yr)	$\bar{x}\pm SE$ (%)	Statistic[c]	
Agathosma apiculata	1985	1	43 ± 6^{AB}	$F_{(2,27)} = 4.35$	**
		2	$59\pm4^{\ B}$		
		3	36 ± 6^{A}		
	1986	0	14 ± 3^{A}	$F_{(2,27)} = 15.16$	***
		1	$39\pm4^{\ B}$		
		2	8 ± 4^{A}		
Agathosma stenopetala	1985	0	64 ± 5[a]	$t_{0.05(13)} = 0.73$	NS
		1	56 ± 7		
	1986	0	39 ± 6	$F_{(2,27)} = 0.73$	NS
		1	47 ± 8		
		2	49 ± 4		
Felicia echinata	1986	0	100 ± 0[a]	$t_{0.05(13)} = 3.04$	**
		1	91 ± 2		
Metalasia muricata	1986	0	82 ± 4[a]	$t_{0.05(13)} = 1.09$	NS
		1	71 ± 7		
	1987	0	63 ± 3	$t_{0.05(18)} = 0.78$	NS
		1	67 ± 7		
Muraltia squarrosa	1986	0	30 ± 8[a]	$t_{0.05(13)} = 4.89$	***
		1	76 ± 5		

[a] n=10 X 5 seed.

[b] 0=current year's crop; 1=one year old; 2=two year old etc.

[c] Significant difference by one-way ANOVA (F value) or t-tests (t value) on arcsine transformations of mean percentages. Different letters (^{A},^{B} etc) indicate significant differences amongst treatments by Tukey's multiple range test. *=p<0.05; **=p<0.01; ***=p<0.001; NS=not significant.

No data available for *Passerina*.

Table 3. Germination response of seeds produced in different years as a measure of year to year variation amongst crops. Comparisons between seed of the same age. Germination conditions were light/dark at 20°C/10°C for 10/14 h over 130 days. Data are mean percentage ± standard error; n=10 X 10 seed unless otherwise indicated[a].

	Crop	Seed[b] age (yr)	x±SE (%)	Statistic[c]	
Agathosma apiculata	1986	0	14±3	$t_{0.05(18)} = 5.16$	***
	1987	0	55±7		
	1985	1	43±6	$t_{0.05(18)} = 0.54$	NS
	1986	1	39±4		
Agathosma stenopetala	1986	0	39±6	$t_{0.01(18)} = 3.15$	**
	1987	0	68±7		
	1985	1	56±7	$t_{0.05(18)} = 0.82$	NS
	1986	1	47±8		
Felicia echinata	1986	0	100 [a]	$t_{0.05(13)} = 2.08$	NS
	1987	0	90±3		
Metalasia muricata	1986	0	82±4[a]	$t_{0.05(13)} = 3.48$	**
	1987	0	63±3		
	1986	1	71±7	$t_{0.05(18)} = 0.36$	NS
	1987	1	67±7		
Muraltia squarrosa	1986	0	30±8[a]	$t_{0.05(13)} = 2.25$	*
	1987	0	12±4		

[a] n=10 X 5 seed.

[b] 0=current year's crop; 1=one year old; 2=two year old etc.

[c] Significant difference by t-tests on arcsine transformations of mean percentages. *=p<0.05; **=p<0.01; ***=p<0.001; NS=not significant.

No data available for *Passerina*.

Table 4. Germination response of different aged seeds from different crops as a simulation of a seed bank exposed to conditions suitable for germination. Germination conditions were light/dark at 20°C/10°C for 10/14 h over 130 days. Data are mean percentage ± standard error; n=10 X 10 seed.

	Crop	Seed[a] age (yr)	x±SE (%)	Statistic[b]	
Agathosma	1986	0	14±3	$t_{0.05(18)}=4.98$	***
apiculata	1985	1	50±6		
Agathosma	1986	0	40±6	$t_{0.05(18)}=2.25$	*
stenopetala	1985	1	62±7		
Felicia	1987	0	93±3	$F_{(2,27)}=1.9$	NS
echinata	1986	1	76±11		
	1985	2	86±3		
Metalasia	1987	0	82±3^{A}	$F_{(2,27)}=35.6$	***
muricata	1986	1	73±6^{A}		
	1985	2	27±4 ^{B}		
Muraltia	1987	0	10±6^{A}	$F_{(2,27)}=21.8$	***
squarrosa	1986	1	82±5 ^{B}		
	1985	2	65±6 ^{B}		
Passerina	1986	1	7±3	$t_{0.05(18)}=0.54$	NS
vulgaris	1985	2	11±4		

[a] 0=current year's crop; 1=one year old; 2=two year old etc.

[b] Significant difference by one-way ANOVA (F value) or t-tests (t value) on arcsine transformations of mean percentages. Different letters (^{A},^{B} etc) indicate significant differences amongst treatments by Tukey's multiple range test. *=$p<0.05$; **=$p<0.01$; ***=$p<0.001$; NS=not significant.

Table 5. Germination of dune fynbos species under variable conditions of light and temperature after 130 days. Data are mean percentage ± standard error; n=10 X 10 seed.

	Treatment[a]		x±SE	Statistic[b]	
	Light Regime	Temp (°C)	(%)		
Agathosma apiculata (2 yr-old seed)	D	10	4 ± 2^{A}	$F_{(4,45)}=19.0$	***
	D/L	20	6 ± 2^{A}		
	D	20	26 ± 4^{B}		
	D	10/20	37 ± 6^{B}		
	D/L	10/20	43 ± 6^{B}		
Agathosma stenopetala (1)	D	20	0^{A}	$F_{(4,45)}=76.0$	***
	D/L	20	0^{A}		
	D	10	7 ± 3^{B}		
	D/L	10/20	40 ± 6^{C}		
	D	10/20	50 ± 3^{C}		
Felicia echinata (0)	D	20	38 ± 4^{A}	$F_{(4,45)}=20.2$	***
	D/L	20	64 ± 5^{B}		
	D	10	79 ± 5^{B}		
	D/L	10/20	90 ± 3^{C}		
	D	10/20	93 ± 3^{C}		
Metalasia muricata (0)	D/L	20	11 ± 3^{A}	$F_{(4,45)}=16.7$	***
	D	20	23 ± 6^{AB}		
	D	10/20	39 ± 4^{B}		
	D	10	41 ± 7^{BC}		
	D/L	10/20	63 ± 3^{C}		

[a] Diurnal regime of 10/14 h: L/D = alternating light/dark; D = continuous dark; 10/20 = alternating temperatures of 10°C/20°C; 10 = continuous 10°C; 20 = continuous 20°C.

[b] Significant difference by one-way ANOVA (F value) or t-tests (t value) on arcsine transformations of mean percentages. Different letters (^{A},^{B} etc) indicate significant differences amongst treatments by Tukey's multiple range test. *=p<0.05; **=p<0.01; ***=p<0.001; NS=not significant.

No data available for *Passerina* and *Muraltia*.

Table 6. Germination success of dune fynbos species at a high (H = 30°C/15°C) and low (L = 20°C/10°C) temperature regime of alternating diurnal temperatures for 10/14 h, light/dark conditions after 60 days. Data are mean percentage ± standard error; n=10 X 10 seed unless otherwise indicated[a]. Where zero germination was recorded, trials were transferred to alternate regime for a further 60 days.

	Temp.regime		Statistic[b]		Trial transfer	
	High	Low			H-L	L-H
Agathosma apiculata (3 yr-old seed)	0	36±6	7.7	***	29±5	-
Agathosma stenopetala (2)	0	49±4	18.9	***	56±7	-
Felicia echinata (1)	39±3	70±10	2.8	**	-	-
Metalasia muricata (1)	31±5	52±3	3.0	**	-	-
Muraltia squarrosa (0)	100±0[a]	87±4[a]	8.1	***	-	-
Passerina vulgaris (2)	10±4	0	2.4	*	-	17±4

[a] n=3 X 10 seed

[b] Significant difference by t-tests on arcsine transformations of mean percentages. *=p<0.05; **=p<0.01; ***=p<0.001.

Table 7. Germination of dune fynbos species subject to various treatments. Conditions were light/dark at 20°C/10°C for 10/14 h over 130 days. Data are mean percentages ± standard errors; n=10 x 10 seed.

	Seed^{a} age (yr)	Treatment^{b}	x±SE	Statistic^{c}	
Agathosma apiculata	0	Control	14 ± 3^{A}	$F_{(3,36)}=37.7$	***
		Charcoal	15 ± 5^{A}		
		Leachate	8 ± 4^{A}		
		Soil medium	80 ± 5^{B}		
	1	Control	48 ± 6^{A}	$F_{(2,27)}=4.5$	*
		Charcoal	36 ± 7^{AB}		
		Leachate	24 ± 5^{B}		
Agathosma stenopetala	0	Control	40 ± 6	$F_{(3,36)}=1.5$	NS
		Charcoal	50 ± 6		
		Leachate	36 ± 7		
		Soil medium	51 ± 7		
Felicia echinata	0	Control	90 ± 3^{A}	$F_{(3,36)}=9.8$	***
		Charcoal	97 ± 2^{A}		
		Leachate	97 ± 2^{A}		
		Soil medium	65 ± 6^{B}		
Metalasia muricata	0	Control	82 ± 3^{AB}	$F_{(4,45)}=9.9$	***
		Control^{d}	62 ± 4^{BC}		
		Charcoal	61 ± 5^{BC}		
		Leachate	86 ± 7^{A}		
		Soil medium	40 ± 8^{C}		
Muraltia squarrosa	0	Control	18 ± 6	$F_{(3,36)}=1.1$	NS
		Charcoal	12 ± 4		
		Leachate	24 ± 8		
		Soil medium	10 ± 3		
	2	Control	64 ± 6^{A}	$F_{(2,27)}=4.9$	**
		Charcoal	36 ± 7^{B}		
		Leachate	38 ± 8^{B}		
Passerina vulgaris	1	Soil medium	8 ± 3^{A}	$F_{(7,72)}=4.4$	***
	2	Acid	3 ± 2^{AB}		
	2	Charcoal	8 ± 4^{AB}		
	2	Leached	6 ± 2^{AB}		
	1	Control	7 ± 3^{ABC}		
	2	Control	11 ± 4^{ABC}		
	1	Scarified	20 ± 5^{BC}		
	1	Leachate	28 ± 7^{C}		

a 0=current crop; 1=one year old; 2=two year old etc.

b Treatment details in text.

c Significant difference by one-way ANOVA on arcsine transformations of mean percentages. Different letters (A,B etc) indicate significant differences amongst treatments by Tukey's multiple range test. *=p<0.05; **=p<0.01; ***=p<0.001; NS=not significant.

d indicates seed from a different population.

Table 8. Germination of dune fynbos seeds subjected to two heat treatments, H1 and H2 with controls C1 and C2 respectively. Conditions were light/dark at 20°C/10°C for 10/14 h over 90 days. Data are mean percentages ± standard errors; n= 10 X 5 seed for H1 and C1; n= 10 X 10 seed for H2 and C2 unless otherwise indicated[a].

	Seed[b] age (yr)	Heat[c] treatment	x±SE (%)	Statistic[d]		
<u>Agathosma apiculata</u>	1	H1 C1	78±2 74±6	$t_{0.05(8)}$	=0.56	NS
	1	H2 C2	71±5 58±5	$t_{0.05(18)}$	=1.77	NS
	2	H2 C2	29±7 16±3	$t_{0.05(18)}$	=0.61	NS
	3	H2 C2	42±8 38±7	$t_{0.05(18)}$	=-0.63	NS
<u>Agathosma stenopetala</u>	1	H1 C1	68±6 64±5	$t_{0.05(8)}$	=0.52	NS
	1	H2 C2	79±4 58±5	$t_{0.05(18)}$	=0.0	NS
	2	H2 C2	65±6 47±6	$t_{0.05(18)}$	=-2.03	NS
<u>Felicia echinata</u>	0	H1 C1	98±2 100±0	$t_{0.05(8)}$	=-1.0	NS
<u>Metalasia muricata</u>	0	H1 C1	86±4 82±4	$t_{0.05(8)}$	=0.73	NS
<u>Muraltia squarrosa</u>	1	H1 C1	12±7 30±8	$t_{0.05(8)}$	=-1.35	NS
	2	H2 C2	2±1[a] 6±1[a]	$t_{0.05(10)}$	=2.53	*
<u>Passerina vulgaris</u>	2	H2 C2	2±1 2±1	$t_{0.05(18)}$	=0.61	NS
	3	H2 C2	2±1 8±2	$t_{0.05(18)}$	=2.12	*

[a] n= 6 X 10 seed.

[b] 0=current year's crop; 1=one year old; 2=two year old etc

[c] H1 = seed heated for 5 min at 80°C and sown on filter paper. C1 = no heat exposure. H2 = seed heated for 20 min at 100°C and sown on soil heated for 1 h at 100°C. C2 = no heat exposure to seed nor soil.

[d] Significant difference by t-tests on arcsine transformations of mean percentages. *=$p<0.05$; NS= not significant.

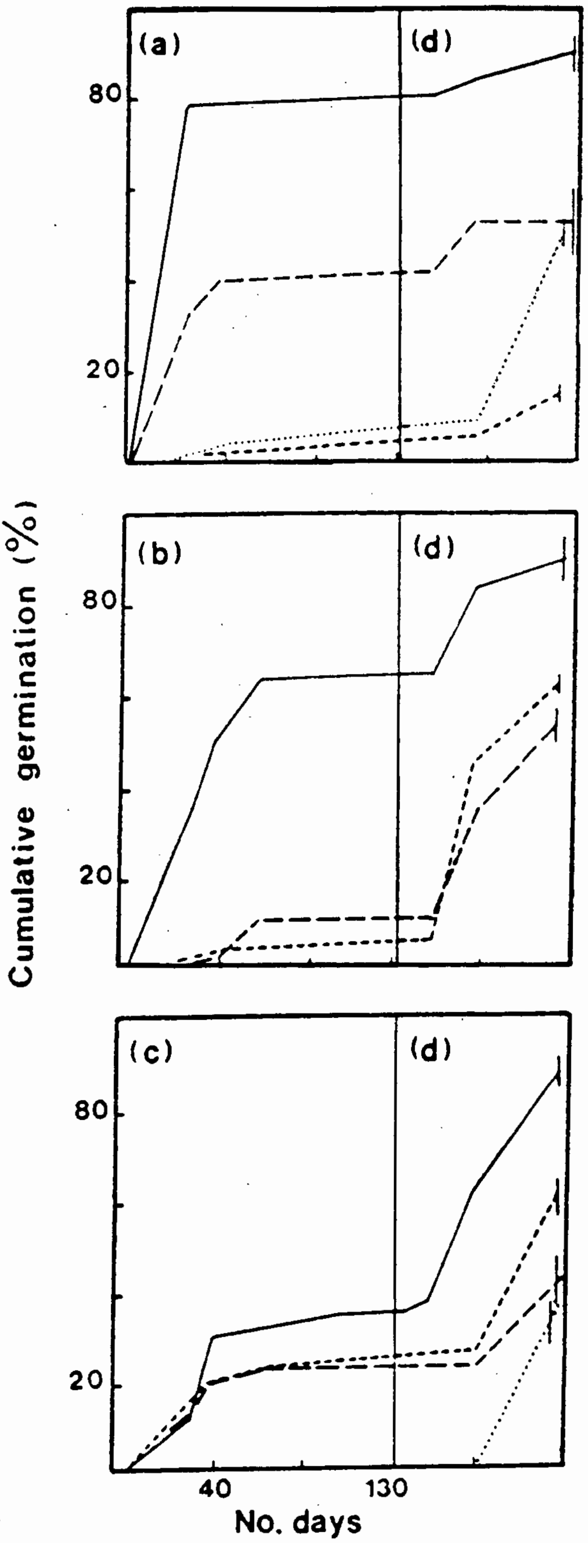


Fig. 1. Cumulative percentage germination of dune fynbos shrubs under changed conditions of temperature and light as follows: (a) constant dark at 10°C; (b) alternating light/dark (14/12 h) at constant 20°C; (c) constant dark at 20°C; changed to (d) alternating light/dark (14/12 h) at 20°C/10°C. Species are: Felica echinata (0) (solid line); Metalasia muricata (0) (long dash); Agathosma apiculata (1) (short dash); A. stenopetala (0) (dotted line). Number in brackets refers to seed age: 0=current year's seed; 1=one year-old etc.. Data=means of 10 replicates of 10 seeds each; vertical lines=standard errors. Under conditions of (b), A. stenopetala showed no response. No data available for Passerina and Muraltia.

DISCUSSION

Fire effects

The hypothesis that germination of fynbos species is fire-stimulated was largely unsupported. Neither heat nor charate treatments resulted in significant enhancement of germination. Also, charate treatment did not break any dark-induced dormancy as found in some chaparral species (Keeley 1987). Studies on other small-leaved shrubs growing in fynbos on acid sands of the Cape Region showed that fire effects induce germination. Heat, as well as ethylene and ammonia treatments simulating fire effects, promoted germination in *Erica hebecalyx* but failed in *E. sessiliflora* (Van de Venter & Esterhuizen 1988). The findings of improved germination after heating of seed of two *Agathosma* species (Blommaert 1972) are unfortunately unclear as seeds of both species were mixed, and statistical analyses were lacking .

Allelopathy has been suggested as a mechanism for inhibiting germination during inter-fire periods (Keeley 1984). An indirect effect of fire is the removal of the shrubs and the breakdown of such allelopathic substances in the soil. There was some support for allelopathic inhibition of germination in seed of *A. apiculata* (one year-old) and

Muraltia (two year-old). However, inhibition was slight, and more detailed investigations are required. Though some inhibitory effects by *Calluna* heathland species have been shown in the laboratory, Hobbs (1984) doubted the importance of allelopathy in the field. The positive response of *Metalasia* seeds and some annual chaparral species to plant leachate, is irreconcilable with allelopathy, but might be a possible response to nitrate levels (Keeley *et al*. 1985). However, recent work reports higher nitrate levels in bare soil relative to vegetated soil (Pons 1989b). The higher nitrates appear to break dormancy, thus acting as a mechanism for gap detection.

Alternating temperature effects

Optimum conditions for germination of all six species were alternating diurnal temperatures of 20°/10°C for the two *Agathosma* species, *Felicia* and *Metalasia*, although *Muraltia* and *Passerina* also responded to a higher regime of 30°/15° C. Both temperature regimes can occur during autumn and early winter in the south eastern Cape when largest diurnal fluctuations are recorded (Chapter 3). The higher regime would be associated with hot, pre-frontal or "berg wind" conditions. The heating of bare soil by radiation could also be important. Soil temperatures of up to 60oC have been recorded in the coastal region of the south western Cape (P. Mustart, 1989, pers. comm.)

Positive germination response to alternating diurnal temperatures is well established in the literature (e.g. Murdoch, Roberts & Goedert 1989). A similar germination response to temperature fluctuation preceding moist conditions has been documented in detail in some members of the Proteaceae in the mediterranean climate of the south western Cape (Brits 1986). In the non-seasonal rainfall region of the south eastern Cape where rain can fall at any time of the year, this "drought-avoiding syndrome" (sensu Angevine & Chabot 1979) would be even more advantageous in ensuring that germination does not occur in response to occasional summer rains.

Recruitment of fynbos seedlings is uncommon under a closed canopy. Some recruitment does occur in open vegetation and in gaps, but most of these seedlings die (Chapter 3). Survivors rarely reach reproductive maturity and fail to contribute to the seed bank (Chapter 3). Removal of the insulating effect of vegetation cover by fire and bushcutting would allow ambient temperature fluctuations to reach soil level (Thompson, Grime & Mason 1977; Brits 1986) which would promote germination with the onset of early winter rains. Alternating temperatures are limited to the uppermost layers of the soil (Koller 1964). For these very small seeds, depth of burial in the soil is critical for emergence (Chapter 4) and therefore response to this cue is especially important.

Light effects

European heath species such as *Calluna vulgaris* and *Erica* species have fairly complex light requirements for germination, dependent on varying intensity and exposure time (Pons 1989a). Dark inhibition would prevent germination under dense canopy and increase chances of incorporation into the soil-stored seed bank (Pons 1989a). The lack of a light requirement in the four study species with soil-stored seed banks (Chapter 4) is therefore unexpected. The singular positive light response by *Metalasia* seed may be an adaptation by wind-dispersed seed for colonization of open patches.

Dormancy and seed ageing

Because shorter lived shrubs are like annuals in having a limited period during which they can contribute to the seed bank, they might be expected to show similar traits such as dormancy (cf. Cohen 1966; Harper 1977; Thompson & Grime 1979). However, this was absent from the relatively short-lived shrub, *Felicia*. Dormancy in the current year's seed of *A. apiculata* could be explained by the timing of its reproductive phenophase. Seeds are produced early in spring

(Table 1; Pierce & Cowling 1984) when soil conditions are still moist. Dormancy would prevent immediate germination and inadequate root development in the short growing season prior to the summer drought. A similar trait has been noted in mediterranean annuals (Thompson 1973). In contrast, *A. stenopetala* and *Passerina* disperse their seeds later, in the early summer prior to the normal fire season. Therefore dormancy in these species would serve no role in drought avoidance. Because some life history attributes are those normally associated with "weedy" annuals in the otherwise long-lived shrub *Metalasia* (ie. widely-dispersed by wind; colonizers of disturbed areas), dormancy was predicted, but not found. Soil-stored seed banks of *Metalasia* and *Felicia* were found to be negligible (Chapter 4) which obviates the need for dormancy. Instead, *Felicia* and *Metalasia* fit closely a model proposed by Venable & Lawlor (1980) which predicts a syndrome of greater dispersibility and decreased seed bank size with increased germinability.

The results for *Passerina* seeds indicated a relatively low viability of about 20% despite varied treatments. It has a wide geographical distribution (Table 1), and has high recruitment relative to the other species after disturbance (Chapter 3). Very high seed production (Chapter 4) might compensate for low viability.

Muraltia seeds had anomalous seasonal behaviour, showing dormancy in seed produced during most of the year, and none in an autumn seed crop. Amongst the Cape Proteaceae, dormancy predominates in myrmecochorous seeds, but is not apparent in non-myrmecochorous species with soil-stored seeds (Slingsby & Bond 1983). Any link between dormancy and ant dispersal and burial is not clear to me. Alternatively, dormancy may not impart any particular selective advantage. It might, for example, simply be the effect of differential embryo development i.e. somatic heterochrony (Silvertown 1984).

The seed deterioration over three years in A. apiculata was unexpected in a species which has soil-stored seed banks Deterioration in three year-old crops of Metalasia and Felicia would have been expected in species with small seed banks (Chapter 4). Ideally germination responses of older seeds (e.g.five, ten and fifteen years old) of all species need to be determined.

Empty seeds

Empty seeds may simply be a casualty of the development of the maternally-derived seed coat independent of embryogenesis (Westoby 1981). Abortion may be due to resource limitation, unsuccessful pollination, lethal genetic recombinations in outcrossers (Wiens et al. 1987) or maternal control in response to environment (cf. Gutterman 1980). Cryptic abortion, where the seed coat remains intact (Nakamura & Stanton 1987) would "cost" the plant more than normal abortion. I suggest the possible advantage of *Muraltia* and *Passerina* producing many empty seeds would be to increase the chances of the plump seed escaping predation (cf. O'Dowd & Gill 1984). Also, for *Muraltia* seeds which bear elaiosomes, continued production of empty seeds would maintain ant interest and thus dispersal. Cafetaria experiments on unsorted seed of these two species showed complete removal by invertebrates (Chapter 5), indicating that both plump and empty seeds were moved.

Comparisons with fire-prone Californian shrublands

No species in this study was comparable to the dominant chaparral shrubs which respond to heat, charate or the effect of light (Keeley 1987). Instead, dune fynbos species are more analogous to coastal sage subshrubs which are similarly independent of fire for recruitment and are able to colonize disturbed sites (Keeley 1987). However, the coastal sage species differ in their ability to resprout. Those chaparral species which are not dependent on fire for germination resemble more closely the thicket component of dune fynbos (Cowling 1984). The latter have relatively short-lived seeds within fruits, lack seed banks and have long distance, directional dispersal by birds and animals (Chapter 6; Knight 1988).

Germination implications for seed banks and coexistence

There was no evidence for great differences in germination requirements as would be predicted for co-existing species (Grubb 1977; Schat 1983); nor was there evidence of highly specialized germination requirements. Instead, the species shared relatively flexible germination requirements. Response to alternating temperatures also allows some inter-fire or "gap detection" germination (*sensu* Thompson, Grime & Mason 1977). A major disadvantage of this germination flexibility is that in open vegetation soil-stored seeds can germinate during inter-fire periods (Chapter 4). This could lead to unsuccessful establishment owing to competition with mature shrubs (Chapter 3). Such inter-fire germination would contribute little to effective population size but effectively deplete the seed bank.

I predict that environmental selection acts on germinable seed quantities rather than on germination responses. Thompson (1973) has argued against genetic plasticity, and suggested instead a remarkable stability in germination responses. In chaparral, previous season's climate appears to affect seed production, seed banks and hence post-fire recruitment (Keeley 1977). This study has shown that each year the seed bank composition of each species comprised a mixture of crops of varying germinability. Therefore in addition to the elements of fire intensity, frequency and season (Gill 1974), year of fire is another important factor in post-fire regeneration. After each fire, varying numbers of recruits of the different species would be favoured according to seed bank composition. This differential recruitment could enable coexistence of the dune fynbos shrubs in the long term (Cowling 1987).

ACKNOWLEDGEMENTS

Technical assistance by D.Barnes, C. Douie, F. Mackay, N. Phillips and S. Steinhobel is gratefully acknowledged. Valuable discussion was provided by N. Phillips, R. M. Cowling and E.J. Moll. The study was supported by the Fynbos Biome Programme, Foundation for Research Development of the CSIR, and the University of Cape Town.

REFERENCES

Angevine, M. W. & Chabot, B. F. (1979). Seed germination syndromes in higher plants. Topics in Plant Population Biology (Ed. by O.T. Solbrig, S. Jain, G.B. Johnson and P.H. Raven), pp. 188-206. Columbia University Press, New York.

Blommaert, K. L. J. (1972). Buchu seed germination. Journal of South African Botany, 38, 237-39.

Bond, W. J. & Breytenbach, G. J. (1985). Ants, rodents and seed predation in Proteaceae. South African Journal of Zoology, 20, 150-54.

Bond, P. & Goldblatt, P. (1984). Plants of the Cape flora. A descriptive catalogue. Journal of South African Botany Supplement 13. Kirstenbosch, Claremont.

Breytenbach, G. J. (1984). Single agedness in fynbos:22; a predation hypothesis. MEDECOS IV (Ed. by B. Dell), pp.14-15. Proceedings of the 4th International Conference on Mediterranean Ecosystems. University of Western Australia, Nedlands.

Brits, G. J. (1986). Influence of fluctuating temperatures and H_2O_2 treatments on germination of Leucospermum cordifolium and Serruria florida (Proteaceae) seeds. South African Journal of Botany, 52, 286-290.

Brits, G. J. & Van Niekerk, M. N. (1986).Effects of air temperature, oxygenating treatments and low storage temperature on seasonal germination response of Leucospermum cordifolium (Proteaceae) seeds. South African Journal of Botany, 52, 207-211.

Cohen, D. (1966). Optimizing reproduction in a randomly varying environment. Journal of Theoretical Biology, 12, 119-29.

Cowling, R. M. (1984). A syntaxonomic and synecological study in the Humansdorp region of the fynbos biome. Bothalia, 15, 175-227.

Cowling, R. M. (1987). Fire and its role in coexistence and speciation in Gondwanan shrublands. South African Journal of Science, 83, 106-112.

Deall, G. B. & Brown, N. A. C. (1981). Seed germination in Protea magnifica Link. South African Journal of Science, 77, 175-76.

Everitt, J. H. (1983). Seed germination characteristics of two woody legumes (retama and twisted acacia) from south Texas. Journal of Range Management, 36, 411-14.

Gill, A. M. (1974). Fire and the Australian flora: a review. Australian Forestry, 38, 4-25.

Grubb, P. J. (1977). The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biological Reviews, 52, 107-145.

Grubb, P. J. (1986). Problems posed by sparse and patchily distributed species in species-rich plant communities. Community Ecology (Ed. by J. Diamond and T.J.Case), pp.207-225. Harper & Row, New York.

Gutterman, Y. (1980). Influences on seed germinability: phenotypic maternal effects during seed maturation. Israel Journal of Botany, 29, 105-117.

Harper, J. L. (1977). Population Biology of Plants. Academic Press, London.

Hobbs, R. J. (1984). Possible chemical interactions among heathland plants. Oikos, 43, 23-29.

Hobbs, R. J. & Gimingham, C. H. (1984). Studies on fire in Scottish heathland communities. I. Fire characteristics. Journal of Ecology, 72, 223-240.

Humphreys, F. R. & Craig, F. G. (1981). Effects of fire on soil chemical, structural and hydrological properties. Fire and the Australian biota (Ed. by A. M. Gill, R. H. Groves and I. R. Noble), pp. 177-200. Australian Academy of Science, Canberra.

Keeley, J.E. (1977). Seed production, seed populations in soil, and seedling production after fire for two congeneric pairs of sprouting and non-sprouting chaparral shrubs. Ecology, 58, 820-29.

Keeley, J. E. (1984). Factors affecting germination of chaparral seeds. Bulletin of Southern Californian Academy of Science, 83, 113-120.

Keeley, J.E. (1987). Role of fire in seed germination of woody taxa in California chaparral. Ecology, 62, 434-43.

Keeley, J. E., Morton, B. A., Pedrosa, A. & Trotter, P. (1985). Role of allelopathy, heat and charred wood in the germination of chaparral herbs and suffrutescents. Journal of Ecology, 73, 445-58.

Keeley, S.C. & Pizzorno, M. (1986). Charred wood stimulated germination of two fire-following herbs of the California chaparral and the role of hemicellulose. American Journal of Botany, 73, 1289-97.

Knight, R. S. (1988). Aspects of plant dispersal in the southwestern Cape with particular reference to the roles of birds as dispersal agents. Ph.D. thesis, University of Cape Town.

Koller, D. (1964). The survival value of germination-regulating mechanisms in the field. Herbage Abstracts, 34, 1-7.

Kruger, F. J. (1984). Fire in fynbos. Ecological Effects of Fire in South African Ecosystems, Ecological Studies 48. (Ed. by P. de V. Booysen and N. M. Tainton), pp. 68-114. Springer-Verlag, Berlin.

Levyns, M. R. (1954). The genus Muraltia. Journal of South African Botany Supplementary Volume II, 1-247.

Murdoch, A. J., Roberts, E. H. & Goedert, C. O. (1989). A model for germination responses to alternating temperatures. Annals of Botany, 63, 97-111.

Nakamura, R.R. & Stanton, M.L. (1987). Cryptic seed abortion and the estimation of ovule fertilization. Canadian Journal of Botany, 65, 2463-65.

O'Dowd, D. J. & Gill, A. M. (1984). Predator satiation and site alteration : mass reproduction of alpine ash (*Eucalyptus delegatensis*) following fire in southeastern Australia. *Ecology*, *65*, 1052-66.

Pierce, S. M. & Cowling, R. M. (1984). Phenology of fynbos, renosterveld and subtropical thicket in the south-eastern Cape. *South African Journal of Botany*, *3*, 1-16.

Pons, T. L. (1989a). Dormancy and germination of *Calluna vularis* (L.) Hull and *Erica tetralix* L. seeds. *Acta Oecologica, Oecologia Plantarum*, *10*, 35-43.

Pons, T. L. (1989b). Breaking of seed dormancy by nitrate as a gap detection mechanism. *Annals of Botany*, *63*, 139-143.

Schat, H. (1983). Germination ecology of some dune slack pioneers. *Acta Botanica Neerlandica*, *32*, 203-212.

Silvertown, J.W. (1984). Phenotypic variety in seed germination behaviour: the ontogeny and evolution of somatic polymorphism in seeds. *American Naturalist*, *124*, 1-16.

Slingsby, P. & Bond, W. J. (1983). Of ants and proteas. African Wildlife, 36, 104-107.

Small, J. G. C. & Garner C.J. (1980). Gibberellin and stratification required for the germination of Erica junonia, an endangered species. Zeitschrift fur Pflanzenphysiologie, 99, 179-182.

Small, J. G. C., Robbertse, P. J., Grobbelaar, N. & Badenhorst, C. M. (1982). The effect of time of application and sterilization method of gibberellic acid, and temperature on the seed germination of Erica junonia, an endangered species. South African Journal of Botany, 1, 139-141.

Thompson, K. & Grime, J. P. (1979). Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. Journal of Ecology, 67, 893-921.

Thompson, K., Grime, J. P. & Mason, G. (1977). Seed germination in response to diurnal fluctuations of temperature. Nature, 267, 147-49.

Thompson, P.A. (1973). Seed germination in relation to ecological and geographical distribution. Taxonomy and Ecology (Ed. by V. H. Heywood), pp 93-119 . Academic Press, London.

Van de Venter, H. A. & Esterhuizen, A. D. (1988). The effect of factors associated with fire on seed germination of Erica sessiliflora and E. hebecalyx (Ericaceae). South African Journal of Botany, 54, 301-304.

Van Staden, J. & Brown, N. A. C. (1977). Studies on the germination of South African Proteaceae - a review. Seed Science and Technology, 5, 633-643.

Van Wilgen, B. W. (1985). The derivation of fire hazard indices and burning prescriptions from climatic and ecological features of the fynbos biome . Ph.D. thesis University of Cape Town.

Venable, D. L. & Lawlor, L. (1980). Delayed germination and dispersal in desert annuals: escape in space and time. Oecologia, 46, 272-282.

Westoby, M. (1981). How diversified seed germination behaviour is selected. American Naturalist, 118, 882-85.

Wiens, D., Calvin, C. L., Wilson, C. A., Davern, C. I., Frank, D. & Seavey, S. R. (1987). Reproductive success, spontaneous embryo abortion, and genetic load in flowering plants. Oecologia, 71, 501-509.

CHAPTER 3

Population structure of non-resprouting dune fynbos shrubs in relation to fire, bushcutting and clearing

ABSTRACT

This study aimed at determining the population structure of six small-leaved, non-resprouting shrub species in mature fynbos, as well as seedling recruitment and survival after fire and bushcutting. Three 13 year-old communities were selected in the coastal dunes of the south eastern Cape: on the north- and south-facing slopes at a moist site (900 mm yr^{-1}) and the third at a drier site (600 mm yr^{-1}). Part of the moist site was burnt; while part of the drier site was bushcut. The few seedlings recorded in permanent plots ($10 \times 1\ m^2$) in the mature vegetation of the two moist stands died, indicating no inter-fire recruitment. In contrast, in plots ($30 \times 1\ m^2$) in the lower, more open vegetation of the drier site, numerous seedlings recruited, with some surviving to contribute to the mixed-age community. These differences were probably due to increased germination of soil-stored seeds in response to greater temperature fluctuations and greater survival under open canopies. Gaps ($5 \times 0.25\ m^2$) cleared in the two moist sites were too small to stimulate recruitment. At the drier site, seedling densities in plots ($15 \times 1\ m^2$) cleared and trenched showed no change after summer drought relative to control plots. However, longer term monitoring showed significant increases in seedling densities in cleared plots. Initial results may have been biased by the most severe summer drought in 90

years. Post-fire seedling densities (20 X 1 m^2) in both moist communities decreased over three years while at the drier site, post-bushcut (15 X 1 m^2) seedling densities increased. The latter increase was due to a gradual reduction in germination inhibition as bushcuttings, insulating the soil surface temperatures, decomposed and/or were removed by wind. Also, possible allelopathic substances would have diminished as cuttings aged. Post-fire seedlings of four species showed no obvious losses to herbivory. Seedling growth rates slowed during the summer/autumn drought period on both slopes. Seedling mortality was significantly greater during the summer drought period for two of the four post-fire species. However, on the north slope, overall rates of mortality were not faster than on the south aspect. Therefore, the prediction of greater moisture stress due to north aspect was not entirely supported, although summer drought-effects were experienced only on this slope. The comparison of aspect effects was complicated by the appearance on the south-facing slope of short-lived herbs which out-competed, and caused etiolation and increased mortality, of shrub seedlings. Post-fire shrub species differed in size of survivors after four years: in two species, a wider size range of seedlings survived; while in the other two species, only the largest seedlings survived.

Nomenclature follows Bond & Goldblatt (1984).

INTRODUCTION

This study investigated determinants of the population structure of non-resprouting shrubs in fire-prone dune fynbos communities, and seedling recruitment and survival after disturbance. Kruger (1979) generalized that the population structure of fynbos communities is even-aged with all recruitment confined to the immediate post-fire period. Most data on the population structure of fynbos shrubs are for the Proteaceae, in which even-agedness is attributed to inter-fire seed predation (Bond 1984; Le Maitre 1988) and herbivory of seedlings (Breytenbach 1984). There are as yet, no published accounts of the population structure of small-leaved shrubs, a major woody component in fynbos communities. Factors such as allelopathy, fire-related germination cues, adult competition, or herbivory have been suggested as determinants of population structure through the control of seedling recruitment and survival (Frost 1984). The first two suggested factors have been explored elsewhere (Chapter 2), while the third and fourth factors were studied here.

This study aimed to determine population age structure and seedling recruitment patterns after disturbance of small-leaved shrubs in dune fynbos communities. Six small-leaved, non-resprouting shrubs, co-occurring in south eastern Cape dune fynbos were selected for study. Although these species shared a broadly similar physiognomy, they had different longevities, phenophases and dispersal modes (Table 1). Firstly, the study aimed to describe and identify the determinants of the population structure of mature fynbos (13 year old) in three communities: a relatively dry site (Cape St Francis with rainfall of 600 mm yr^{-1}); and north- and south-facing slope communities at a moister site (Brandewynkop with 900 mm yr^{1}). Mature individuals and seedling numbers were monitored over three years. Small gaps were made in mature vegetation in the moist site to determine if seedling recruitment was gap-related. At the drier site, quadrats were cleared of mature shrubs and trenched to determine if seedling survival was higher than in the presence of adults over the summer/autumn drought period.

Secondly, the study aimed to determine seedling recruitment patterns after different disturbances of fire and bushcutting. Dune vegetation in the south eastern Cape is burnt every 10-20 years, although frequencies can vary widely from four to greater than 40 years. In the last 50 years, some areas of dune fynbos have been bushcut by pastoralists on a four year rotation to remove unpalatable shrubs and to encourage grasses for grazing.

Thirdly, seasonal drought as a determinant of post-fire seedling mortality was investigated. Higher rates of seedling mortality would be expected in the summer/autumn drought period of the south eastern Cape. Furthermore, a warmer, north-facing slope would be more moisture-stressed than a south-facing slope (Holland & Steyn 1975; O'Leary 1988), and faster seedling mortality rates would be predicted for the former. Seedling densities in randomly located quadrats were counted at intervals after a fire on both slopes to determine mortality rates. Tagged seedlings of each of four species were monitored to derive survival curves, and determine growth rates and size at death.

METHODS

Study sites

Two study sites, Brandewynkop and Cape St Francis, were located in South Coast Dune Fynbos (*sensu* Cowling 1984) in the coastal dunefields of the Humansdorp (34°02'S;24°47'E) region of the south eastern Cape. The dunes are vegetated, with a mosaic of Cape fynbos, and subtropical grassland and thicket. Further descriptions of the region are given in Cowling (1984).

Detailed studies on population structure were carried out at both sites. The drier site at Cape St Francis receives ca. 600 mm yr^{-1} (see Fig.1c), while the moister site at the farm Brandewynkop, near Oyster Bay receives ca. 900 mm yr^{-1} (Fig1d).

The site at Brandewynkop comprised a north-facing slope (18°) and a south-facing slope (25°) of a valley formed between two parallel dune ridges. Hereafter they are referred to as north (N) and south (S) slopes respectively. Although radiation flux density shows little variation with slope in mid-summer (N=31 10^6J m^{-2} day^{-1}; S=29 10^6J m^{-2} day^{-1}), at the equinoxes, N=27 10^6J m^{-2} day^{-1} and S= 14 10^6J m^{-2} day^{-1}, and through into winter when N=17 10^6J m^{-2} day^{-1} and S= 3 10^6J m^{-2} day^{-1}, there is a trend for increasing radiation on steep north facing slopes and decreasing radiation on steep south slopes at 34°S (from Schulze 1975; Cowling 1984). Solar radiation on slopes has important ecological effects at latitude 34°S (Schulze 1975) in affecting soil moisture (Holland & Steyn 1975; Holland, Steyn & Fuggle 1977).

Soils were uniformly deep, calcareous sands. Fynbos communities were dominated by *Metalasia muricata* and *Passerina vulgaris*. Adult individuals of *Felicia echinata* were rare on the two slopes, while *Muraltia squarrosa*, though dense on the north slope, was absent from the south slope. Both slopes had been lightly grazed by cattle and burnt in 1972. A portion of both slopes had been burnt again in March 1984. The study site comprised four homogeneous areas of ca. 50 X 50 m on each slope and in both burnt and unburnt vegetation.

The site at Cape St Francis was a homogeneous area of ca. 50 X 50 m dune fynbos dominated by *Agathosma apiculata*, and *Metalasia muricata* which had previously been burnt in 1972. A portion of the area was bush cut in May 1985.

Climate

Radiation and evaporation data from the nearest available source (Fig.1a) and the Walter-Lieth climate diagram (Fig.1b) indicate a mediterranean climate typified by moisture surpluses in winter and deficits in summer (Fig. 1b). Temperatures are mild and the area is frost-free. The warmest month at Cape St Francis is February (mean monthly temperature of 19.9°C) and the coolest month is July (14.2°C). Largest diurnal temperature fluctuations of ca. 8°C are generally experienced in May, June and July. During the study period, the region suffered the most severe drought recorded in 90 years during the summer of 1987-88 (Weather Bureau, unpubl. data). This shortfall is clear in the rainfall/temperature graph for Cape St Francis (Fig.1c).

Population age structure of mature vegetation

On both north and south slopes at Brandewynkop, ten permanent 1 m^2 quadrats were marked in mature vegetation (13 year-old). During the period between January 1985 and February 1987 the numbers of seedlings (approximately less than 2 years old) and adults (reproductive) were recorded, live and dead. At the Cape St Francis site, the number of adults was recorded in 30 X 1 m^2 quadrats in November 1987, March 1988 and September 1988, and dead and senescent individuals were noted. Numbers of seedlings were counted simultaneously in half of these randomly and independently located plots: 15 X 1 m^2.

In addition, the population size structure of two Agathosma spp. was sampled in an adjacent mature dune fynbos community. Owing to the marked seasonality and growth habit of these two species (Pierce & Cowling 1984), the age of individuals could be estimated from counts of growth nodes. For each species, all individuals were counted and aged from node counts in a randomly located strip of thirty contiguous 1 m^2 plots.

Gap and clearing effects in mature vegetation

In March 1985, five quadrats (0.25 m^2), randomly located, on each slope at Brandewynkop were marked, cleared of vegetation (primarily ground layer) and monitored at intervals until September 1988 to determine seedling recruitment in gaps. Differences among densities at sampling times were analysed by means of the Kruskal-Wallis analysis of variance by ranks (Siegel 1956) as data were not normally distributed.

The hypothesis that inter-fire seedling mortality is the result of unsuccessful competition with established adult plants for soil moisture was tested as follows. In November 1987, seedling counts were made in 30 X 1 m^2 quadrats randomly located in mature vegetation at Cape St Francis. One randomly selected sub-set of 15 quadrats was then subjected to a treatment of bushcutting which included: removal of all plants except seedlings; bush-clearing 0.5 m around each quadrat periphery;and trenching to 400 mm depth all around to prevent root interference. In March 1988, after four months of summer drought, seedling densities were counted in the treatment quadrats and compared with counts in 15 newly located (random) quadrats in the mature fynbos. If seedling densities were lower in uncleared quadrats then seedling mortality due to competition with adults would be assumed. A significant difference in seedling numbers between bushcut and uncleared quadrats was predicted. Later, in September 1988, the treatment quadrats were again counted and their seedling densities compared against a further 15 quadrats in untreated mature vegetation. Differences between treatments and controls were analysed by means of the Mann-Whitney U test (Siegel 1956); this non-parametric test was chosen as data were not normally distributed.

Effects of disturbance and seedling survivorship

Bushcutting

Recovery from bushcutting carried out in May of 1985 was recorded by counting seedling numbers in thirty 1 m² randomly located and independently placed plots in February 1986, March 1987, and March 1988. Differences among sampling times were analysed using the Kruskal-Wallis analysis of variance by ranks (Siegel 1956); this non-parametric test was chosen as data were not normally distributed.

Fire

In the burnt area of the Brandewynkop site, post-fire recovery was monitored by counting seedlings in 20 X 1 m² quadrats randomly located on each of the north and south slopes in January 1985, January 1987 and March 1988. Differences in mortality rates on the two slopes were analysed by means of the Kolmogorov-Smirnov two sample test (Siegel 1956).

Also, detailed records were kept of survival and height of tagged seedlings occurring within three permanent plots (0.25 m²) on each slope, and where necessary, outside the plots, so that at least 30 seedlings of each study species were monitored.

On the south slope, Metalasia were very infrequent, and only one seedling was tagged. In addition the plots were monitored for any subsequent recruitment. Twelve such measures were made at intervals between January 1985 and March 1988. To test if mortality was higher in the summer/autumn season, observed cumulative numbers of deaths over time should differ significantly from an expected linear increase. The Kolmogorov-Smirnov one sample test was used as samples were not independent. Survival curves as percentages of initially tagged numbers were drawn as well as growth rates over time. The tagged seedling data were also used to determine seedling size frequencies at death and size frequencies of survivors at last sampling.

RESULTS

Population age structure of mature vegetation, gap and clearing effects

Brandewynkop

Analysis of the population structure of mature (13 yr-old) vegetation at Brandewynkop over a period of 3 years showed a decline in number of adults of Passerina and Muraltia on both slopes (Fig. 2). No individuals of Felicia and no changes in *Metalasia* shrub populations were recorded. Seedlings of *Passerina* and *Muraltia* were present, but in extremely low numbers which varied slightly with season. No *Agathosma* species were recorded in the plots although occasional adults were present on the south slope.

In the cleared gaps (0.25 m^2), seedling recruitment was negligible. On the north slope, a total of three *Passerina* seedlings appeared. On the south slope, two *Felicia* seedlings appeared. However, none of the new recruits survived. Other species, such as the short-lived, pioneer shrub, *Anthospermum aethiopicum*, and also resprouting species (grasses and restioids) were more successful in the gaps.

Cape St Francis

At the drier site at Cape St Francis, adults showed no sign of senescence and their numbers remained unchanged during the monitoring period. Densities were (no.m^{-2} ±standard deviation;n=30): *Agathosma apiculata* 1.0±0.4; *A. stenopetala* 1.1±0.4; *Felicia* 0.1±0.3; *Metalasia* 0.2±0.2; *Muraltia* 0.1±0.3; *Passerina* 1.8±2.8. The slight differences amongst seedling numbers with time were not significant, except for *Passerina* (Table 2).

Analysis of Agathosma apiculata and A. stenopetala in the mature Cape St Francis community showed clearly unevenness in population age structure although most individuals (48% and 38% respectively) were recruited soon after fire (Table 3).

Clearing experiment

Contrary to the prediction, there were no significant differences in seedling densities between the quadrats which had been cleared of vegetation, and the controls after the summer drought (Table 4). However, later, in September, after the following cool, wet season, seedling establishment was significantly higher in the cleared versus the uncleared quadrats.

Effects of disturbance on seedling establishment and survivorship

Post-bushcutting effects

Post-bushcutting seedling densities at Cape St Francis showed significant increases from initial sampling to three years later (Table 5). However, the increase in Muraltia seedling densities was not significant.

Post-fire effects

Post-fire seedling densities decreased over time on both north-facing and south-facing slopes at Brandewynkop, with the south slope showing lower densities of the species shared by both slopes (Table 6). There were no significant differences in mortality rates for all four species between the north- and south-slopes (Table 6). After four years, densities of all species had decreased by about half, except for the very low, almost constant densities of *Metalasia*.

Survival curves of tagged *Passerina* seedlings indicated no differences between north and south slopes until the summer of 1988 when south slope numbers dropped more rapidly (Fig.3). Growth rates on the two slopes were almost identical (Fig. 3). However, statistical analyses showed that *Passerina* seedling mortality showed no significant differences (NS) with season (north slope : $D=0.13$, $n=12$, $p \geq 0.05$, NS; south slope : $D=0.35$, $n=12$, $p \geq 0.05$, NS). For the other three species, growth rates slowed during the autumn periods of 1986 and 1987 and highest mortality appeared to coincide with the autumn of 1986 (Fig. 4). Although seedling mortality of *Felicia* on the south slope was highest prior to July 1986, the difference was not significant ($D=0.33$, $n=12$, $p \geq 0.05$; NS). However significant differences were found for north slope *Metalasia* seedlings ($D=0.50$, $n=12$, $p \geq 0.01$) and for north slope

Muraltia seedlings (D=0.46, n=12, $p \geq 0.01$). The decline in *Metalasia* seedling densities on the north slope was apparent in both quadrat samples and from tagged individuals: unfortunately the lack of tagged data on the south slope disallowed further detail on the almost constant densities monitored in the quadrat samples (Table 6).

Although height is generally not a good measure of size, the simple, unbranched growth form of the seedlings qualified height as an adequate measure of size for this study. Size frequency distributions of seedlings at death and of survivors at the time of last sampling indicated that for *Passerina* and *Muraltia*, survivors were from a wide range of size classes; whereas for *Felicia* and *Metalasia*, only the largest seedlings survived (Fig. 5).

Detailed observations of the permanent quadrats showed that new seedling appearance in the period of ten months to four years after the fire was negligible.

Table 1. Characteristics of the study species.

Species [a]	Family	No.spp.[b] in Cape flora	Distribution[b]	Shrub height (m)	Shrub longevity (yr)	Pollination	Dispersal	Seed prodn [d]	Seed mass (mg) (x±SE)
Agathosma apiculata	Rutaceae	135	Riversdale to Port Elizabeth	0.8	25	Insect	Ballistic and myrmecochory	May-Oct	4.6±0.2 (n=38)
Agathosma stenopetala	Rutaceae	135	Humansdorp to Port Elizabeth	0.6	20	Insect	Ballistic and myrmecochory	Sep-Dec	2.1±0.03 (n=50)
Felicia echinata	Asteraceae	83	Mossel Bay to Port Alfred	0.1	5	Insect	Wind	May-Sep	0.4±0.03 (n=300)
Metalasia muricata	Asteraceae	50	Cape to Drakensberg	2.3	>30	Insect	Wind	May-Jul	0.6±0.03 (n=50)
Muraltia squarrosa	Polygalaceae	115	Mossel Bay to Port Elizabeth	0.8	14	Insect/[c] self	Myrmecochory	All year	3.7±0.1 (n=50)
Passerina vulgaris	Thymelaeaceae	18	Cape to Drakensberg	1.5	14	Wind	Unspecialized	Oct-Feb	1.3±0.03 (n=47)

[a] Nomenclature after Bond & Goldblatt (1984).
[b] From Bond & Goldblatt (1984).
[c] Levyns (1954).
[d] Pierce & Cowling (1984) and this study.

Table 2. Population structure of seedlings in mature (13 yr-old) dune fynbos at Cape St Francis. Data are means±standard deviations; n=15. Differences tested by Kruskal-Wallis ANOVA by ranks (*H*); * = $p \leq 0.05$; NS= not significant.

	No.seedlings (m^{-2})				
	Nov 1987	Mar 1988	Sep 1988	*H*	
Agathosma apiculata	1.50±1.98	1.30±1.98	2.23±1.99	5.6	NS
A. stenopetala	0.53±0.80	0.76±0.94	0.60±1.22	2.5	NS
Felicia	0	0	0.23±0.43	-	
Metalasia	0.03±0.18	0	0.10±0.31	-	
Muraltia	0.33±0.71	0.07±0.25	0.03±0.18	4.3	NS
Passerina	2.07±2.27	1.30±1.62	0.87±1.55	7.3	*
Total spp.	4.43±2.79	3.33±2.59	4.10±2.56	4.7	NS

Table 3. Population structure of two *Agathosma* species in mature (13 yr-old) dune fynbos at Cape St. Francis. Data are totals from contiguous quadrats; $n=30 \times 1\ m^2$.

	Age classes (yr)			
	1-3	4-6	7-9	10-12
Agathosma apiculata	9	5	12	24
A. stenopetala	10	7	15	20

Table 4. Response of seedling numbers of selected shrub species to clearing treatments (November 1987) in mature (13 yr-old) dune fynbos at Cape St Francis. Data are means±standard deviations; n=15. Significant differences by Mann-Whitney *U* tests; ***=$p \leq 0.001$; NS= not significant.

	Control	Clearing		
	No. seedlings (m^{-2})		*U*	
Mar 1988	2.3±2.7	3.2±2.9	152	NS
Sep 1988	15.9±20.4	77.4±68.9	16	***

Table 5. Seedling densities of selected shrub species monitored after bushcutting (May 1985) at Cape St Francis. Data are means±standard deviations; n=30. Significant differences by Kruskal-Wallis analysis of variance by ranks (*H*); *= $p \leq 0.05$; **=$p \leq 0.01$; ***=$p \leq 0.001$; NS = not significant.

	No. seedlings (m^{-2})				
	Feb 1986	Mar 1987	Mar 1988	*H*	
Agathosma apiculata	0.10±0.31	7.47±9.83	6.17±7.81	40.2	***
A.stenopetala	0.07±0.37	2.33±3.72	3.23±4.62	24.4	***
Felicia	0.07±0.37	0.63±1.50	0.50±0.83	9.5	*
Metalasia	0.17±0.65	2.77±3.24	3.30±4.21	25.7	***
Muraltia	0.20±0.81	0.43±0.73	0.67±1.35	6.8	NS
Passerina	0.37±1.03	3.97±4.10	3.50±4.80	24.3	***
Total spp.	1.00±2.48	16.03±12.42	17.33±15.30	57.3	***

Table 6. Seedling densities of selected dune fynbos species recorded on north- (N) and south-facing (S) slopes monitored after a fire (March 1984) at Brandewynkop. Data are means±standard deviations; n=20. Significant differences in mortality rates on the two slopes tested by Kolmogorov-Smirnov (*D*) two-sample test; NS= not signifcant.

		No.seedlings (m^{-2})				
		Jan 1985	Jan 1987	Mar 1988	*D*	
Felicia	N	30±26	18±18	13±13	-	
	S	0	0	0		
Metalasia	N	1.2±3.2	1.2±2.3	0.2±0.9	0.67	NS
	S	0.4±1.2	0.2±0.8	0.6±1.5		
Muraltia	N	27±27	27±21	15±13	-	
	S [a]	0	0	0		
Passerina	N	72±69	42±28	38±53	0.67	NS
	S	60±58	30±25	23±33		
Total spp.	N	95±68	70±34	53±59	0.67	NS
	S	90±62	49±30	37±37		

[a] Adults absent from slope

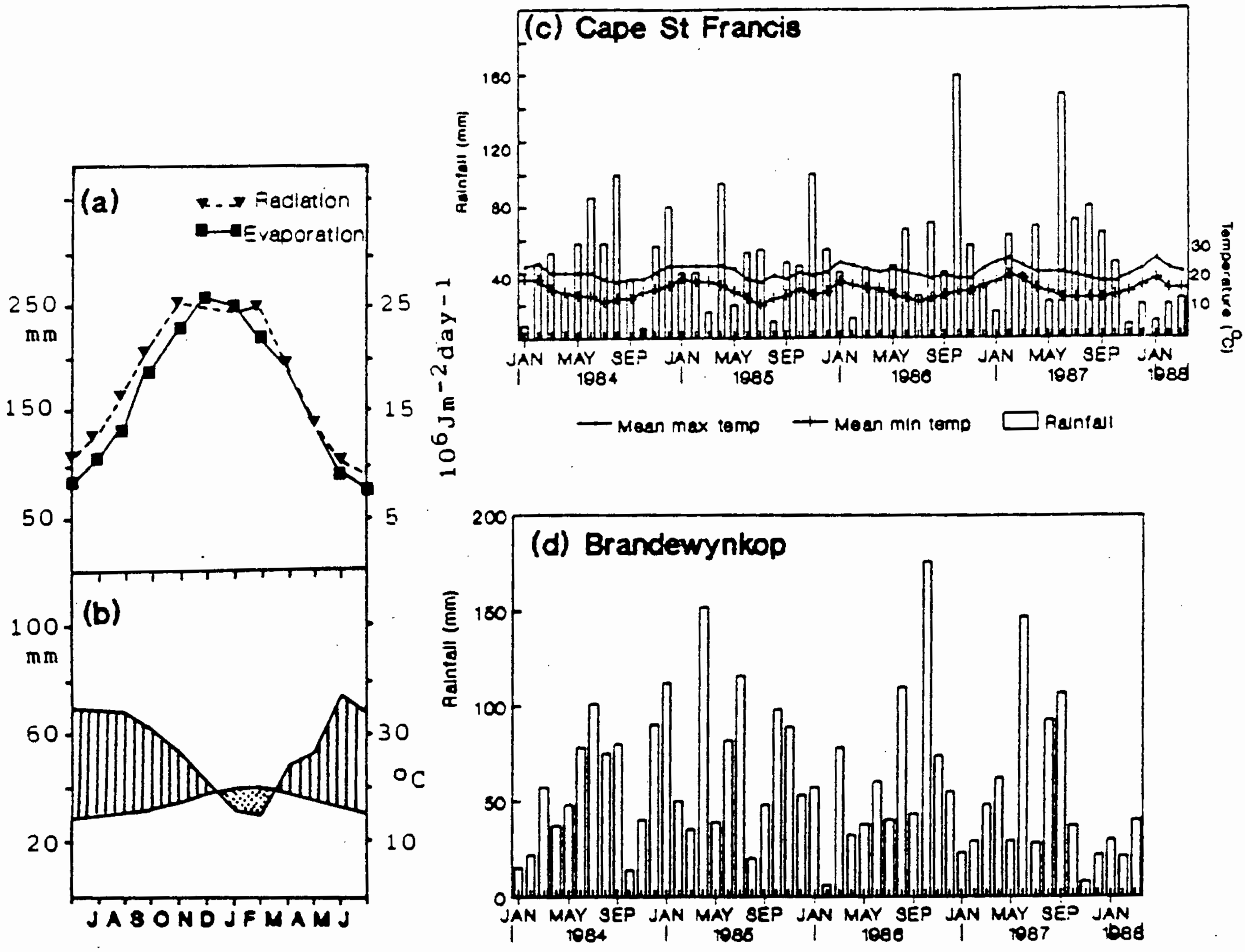


Fig.1. Climate of the study sites. (a) Mean monthly solar radiation (earth's surface) and mean monthly evaporation (American Class "A" Evaporation Pans) from Port Elizabeth (1957-58 and 1957-61 respectively) (McCallum 1972). (b) Walter-Lieth climate diagram for Cape St Francis (Heydorn & Tinley 1980). (c) Rainfall, mean maximum and minimum temperatures during study period at Cape St Francis (Weather Bureau, unpubl. data). (d) Rainfall at Brandewynkop during study period (unpubl. data).

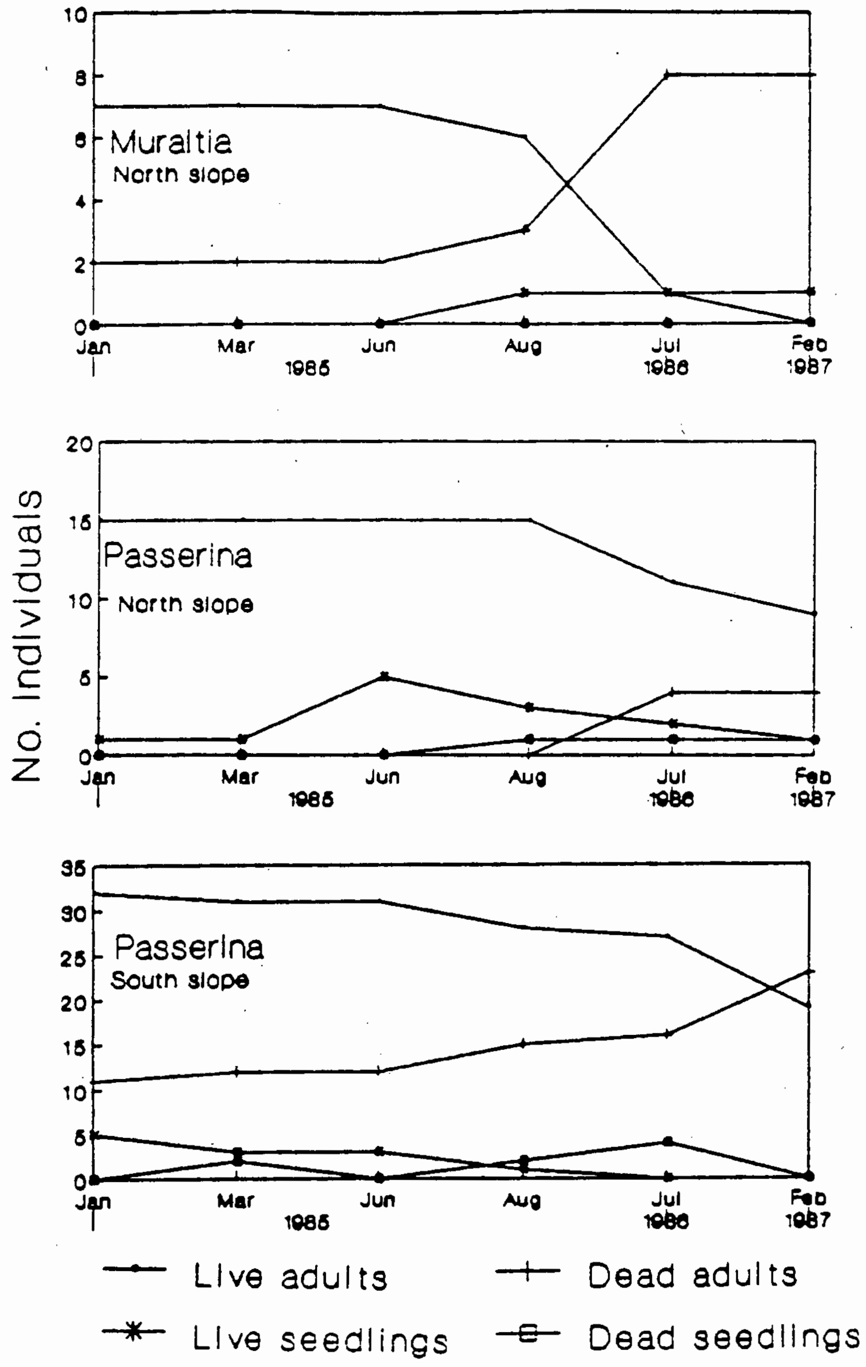


Fig. 2. Population structure of selected shrub species in mature (13 year-old) dune fynbos on north and south slopes at Brandewynkop. Data are total no. individuals in 10 X 1 m² quadrats.

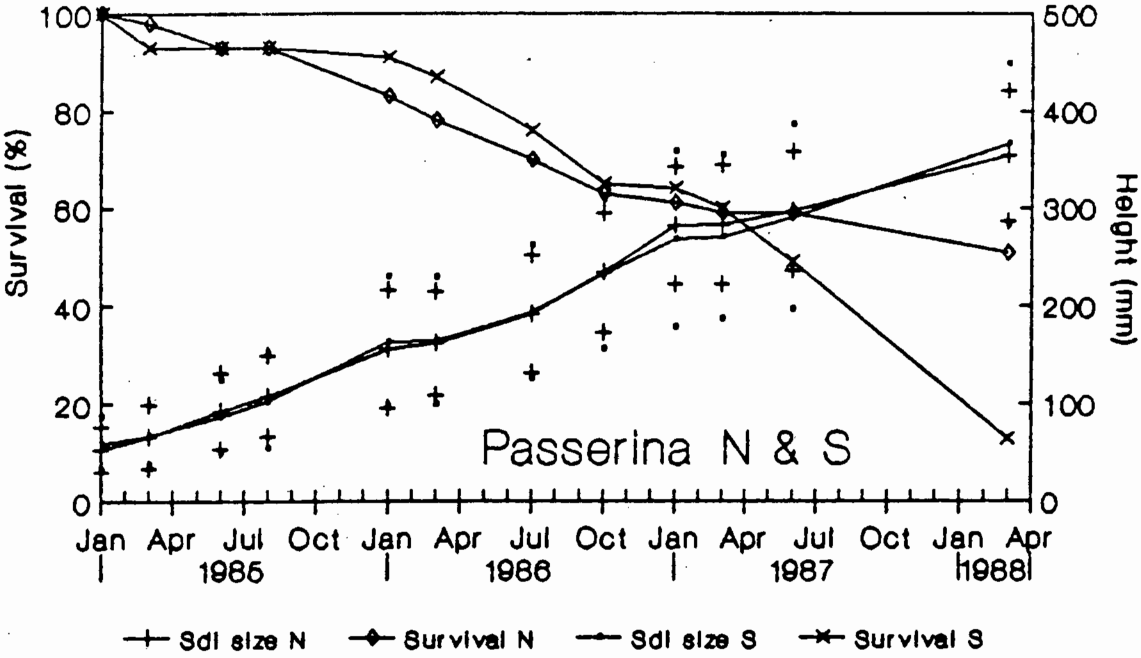


Fig. 3. Passerina seedling survival (%) and size (mm) on the north- (N) and south-facing (S) slopes at Brandewynkop after a fire (March 1984). No. individuals monitored decreased from start to end; (N):n=41 to 21; (S): n=55 to 7. Dots and pluses indicate ± standard deviations of mean seedling size for (S) and (N) respectively.

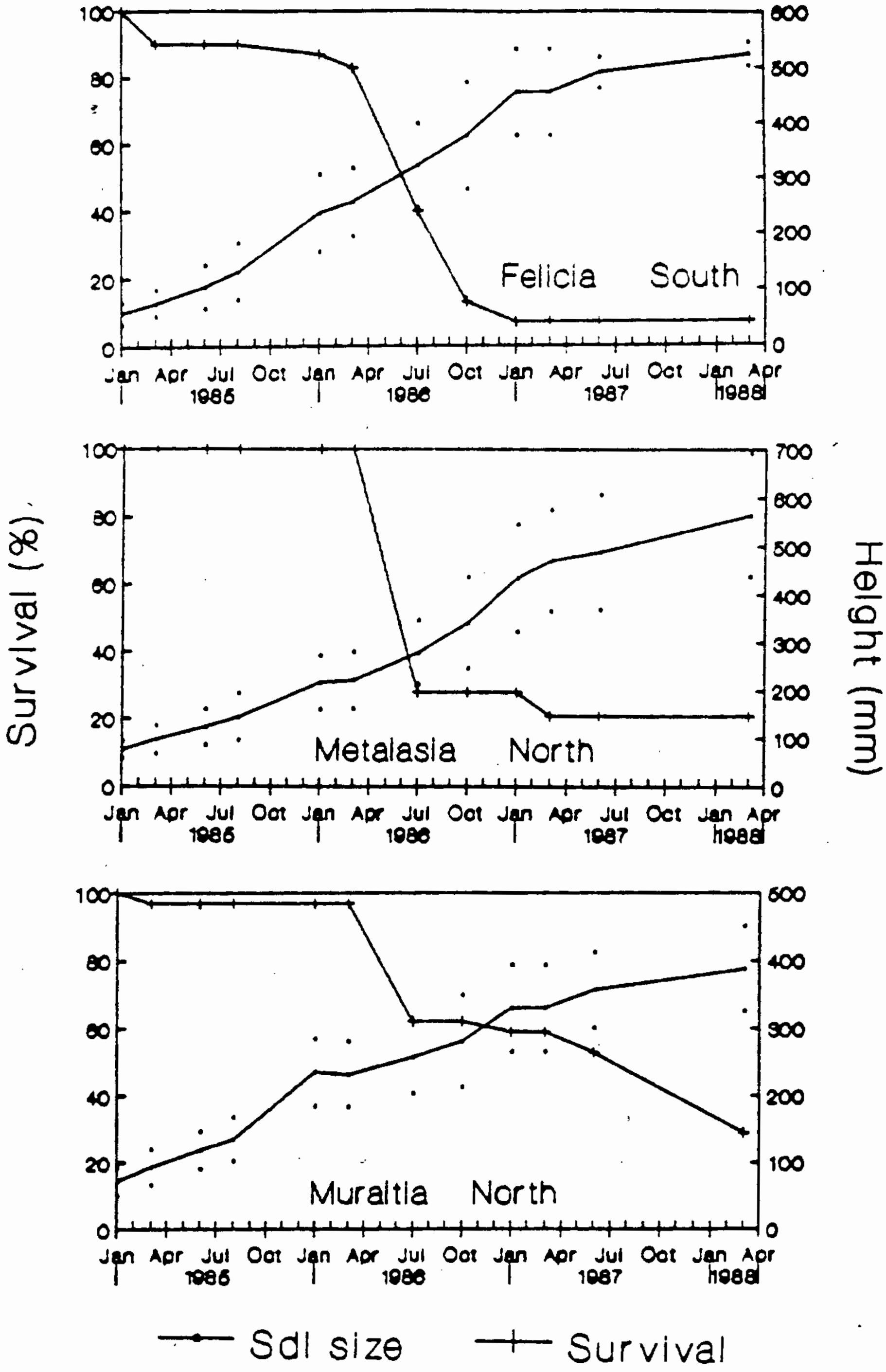


Fig. 4. Seedling survival (%) and size (mm) on the north- and south-facing slopes at Brandewynkop. No.of individuals monitored decreased from start to end; Felicia n=30 to 2; Metalasia n=29 to 6; Muraltia n=34 to 10. Dots indicate ±standard deviations of mean seedling size.

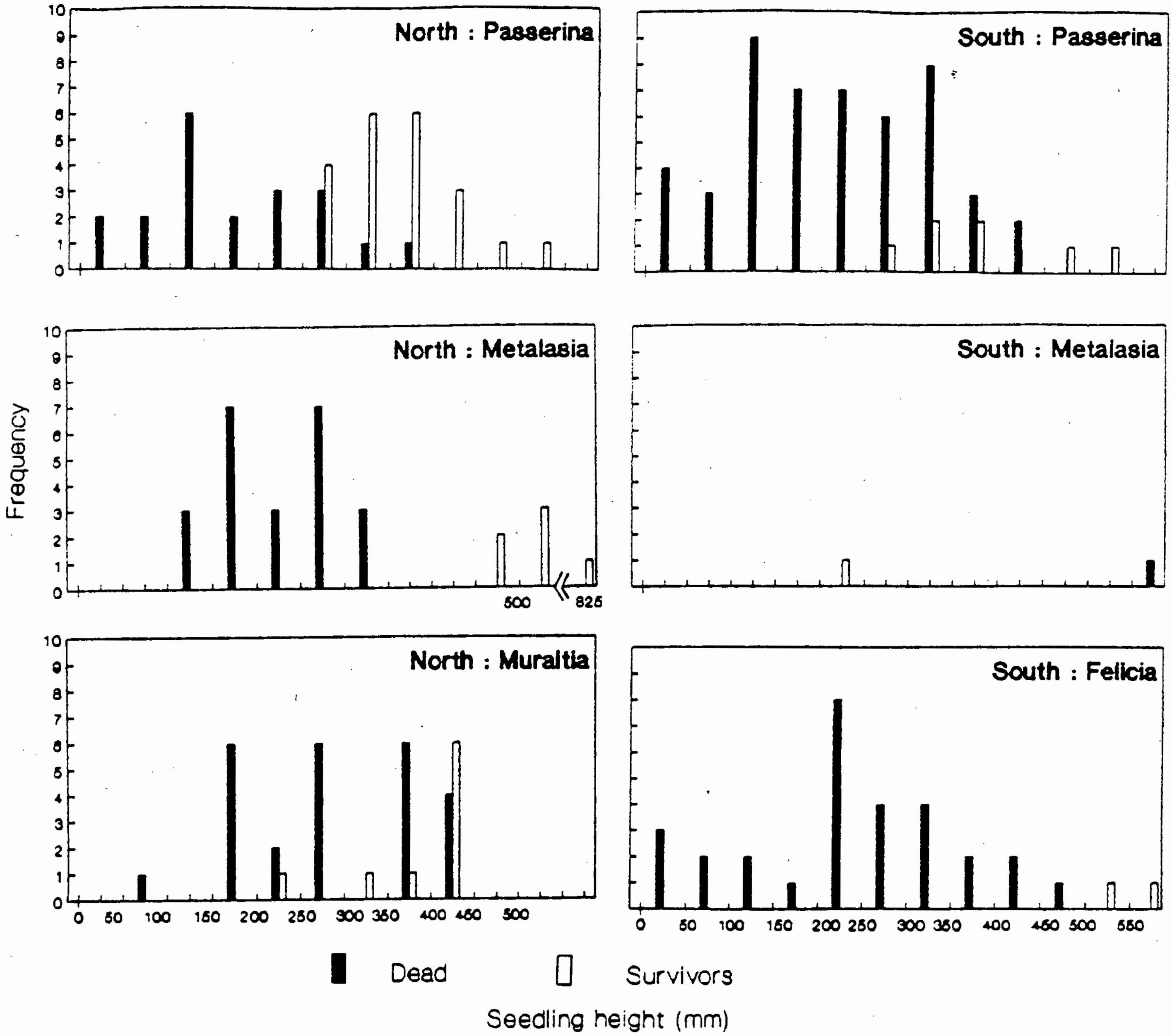


Fig. 5. Size frequency distributions of seedlings: at death during the four year period after fire (March 1984); and of survivors at the time of last recording of selected dune fynbos species at Brandewynkop.

DISCUSSION

Population structure of mature dune fynbos communities.

Contrary to expectations, shrub population structure of the three dune fynbos communities was not consistently even-aged nor lacking in inter-fire recruitment. In the mature community at the moist Brandewynkop site, the few seedlings present died before reaching reproductive maturity. Inter-fire recruitment was clearly unimportant in contributing to population structure. Similarly in south western Cape fynbos communities, Wicht (1948) reported that seedlings established in mature fynbos in winter but that few survived in summer. A similar trend was noted for chaparral (Montygierd-Loyba & Keeley 1987), a vegetation type broadly analogous to fynbos in being a mediterranean shrubland prone to fire. In contrast, at the drier Cape St Francis site, numerous seedlings were present in the mature inter-fire vegetation. Despite some mortality during summer drought, some seedlings appeared to survive to reproductive age, and contribute to the uneven aged population structure.

To explain these differences in population structure between the Brandewynkop and Cape St Francis communities, seed germination requirements were invoked. Maximum germination response of the dune fynbos shrub species resulted from alternating diurnal temperatures of 20°C/10°C (Chapter 2). More soil-stored seeds would germinate under the open canopy of the drier site where fluctuations in diurnal temperatures are wider than under a closed canopy. Brits (1986a) has shown clearly the increasing amplitude in diurnal temperature fluctuations under a gradient of canopy cover from dense, through open, to sparse, in fynbos. Poor recruitment in the gaps cleared in mature vegetation at Brandewynkop may have been the result of inadequate openings for the required temperature fluctuations (cf. Goldberg & Werner 1983).

The attempt to determine the role of adult competition for soil moisture in determining seedling establishment in the mature dune fynbos at Cape St Francis was unfortunate in coinciding with the driest period in 90 years. Rainfall in the hottest months from November 1987 to March 1988 was exceptionally low (see Fig. 1). The expected higher survival in clearings was not found. However, after continuing the experiment, results supported the hypothesis that establishment is higher in cleared than in uncleared vegetation, probably due to soil moisture increases. In their review, Schlesinger et al. (1982), found that soil moisture content was higher for one year after fire in burned than unburned stands of chaparral; thereafter, it declined to previous levels with vegetation regrowth.

Ideally the experiment should have continued through the next dry season to test for higher long term survival in clearings. The hypothesis that higher establishment is possible due to decreased competition with adult plants for soil moisture requires more rigorous testing by comparing water stress of seedlings under mature vegetation with that of seedlings in clearings.

In the moist site, both *Muraltia* and *Passerina* showed obvious signs of becoming moribund and senescing. This behaviour is consistent with the pattern of succession in dune fynbos (Appendix 1). Senescence is a commonly recognized phenomenon in fynbos (Kruger & Bigalke 1984). There is anecdotal evidence that Californian chaparral also senesces, in some cases after 30-40 years (Montygierd-Loyba & Keeley 1987). However, the size structure of stands of very old *Ceanothus megacarpus*, which had highest mortality amongst smaller plants and highest survival amongst larger plants, was interpreted as intraspecific competitive effects, rather than programmed senescence. In fynbos, vegetation senescence would be followed by succession to forest or by fire (Kruger & Bigalke 1984).

Seedling responses to fire and bushcutting

Seedling populations responded differently over time to different disturbances : shortly after fire, seedling densities were highest and gradually decreased over the next three years. Conversely, after bushcutting, seedling numbers gradually increased over three years of monitoring. To explain these differences, I considered possible differences in available seed and differences in favourable conditions for germination and seedling establishment. An analysis of seed available for recruitment revealed that relative to the Cape St. Francis site, there were adequate soil-stored seed banks for inter-fire recruitment at Brandewynkop (Chapter 4). Therefore available seed was not considered a limiting factor here. In Californian coastal scrub, recruitment in the second year after fire was attributed to new (eg. *Salvia* spp.), as well as pre-fire seed banks (Keeley & Keeley 1984). At Brandewynkop, *Felicia* individuals which had recruited shortly after fire in March 1984, reproduced after 18 months and contributed to the seed banks (Chapter 4). However, this input had no apparent effect on subsequent inter-fire recruitment: further establishment after the initial post-fire cohort of the four study species was negligible. Christenson & Muller (1975) attributed the increased germination of shrub and herb seeds in chaparral soil in the first few years after fire to dormancy-breaking by heat and the denaturing of inhibiting substances, and secondly to the removal of the source of chemical compounds which enforce dormancy in otherwise non-dormant seeds. Brits (1986b) has proposed that inter-fire accumulation of decaying plant material reduces oxygen partial pressure in the soil and that a fire would alter these conditions which inhibit germination. However, the work of Christenson & Muller (1975) failed to corroborate the hypothesis that microbial depletion of soil oxygen in unburned chaparral inhibits seed germination.

The explanation for increasing seedling densities after bushcutting is sought in terms of germination cues. Plant material left on the ground after bushcutting, insulates soil surface temperatures against wide temperature fluctuations, and would hence inhibit germination. This insulation, however, would gradually be lost through decomposition and wind removal, and germination would be increasingly favoured. Allelopathic effects of dominant species may also be important in inhibiting germination (Chapter 2). Such substances would also denature with time. Finally, the timing of the bushcutting in May may have been too late for temperature fluctuations optimal for germination (Chapter 2).

In contrast the fire at Brandewynkop was a "clean burn", and removed all cover. The resultant post-fire soil temperature extremes would encourage maximum germination. After the Brandewynkop fire, seed banks were considerably reduced (Chapter 4) and further establishment after the initially recorded cohort was negligible.

Seedling responses to seasonal drought

In determining the cause of seedling mortality, it is not always possible to separate contributory causes, e.g. greater susceptibility of seedlings to pathogens when drought stressed (Fenner 1987). Detailed studies on tagged seedlings showed no obvious losses to predation which can be an important determinant in seedling establishment (Breytenbach 1984; Cook 1979; Le Maitre 1988; but see Bond 1984). Maximum seedling losses in some species were related to the summer/autumn drought. Also, lower seedling densities were recorded in autumn relative to spring in the clearing experiment.

Seedling responses to aspect

The prediction that seedling mortality rates should be higher on the north- than the south-facing slope due to higher radiation and therefore higher moisture stress, was not supported here. However, any seasonal drought effects were apparent on the north and not the south slope. Initial records of south slope densities for shared species were lower than on the north slope, although their seed banks did not show this tendency (Chapter 4). On the south slope, lower radiation and hence narrower soil temperature amplitudes would not have favoured optimal germination. Nevertheless, rates of seedling mortality were not different on the two slopes. However, biotic effects may have played a compensatory role on the south slope. After the fire, this slope was dominated by early colonizing, ephemeral herbs (Appendix 1) which outgrew and outshaded the shrub species. Etiolation was obvious on the south slope but absent on the north. Competition for soil moisture could also have decreased shrub seedling numbers. In chaparral, highest shrub seedling mortality occurred where highest numbers of post-fire herbs appeared (Schlesinger et al. 1982; Keeley & Soderstrom 1986). These mechanisms need to be tested by comparing seedling density responses to shaded and weeded quadrats with controls.

Seedling population size structure

In general the size hierarchy of young populations of plants in the post-fire period conformed to the predictions of White & Harper (1970): skewness decreased with age as the smallest size classes died and the growth of the larger plants continued. The size hierarchies (defined as "characteristics of the size distribution" - Weiner & Solbrig 1984) of all species moved towards size equality over time. Size hierarchies are not solely determined by competition (Weiner & Solbrig 1984), but are rather the result of the interaction between size-specific growth and death rates, competition and size-specific herbivory (Hutchings 1986). Density-dependence is difficult to invoke as a factor here without manipulative experiments (Hickman 1979). Post-fire seedlings tended to be aggregated into dense clumps (e.g. up to five individuals in 10 mm^2) which is possibly more an indication of "safe sites" (sensu Harper 1977), rather than a case of possible germination facilitation due to clumping of seeds (cf. Fowler 1988).

Although mortality is not unique to any particular size class of individuals, the smaller sizes were more vulnerable. Cook (1979) predicted that with smaller individuals suffering greater mortality, selection should minimize the vulnerable stage by maximising potential growth rate of plants. He also suggested an alternative path : species may be adapted to survive over a longer susceptible juvenile period. In two species, Felicia and Metalasia, the longest surviving seedlings were in the largest size classes, whilst in Muraltia and Passerina, seedling survivors were spread over a wider size range. Thus Metalasia and Felicia exhibit Cook's (1979) fast growth behaviour, while Muraltia and Passerina fit the alternative model. Seedling counts on the south slope showed that Metalasia behaved differently relative to the other shrub species: considerably fewer seedlings recruited yet these extremely low densities remained relatively constant after four years, although tagged seedlings (Fig. 4) failed to show a similar pattern.

Unfortunately collection of data on on time of germination and emergence in the field after disturbance was not possible, disallowing the determination of possible advantages of early germination and establishment (Ross & Harper 1972; Fenner 1987; Fowler 1988). Wilson (1988) has shown no initial size advantage amongst different sized seedlings in competition for nutrients based on rooting behaviour. Similarly, above-ground size, though important in light capture, may not be important in below-ground competition for soil moisture.

Conclusions

Keeley & Keeley (1989) developed a model to explain the post-fire appearance of herb species, and their later absence in mature chaparral. They inferred that biotic and abiotic conditions were acting not on germination inhibition, but rather on reduction of seedling survival. This would have selected for dormancy to minimize germination at times when seedling survival chances were low. Other species lacking this dormancy are often associated with gaps and have evolved an alternative mechanism : inhibition by allelopathic compounds to ensure germination in a suitable site. In contrast, in dune fynbos shrub species, seed germination is not directly fire-stimulated and dormancy is weakly developed (Chapter 2). Germination is common under an open canopy, which would result in reduced seed pools (Chapters 3 and 4). Germination was inhibited, and seedling survival was reduced only under a dense canopy. A logical explanation for this anomalous, and apparently non-adaptive behaviour has not yet been formulated. A review of regeneration strategies in chaparral led Zedler & Zammit (1989) to conclude that there was " little demographic evidence" for selection by fire. Similarly, fire may not have been the major selective force in dune fynbos.

Dune fynbos population structure was found to be dependent on available seed reserves at the time of disturbance, seed germination requirements being met after disturbance, and the susceptibility of seedlings to causes of mortality (cf. Purdie 1977) by seasonal and stochastic drought events (Specht 1981). It would appear from these field studies and from germination trials (Chapter 2), that regeneration is cued to effects of vegetation removal rather than to fire per se. This has allowed the regeneration of dune fynbos shrubs after the artificial disturbance of bushcutting. However, too frequent bushcutting, as with fire, can drastically reduce the population size of fynbos shrubs (Chapters 6 and 7).

ACKNOWLEDGEMENTS

I thank the landowners Johan and Francis Linstrom, O. Nauhaus and the former Humansdorp Divisional Council for permission to work on their land. R. M. Cowling kindly helped with clearing experiments. The financial support of the Fynbos Biome Program, Foundation for Research Development of the CSIR, administered through the University of Cape Town is gratefully acknowledged.

REFERENCES

Bond, W. J. (1984). Fire survival of Cape Proteaceae - influence of fire season and seed predators. Vegetatio, 56, 65-74.

Bond, P. & Goldblatt, P. (1984).Plants of the Cape flora. A descriptive catatogue. Journal of South African Botany Supplement 13. Kirstenbosch, Claremont.

Breytenbach, G. J. (1984). Single-agedness in fynbos : a predation hypothesis. MEDECOS IV. (Ed. by B. Dell), pp. 14-15. Proceedings of the 4th International Conference on Mediterranean Ecosystems. University of Western Australia, Nedlands.

Brits, G. J. (1986a). Influence of fluctuating temperatures and H_2O_2 treatment on germination of Leucospermum cordifolium and Serruria florida (Proteaceae) seeds. South African Journal of Botany, 52, 286-90.

Brits, G. J. (1986b). The effect of hydrogen peroxide treatment on germination in Proteaceae species with serotinous and nut-like achenes. South African Journal of Botany, 52, 291-93.

Christenson, N.L. & Muller, C.H. (1975). Effects of fire on factors controlling plant growth in Adenostoma chaparral. Ecological Monographs, 45, 29-55.

Cook, R.E. (1979). Patterns of juvenile mortality and recruitment in plants. Topics in Plant Population Biology.(Ed. by O.T. Solbrig, S. Jain, G.B. Johnson and P.H Raven),pp.207-231. Columbia University Press, New York.

Cowling, R. M. (1984). A syntaxonomic and synecological study in the Humansdorp region of the fynbos biome. Bothalia, 15, 175-227.

Fenner, M. (1987). Seedlings. New Phytologist, 106, 35-47.

Fowler, N. L. (1988). What is a safe site? Neighbour, litter, germination date, and patch effects. Ecology, 69, 947-961.

Frost, P. G. H. (1984). The responses and survival of organisms in fire-prone environments. Ecological Effects of Fire in South African Ecosystems. Ecological Studies 48. (Ed. by P. de V. Booysen & N. M. Tainton).pp. 273-310. Springer-Verlag, Berlin.

Goldberg, D. E & Werner, P. A. (1983). The effects of size of opening in vegetation and litter cover on seedling establishment of goldenrods (Solidago spp.). Oecologia (Berlin), 60, 149-155.

Harper, J. L. (1977). Population Biology of Plants. Academic Press, London.

Heydorn, A. E. F. & Tinley, K. L. (1980). Estuaries of the Cape. Part 1. Synopsis of the Cape. CSIR Research Report 380, Pretoria.

Hickman, J. C. (1979). The basic biology of plant numbers. Topics in Plant Population Biology.(Ed. by O.T. Solbrig, S. Jain, G.B. Johnson and P.H Raven),pp.232-263. Columbia University Press, New York.

Holland, P. G. & Steyn, D. G. (1975). Vegetational responses to latitudinal variations in slope angle and aspect. Journal of Biogeography, 2, 179-183.

Holland, P. G., Steyn, D. G. & Fuggle, R. F. (1977). Habitat occupation by Aloe ferox Mill. (Liliaceae) in relation to topographic variations in direct beam solar radiation income. Journal of Biogeography, 4, 61-72.

Hutchings, M. J. (1986). The structure of plant populations. Plant Ecology (Ed. by M. J.Crawley),pp.97-136.Blackwell Scientific Publications, London.

Keeley, J.E. & Keeley, S.C. (1984). Postfire recovery of Californian coastal scrub. American Midland Naturalist, 111, 105-117.

Keeley, J. E. & Keeley, S. C. (1989). Allelopathy and the fire-induced herb cycle. The Californian Chaparral. Paradigms Reexamined. No. 34. Science Series. (Ed. by S. C. Keeley), pp. 65-72. Natural History Museum, Los Angeles.

Keeley, J. E. & Soderstrom T. J. (1986). Postfire recovery of chaparral along an elevational gradient in southern California. The Southwestern Naturalist, 31, 177-184.

Kruger, F. J. (1979). South African heathlands. Ecosystems of the World, Vol.9A. Heathlands and related shrublands : descriptive studies (Ed. by R. L. Specht), pp.19-80. Elsevier, Amsterdam.

Kruger, F.J. & Bigalke, R. C. (1984). Fire in fynbos. Ecological Effects of Fire in South African Ecosystems. Ecological Studies 48. (Ed. by P. de V. Booysen & N. M. Tainton), pp. 69-114. Springer-Verlag, Berlin.

Le Maitre, D. C. (1988). Effects of season of burn in the regeneration of two Proteaceae with soil-stored seed. South African Journal of Botany, 54, 575-80.

Levyns, M.R. (1954). see p. 61.

McCallum, D. M. (Ed.)(1972). Meteorology. Environmental Study, Swartkops River Basin. Hill, Kaplan, Scott and Partners, Cape Town.

Montygierd-Loyba, T. M. & Keeley, J. E. (1987). Demographic structure of Ceanothus megacarpus chaparral in the long absence of fire. Ecology, 68, 211-13.

O'Leary, J. F. (1988). Habitat differentiation among herbs in postburn Californian chaparral and coastal sage scrub. American Midland Naturalist, 120, 41-49.

Pierce, S. M. & Cowling, R. M. (1984). Phenology of fynbos, renosterveld and subtropical thicket in the south eastern Cape. South African Journal of Botany, 3, 1-16.

Purdie, R. W. (1977). Early stages of regeneration after burning in dry sclerophyll vegetation. II Regeneration by seed germination. Australian Journal of Botany, 25, 35-46.

Ross, M. A. and & Harper, J. L. (1972). Occupation of biological space during seedling establishment. Journal of Ecology, 60, 77-88.

Siegel, S. (1956). Nonparametric Statistics. For the Behavioural Sciences. McGraw- Hill, London.

Schlesinger, W. H., Gray, J. T., Gill D.S. and Mahall, B.E. (1982). Ceanothus megacarpus chaparral : a synthesis of ecosystem processes during development and annual growth. Botanical Review, 48, 71-117.

Schulze, R. E. (1975). Incoming radiation on sloping terrain: a general model for use in southern Africa. Agrochemophysika, 7, 55-61.

Specht, R. L. (1981). Responses to fire in heathlands and related shrublands. Fire and the Australian Biota (Ed. by A. M. Gill, R. H. Groves and I. R. Noble), pp.395-415. Australian Academy of Sciences, Canberra.

Weiner, J. & Solbrig, O. T. (1984). The meaning and measurement of size hierarchies in plant populations. Oecologia, 61, 334-36.

White, J. & Harper, J.L. (1970). Correlated changes in plant size and number in plant populations. Journal of Ecology, 58, 467-85.

Wicht, C. L. (1948). A statistically designed experiment to test the effects of burning on the sclerophyll scrub community. 1. Preliminary account. Transactions of the Royal Society of South Africa, 31, 479-501.

Wilson, J.B. (1988). The effect of initial advantage on the course of plant competition. Oikos, 51, 19-24.

Zedler, P. H. & Zammit, C. A. (1989). A population-based critique of concepts of change in the chaparral. The Californian Chaparral. Paradigms Reexamined. No. 34. Science Series. (Ed. by S. C. Keeley), pp. 73-83. Natural History Museum, Los Angeles.

CHAPTER 4

Dynamics of soil-stored seed banks of six shrubs in fire-prone dune fynbos

ABSTRACT

This study investigated the size of soil-stored seed banks of six non-sprouting shrubs in mature (13 yr-old) dune fynbos and related these findings to patterns of post-fire recruitment. Shrub and community seed banks were determined from seed counts of 50 soil cores in three communities each autumn for three successive years. Instead of the large soil stores expected in fire-prone vegetation, the dominant shrubs had relatively small seed banks i.e. highest mean seed density recorded was 825 ± 1187 seed m^{-2} (mean±S.D., n=50). Shrub and community seed banks showed no significant increments over three years. A comparison of methods of estimating seed banks by counting seeds versus counting germinants showed neither method to be superior; a knowledge of germination cues was essential in evaluating results. After a fire, seed banks were depleted by more than half. Species differences in seed bank sizes related to life history attributes (e.g. dispersal, germination requirements), therefore the trait of obligate reseeding as a criterion for a guild is too simplistic. Seed burials showed that seed bank losses due to decay and germination varied widely amongst species and with crop age, with losses ranging from 12-93%. The small and non-persistent seed banks of dune fynbos shrubs, leading to varying proportions

of species replacements after fire, might help to explain the maintenance of species richness in Cape fynbos.

Nomenclature according to Bond & Goldblatt (1984).

INTRODUCTION

In fire-prone vegetation, plant populations of different species may be determined by the relative availability of their seeds at the time of fire. In the fire-prone shrublands of the Cape Region, regeneration of non-sprouting shrubs is apparently dependent on soil-and canopy-stored seed banks (Kruger 1984). Until now, soil-stored seed banks in fynbos have not been studied. There have been a number of studies on the soil-stored seed banks of shrubs which grow in other fire-prone vegetation. These include Australian acacias (Auld 1986), chaparral shrubs (Keeley 1977; 1987; Zammit & Zedler 1988), and European Calluna heath (Mallik, Hobbs & Legg 1984; Willems 1988). In these systems, the shrubs have large and persistent seed banks which enable the replacement of dominant species after fire.

This study aimed to determine seed bank size as well as inputs and losses for members of non-resprouting, small-leaved shrubs predominant in Cape fynbos. Six species of dune fynbos were selected (Table 1) as members of genera well-represented in Cape fynbos (Chapter 2). An aim of this study was to determine whether fynbos was similar to other fire-prone shrublands in having shrubs with large, reliable soil-stored seed banks which accumulate with each year's seed input. The study also aimed to determine seed losses after dispersal and before germination, a serious gap in the literature (Cavers 1983; Fenner 1987). The extent of seed bank depletion after post-fire seedling recruitment was also investigated. These questions required the measurement of seed production by different aged plants, annual crop variation, and seed survival in soil-storage after decay and failed germination. Estimates of seed predation and seedling establishment are reported elsewhere (Chapters 5 and 3 respectively).

Soil-stored seed banks were determined from counts of seed under a microscope in soil cores sampled in the autumn fire season of three successive years. Extra samples in the third year were incubated and counts of germinants allowed a comparison of the two methods of seed bank estimation. Seed production was determined from bagging plants. Seeds in net bags were buried in the field to determine seed survival in soil storage.

The study also aimed at relating the nature of the species' seed banks to other life-history attributes. Finally, the implications of the nature of the seed banks for fynbos dynamics were discussed.

METHODS

Study sites

The study was carried out in the vegetated coastal dunes in the Humansdorp (34°02'S; 24°47'N) region of the south eastern Cape. The vegetation, South Coast Dune Fynbos (Cowling 1984), comprises a fine-leaved shrubland with a field layer of sedges and restioids. The climate is mild and it can rain at any time of year. However, there are generally moisture surpluses in winter, and deficits in late summer/autumn (see Chapter 3 for details). The autumn period is, hence, the most fire-prone season. The study sites included a south- and a north- facing slope at Brandewynkop (ca. 900 mm yr^{-1}), and a drier site at Cape St. Francis (ca. 600 mm yr^{-1}). Hereafter the slopes are referred to as south and north slopes respectively. Solar radiation differences on the two slopes are greatest in winter and at the equinoxes and in winter, with increased radiation on the north slope and decreased radiation on the south slope (from Schulze 1975; see Chapter 3). These differences affect soil moisture correspondingly (Holland & Steyn 1975; Holland, Steyn & Fuggle 1977). All three communities were 13 years old.

Soils were deep, calcareous sands and were uniform on both slopes. Vegetation communities on both slopes at Brandewykop were dominated by Metalasia muricata and Passerina vulgaris. Adult individuals of Felicia echinata were extremely rare on both slopes, while Muraltia squarrosa, though dense on the north slope, was absent from the south slope. A portion of both slopes had been burnt in March 1984. The study site comprised four homogeneous areas of ca. 50 X 50 m on both slopes and in both burnt and unburnt vegetation.

The site at Cape St. Francis was a homogeneous area of ca. 50 X 50 m dominated by Agathosma apiculata and Metalasia muricata. A portion of the area was bushcut in May 1985. As the two Agathosma species were very infrequent at the Brandewynkop site, they were studied in detail at the Cape St. Francis site only.

Estimation of seed production

In 1985/1986, seed production of 3&4 and 13&14 year-old plants was measured at Brandewynkop. At Cape St. Francis, only 13/14 year old shrubs of Agathosma spp. were measured due to unavailabiliy of young plants. Different methods were used due to individual differences in growth habit, and differences in flowering behaviour of the species. Except for Muraltia, all species had definite flowering seasons

(Table 1). In the case of *Metalasia* and *Passerina*, number of seeds produced per canopy area was determined by bagging whole, or part of, individual shrubs during the reproductive phenophase. Terylene netting was secured around whole shrubs to capture dispersed seed while still exposing flowers to pollinators. For the *Agathosma* species, whole shrubs and branches were bagged at the stage of immature fruit until all seeds had been released ballistically. *Felicia* inflorescences were bagged at the immature seed stage. *Muraltia* species are self-pollinated (Levyns 1954). Hence it was possible to bag branchlets of *Muraltia* for a year at a time due to the erratic and low, year-round production of seed. For each species each year, fifty baggings were replicated, with up to five per shrub. However, many replicates were lost to rodent damage. As some species form a seed coat regardless of whether the ovule has been fertilized, plump seed (assumed to be viable) were distinguished from empty seeds by applying light pressure to each seed (see also Chapter 2). Seed production was estimated as number of seeds (total and plump) produced per 100 X 100 mm of canopy cover per year. Seed number (plump) produced per individual was also determined from estimates of mean cover of individuals.

Estimation of seed banks

In general, seed density in the soil profile declines dramatically below 50 mm depth (Roberts 1981). In this study on dune fynbos, soil-stored seed banks were sampled to a depth of 50 mm. I assumed that seeds buried any deeper would not reach the soil surface for successful establishment, and therefore this sampling depth should adequately reflect the seed store for potential recruitment. This assumption was tested by monitoring seedling emergence from seeds buried at 50 mm depth. This emergence was compared with an expected emergence, determined as germination success from surface sowing under control conditions. Seeds of the study species were planted at 50 mm depth in pots of soil and incubated at the optimum regime of 10°C/20°C (Chapter 2). Trials of study species consisted of ten replicates of five seed (10X5); except for A.apiculata (7X5) and Passerina (9X5). After 12 weeks seedling emergence was determined and non-emerged seed were sieved from the soil and examined.

Seed bank densities were determined from seed counts using a dissecting microscope of soil cores collected at each study site. Soil cores of 50 mm depth (see above) and 70 mm diameter (see Thompson 1986) were used initially; thereafter, 50 mm diameter cores proved easier to use in the sandy soil. Seed banks under mature communities at the three sites were sampled with 50 cores randomly located in March of 1985, 1986 and 1987. In addition, soil-stored seed banks were measured in early post-fire sites (north and south slope, 27 months after fire) in June 1986. Annual variation in seed bank densities (expressed as seed numbers m^{-2} each year) for each selected species as well as for other species and for total species were tested for significance using Kruskal-Wallis one-way analysis of variance by ranks (Siegel 1956), as data were not normally distributed.

The method of determining seed banks by seed count was compared with the method of counting germinants to assess the accuracy of the former method used here. A further 50 soil cores sampled in March 1987 on each of the north and south slopes at Brandewynkop, were placed on the surface of separate pots of sterile soil in an open greenhouse (details in Chapter 6). Differences between estimates of selected species seed banks were tested using the Mann-Whitney $\underline{z}$ test for large samples. Data for total species were grouped into ten replicates of five samples each and differences were tested for significance using the Mann-Whitney $\underline{U}$ test for small samples (Siegel 1956).

The depletion of seed banks by post-fire recruitment was determined by comparing post-fire seed banks (June 1986) with mature vegetation seed banks (March 1986) on north and south slopes at Brandewynkop. The Mann-Whitney *z* test for large samples (Siegel 1956) was used to test for significant differences.

Estimation of deterioration after storage: laboratory and field studies

Seed (n=50) of each study species were selected for plumpness (see above) and stored in the laboratory . After a year, seed were again assessed for plumpness.

Fresh seeds of the study species were buried separately in net bags at 10 mm depth under mature fynbos at Cape St. Francis. Seed numbers were : *A. apiculata* n=380; *A. stenopetala* n=200; *Felicia* n=600; *Metalasia* n=570; *Muraltia* n=34; *Passerina* n=134. After 14 months, bags of seed were recovered and whole seed counted. A second seed burial experiment was carried out with older seed buried at Cape St. Francis for only six months during the cooler, wetter season to determine seed bank losses to germination under mature fynbos. Experiments involved replicate bags X number of seed of different ages (in brackets) as follows: *A. apiculata* n=10X10 seed (seven months), n=10X10 seed (1 yr 7 months) ; *A. stenopetala* n=10X10 (seven months), 7X10 seed (2 yr 6 months); *Felicia* n=10X10 seed (six months); *Metalasia* n=10X10 seed (9 months); *Muraltia* n=5X5 seed (2 yr 6 months); *Passerina* n=10X10 seed (1 yr 4 months); n=10X10 seed (2 yr 4 months). Seed selection was limited by availability of germinable seed (Chapter 2).

RESULTS

Seed production

Seed production of both young and old dune fynbos shrubs varied greatly between the two years with no consistent pattern between species (Table 2). When seed production is expressed per unit area of canopy, *Passerina* showed the highest value. When expressed on an individual shrub basis, the larger canopy of the older *Metalasia* shrubs made this the most productive species. *Muraltia* shrubs produced the fewest seeds.

Seedling emergence from 50 mm depth

No seedlings emerged from seeds buried at 50 mm soil depth. These results justified the use of seed bank soil core samples of this depth. Whole seed survival was as follows (mean percentage±standard deviation with n=10X5 unless otherwise indicated) : *Agathosma apiculata* 100% (7X5); *A. stenopetala* 96±8%; *Muraltia* 90±22%; *Felica* 84±35%; *Passerina* 80±28% (9X5); *Metalasia* 36±44%.

Seed bank size

Seed bank size at the three sites did not show consistent annual variation (Table 3). No species showed significant increments in seed densities over three years. Annual variation was significant for *Felica* (south slope and Cape St. Francis sites) and for *Muraltia* (north slope) in which densities decreased over the three years. Other significant differences showed inconsistent patterns.

Comparison of methods : seed counts versus germinant counts

Comparisons of seed counts versus germinant counts as different methods of determining seed bank size showed significant differences for south slope seed banks but generally no differences for the north slope (Table 4). These differences were not consistent, in that results from one method were not always higher than the other methods results. *Passerina* seed banks were the exception, in that seed counts were significantly higher than germination counts.

Post-fire versus mature vegetation seed banks

Seed banks measured shortly after fire, were generally considerably smaller than in the mature vegetation (Table 5). Exceptions included seed banks of species other than the selected study species on the north slope, which were not significantly different. Also, Felicia showed a significant increase on the south slope, while on both north and south slopes, Metalasia showed no change. Muraltia seed banks on the north slope were almost depleted.

Deterioration after storage: laboratory and field

Deterioration after a year's storage of plump seed was negligible: four species showed 100% plumpness ; while Passerina plump seed was 94±6% (mean±standard deviation) and Muraltia was 96±6%, (n=50).

After 14 months' burial of fresh seed at 10 mm depth in the field, deterioration varied according to species. Whole surviving seeds (%) were as follows (mean±standard deviation): Agathosma apiculata 88±58,n=380; A. stenopetala 57±71, n=200; Felicia 79±98, n=600; Metalasia 49±72, n=570; Muraltia 53±99, n=34; Passerina 57±69, n=134.

After six months' burial of older seed, survival of whole seed of different species also varied (Table 6). Seed bank losses to successful germination were apparent (Table 6). Seed deaths were high for the Agathosma spp. and lowest for Muraltia, Passerina and Felicia. Failed germination and/or seed decay could not be distinguished, and were lumped as causes of seed death.

Table 1. Characteristics of dune fynbos shrubs. Data on seed size are means ± standard deviations.

	Life-span (yr)	Juv. period (yr)	Seed prodn.	Dispersal mode	Seed mass (mg)
Agathosma apiculata	25	4	Aug-Oct	ballistic/ ant	4.6±1.2 (n=38)
Agathosma stenopetala	20	4	Nov-Dec	ballistic/ ant	2.1±0.2 (n=50)
Felicia echinata	5	1.5	Aug-Oct	wind	0.4±0.5 (n=300)
Metalasia muricata	>30	4	May-Jun	wind	0.6±0.2 (n=50)
Muraltia squarrosa	15	1.5	All year	ant	3.7±0.7 (n=50)
Passerina vulgaris	15	2.5	Nov-Feb	unspecialized	1.3±0.2 (n=47)

Table 2. Seed production of young (3 and 4 yr-old) and mature (13 and 14 yr-old) shrubs of dune fynbos species over two years. Data are means±standard deviations.

	Shrub age (yr)	Total no. seed per 100 cm2 canopy		No.plump seed per 100 cm2 canopy		Mean plump seed produced per individual	
		1985	1986	1985	1986	1985	1986
Cape St. Francis							
Agathosma apiculata	13/14	108±9 (n=23)	24±4 (n=50)	87±7	21±3	3932	949
Agathosma stenopetala	13/14	125±40 (n=10)	420±90 (n=29)	97±32	363±89	775	2900
Brandewynkop							
Felicia echinata	3/4	224±26 (n=47)	2037±183 (n=24)	216±24	1465±118	1527	10358
	13/14	168±26 (n=36)	380±42 (n=28)	159±22	109±20	1331	9024
Metalasia muricata	3/4	102±23 (n=30)	193±22 (n=50)	62±16	64±12	1217	1256
	13/14	168±36 (n=30)	899±95 (n=50)	148±32	217±46	23110	33885
Muraltia squarrosa	3/4	153±90 (n=5)	17±5 (n=24)	23±14	3±1	163	21
	13/14	7±1 (n=11)	17±4 (n=20)	1±0	3±1	26	79
Passerina vulgaris	3/4	2423±304 (n=40)	402±47 (n=34)	2132±268	354±42	26799	2503
	13/14	137±65 (n=16)	863±350 (n=22)	120±58	759±308	1908	12068

Table 3. Annual variation in seed bank size (no. seed m-2) in dune fynbos communities in March of three successive years. Data are means ± standard deviations; n=50 unless otherwise indicated. Differences tested by Kruskal-Wallis one-way ANOVA by ranks (*H*); *=0.05; **=p≤0.01: ***=p≤0.001; NS=not significant.

Cape St Francis

	1985	1986	1987	*H*	Signif.
A. apiculata	52± 174	81± 280	51± 153	0.06	NS
A. stenopetala	5± 36	20± 102	31± 122	1.09	NS
Felicia echinata	54± 138	41± 138	10± 71	10.03	**
Metalasia muricata	26± 94	10± 71	132± 321	8.19	**
Muraltia squarrosa	177± 380	114± 280	51± 183	5.53	NS
Passerina vulgaris [a]	0	0	0		
Other spp.	712± 829	367± 474	896± 973	10.22	**
Total spp	1024± 1099	698± 845	1182± 1064	4.93	NS

Brandewynkop

South slope

	1985 [b]	1986	1987		
Agathosma apiculata [a]	0	0	0		
A. stenopetala [a]	7± 20	0	0		
Felicia echinata	37± 112	20± 101	0	6.17	*
Metalasia muricata	141± 278	143± 386	316± 599	2.50	NS
Muraltia squarrosa [a]	0	0	0		
Passerina vulgaris	549± 671	764± 1171	469± 591	3.04	NS
Other spp.	5340± 7153	8587± 7986	6692± 5628	9.81	**
Total spp	6068± 7569	9514± 8225	7477± 5602	9.04	*

North slope

	1985 [c]	1986	1987		
A. apiculata [a]	52± 135	0	0		
A. stenopetala [a]	0	0	0		
Felicia echinata	0	0	0		
Metalasia muricata	80± 232	81± 260	41± 226	4.13	NS
Muraltia squarrosa	127± 309	71± 206	41± 173	6.34	*
Passerina vulgaris	593± 1421	825± 1187	469± 633	3.99	NS
Other spp.	1166± 1881	845± 1371	957± 1594	1.05	NS
Total spp	2020± 2522	1833± 1879	1507± 1849	1.18	NS

[a] Adults absent from mature vegetation.
[b] n=35
[c] n=39

Table 4. Comparison of seed bank size (no.seed m-2) determined by seed counts and by germination. Samples collected at Brandewynkop in March 1987. Data are means ± stand deviations; n=50 unless otherwise stated. Differences tested by Mann-Whitney test (one-tailed) for large samples of individual species (*z* statistic) where n=50; and *U* test for total species where n=10 replicates X 5 clumped cores [a] ; $*=p\leq0.05$; $***=p\leq0.001$; NS=not significant.

	South slope				North slope			
	Seed count	Germn. count	Statistic	Signif.	Seed count	Germn. count	Statistic	Signif.
Agathosma stenopetala	0	10±32	-	-	0	0	-	
Felicia echinata	0	10±32	-	-	0	10±32	-	
Metalasia muricata	316±599	81±188	*z*=1.9	*	41±226	173±647	*z*=1.7	NS
Muraltia squarrosa	0	0	-	-	41±173	31±158	*z*=-0.4	NS
Passerina vulgaris	469±591	132±336	*z*=-3.6	***	469±633	163±331	*z*=-3.3	***
Total spp.[a]	7527±2153	4518±954	U=9	***	1573+793	1683+820	U=51	NS

[a] n=10X50

Table 5. Comparison of seed bank size (no.seed m-2) in mature (13 yr-old) and post-fire (2 yr 9 month) dune fynbos communities. Mature and post-fire community seed banks sampled in March 1986 and June 1986 respectively. Data are means ± standard deviations; n=50. Significant difference by Mann-Whitney test (*z*) for large samples, 2-tailed. *=0.05; **=p≤0.01: ***=p≤0.001; NS=not significant.

South slope

	Mature	Post-fire	*z*	Significance
Agathosma apiculata	0	0		
A. stenopetala	0	0		
Felicia echinata	20±101	153±360	-2.68	**
Metalasia muricata	143±386	81±260	0.85	NS
Muraltia squarrosa	0	0		
Passerina vulgaris	764±1171	224±413	3.91	***
Other spp.	8587±7986	4553±6524	4.16	***
Total spp.	9514±8225	5052±6616	-9.51	***

North slope

	Mature	Post-fire		
A. apiculata	0	0		
A. stenopetala	0	0		
Felicia echinata	0	0		
Metalasia muricata	81±260	10±72	-1.69	NS
Muraltia squarrosa	71±206	10±72	-1.95	*
Passerina vulgaris	825±1187	153±440	-4.82	***
Other spp.	845±1371	642±749	-0.32	NS
Total spp.	1833±1879	753±856	3.36	***

Table 6. Response of seed of dune fynbos species to burial (10mm depth) in the field from April-September 1988. Data are mean % ± standard deviations; n=10 replicates X 10 seed (10X10) unless otherwise indicated.

	Seed age (months)	Seed survival (x%±SD)	Seed decay (x%±SD)	Successful germn (x%±SD)
Agathosma apiculata	7	7± 9	85±18	8±18
	19	29± 21	71±21	0
Agathosma stenopetala	6	49±29	38±26	12±11
	30 [a]	17±18	74±21	9±12
Felicia echinata	6	55±29	0	45±29
Metalasia muricata	9	63±28	26±28	11± 9
Muraltia squarrosa	30 [b]	96± 9	4± 9	0
Passerina vulgaris	16	97± 5	2± 4	1±3
	28	87±15	12±14	1±3

[a] 7X10
[b] 5X5

DISCUSSION

Seed banks of dune fynbos shrubs were unexpectedly small, and showed no significant annual increments under 13-15 year-old vegetation. By far the largest shrub seed bank recorded was ca. 830±1187 seed m-2 (Passerina, Table 3). By comparison, in maturing British heath, seed bank size of dominant shrub species were up to tenfold larger: Calluna vulgaris with 2000-3000 seeds m^{-2} and Erica cinerea with 2000-6000 seeds m^{-2} (Mallik, Hobbs & Legg 1984). In ten year-old chaparral, maximum seed densities of 2000-3000 seeds m^{-2} were recorded for Adenostoma fasciculatum (Zammit & Zedler 1988). The size of the seed banks of the last mentioned species increases with vegetation age, which can reach about 85 years in chaparral. Therefore, much larger seed banks can accumulate there than in dune fynbos which starts to senesce at about 13 years old. Metalasia and Felicia had negligible soil-stored seed banks, while the other four species in this study behaved more like another important chaparral shrub, Ceanothus greggii. This species has smaller seed banks ranging up to 300 seeds m^{-2} (Keeley 1977), which do not accumulate proportionally with time (Zammit & Zedler 1988). It is apparently dependent on the most recent years' seed inputs for recruitment after disturbance (Keeley 1977; Zammit & Zedler 1988).

Total species' seed banks are highly clumped (variance/mean ratios=V/M>>1) (from Whittaker 1975). This agrees with other findings for soil-stored seed banks (Thompson 1986). As expected for the wind-dispersed species, *Metalasia* and *Felicia*, seed distributions were randomly dispersed (V/M close to 1). However, the distributions of elaiosome-bearing seeds (i.e. *Agathosma* spp., *Muraltia*; see also Chapter 5), were randomly dispersed, and not clumped in ant nests, as expected. *Passerina* seeds, which have an unspecialized mode of dispersal, had distribution patterns ranging widely from random to clumped dispersion.

Seed inputs and losses

Seed banks were small relative to their very variable but sometimes very high seed inputs (see Keeley 1977). Determinants of seed bank size include losses to predation, inherent seed decay or pathogens, and germination (Harper 1977, Cook 1980). Seed production of the study species varied considerably over two years, but without any consistent annual pattern. Therefore, climate was not seen as responsible for annual fluctuations, as inferred for some chaparral shrubs (Keeley 1977). Causes for variable seed production have been ascribed to limited resources (including maternal control) and unsuccessful pollination (Haig & Westoby 1988). Seed production per individual was higher for younger shrubs of the shorter lived species, *Felicia* and *Passerina*. *Muraltia's* seed production diminished in the older shrubs, many of which showed clear signs of senescence (decreasing leaf cover) (see Chapter 3). *Metalasia*, however, which is the most long-lived, showed increased production per unit area of canopy and with increasing size and age.

Losses to predators after seed release and before burial (passively or by ants) were assumed to be very high (Chapter 5), although levels of predation do vary in time and space with variation in faunal density and other food resources (Watkinson 1978). Predation was found to be a major factor in determining the seed banks of two *Arctostaphylos* spp. in chaparral (Keeley & Hayes 1976). However, once seeds are buried, predation is a negligible threat (Thompson 1987).

With regard to seed decay by internal pathogens (cf. Benic & Knox-Davies 1983), plump seed stored in the laboratory showed negligible decay. However, in the soil, pathogen activity could cause high seed losses (Cook 1980). In the measurement of seed losses during burial trials, it was not possible to distinguish whether pathogens caused the loss of intact, dormant seeds or of imbibed, germinating seeds.

Some 62-89% of seed of total species in the soil was empty. *Passerina* seed banks comprised ca. 94% empty seed. These results were similar to preliminary findings for a south western Cape congener, Passerina palacea, with 92% empty seed (D. J. Kilian, 1989, pers. comm).

Seed bank losses to germination are widely reported in the literature (Cook 1980; Thompson 1987). In dune fynbos, successful germination during the wetter season varied widely with species. Ultimately, most of these germinations can be regarded as losses from the seed pool as many of these seedlings died in the following dry summer period (see Chapter 3). In open vegetation, such as at Cape St. Francis, in the absence of a dense insulating cover, wide fluctuations in soil surface temperatures would favour germination of shrub seeds (Chapters 2 and 3). Hence, seed bank losses to failed germination would be high. In young vegetation regenerating after disturbance, similarly open in structure, seed banks would accumulate slowly due to germination losses. With time, in sites where dense canopies develop, seed banks would start to accumulate at faster rates as the losses to germination diminished. This might explain in part why the seed banks of the study species at Cape St. Francis were almost half the size of those at the Brandewynkop sites.

Methods of seed bank estimation

The problem of adequate seed bank sampling has been discussed elsewhere (Chapter 6). Application of the guidelines for adequate sampling recommmended by Thompson (1986) (within 20% error of the mean) showed that 50 samples were adequate for total species' seed banks, and for species with large seed banks such as *Passerina*, . However, for species with sparse seed banks, the recommended sampling intensity would have been prohibitive (see also Auld 1986).

Seed counts versus germinant counts

There have been no published accounts of comparisons between the different methods of seed bank estimation. Both methods have associated flaws: in seed counts, seeds are not necessarily viable; in germination counts, germination requirements may be under- or over-supplied (i.e. much more favourable) relative to field conditions. Seed sorted from soil cores were too few for germination trials, and too small to lend themselves to tetrazolium viability tests. While seed counts might overestimate seed numbers and germination might yield underestimates, results also depended largely on life history traits of the component species. Thus *Passerina* seed banks were significantly lower when determined by germination than by seed count, due to below-optimum temperatures for germination (see Chapter 2). Germination estimates of *Metalasia* (south) seed banks were lower than from counts, but in view of decreasing germinability with age (Chapter 2), the estimate by germination is probably more accurate.

For total species' seed banks on the north slope, there was no difference between estimates suggesting most species lack dormancy. In contrast on the south slope, germination estimates were almost half those from counts. After fire, this slope supported an ephemeral community of short-lived "weedy" (ie. colonizing) species (Appendix 1 and Chapter 6). These species could have well-developed dormancy mechanisms, such as the post-fire ephemerals in chaparral (Keeley & Pizzorno 1986).

Seed banks in relation to other life history attributes

How did individual species' seed banks relate to other life history attributes? This study has shown that the guild of small-leaved obligate reseeders is too simplistic in encompassing species with wide ranges in seed bank size.

As both *Felicia* and *Metalasia* have highly germinable seed (Chapter 2), seed bank estimates by germination were considered here. Both had very small soil-stored seed banks, being reliant on their numerous, highly germinable wind-borne seeds. *Felicia* has a short juvenile period (ca. 1 yr 5 months) and is short-lived (Table 1), and scarce in 13 year-old stands. In contrast, Metalasia has a longer juvenile period (4 years) and lives for >30 years. Its numerous and extremely small seed (Table 1), together with its wide dispersion, would aid in avoiding predation by invertebrates (Thompson 1987).

However, the other four species had larger soil-stored seeds banks. In the non-myrmecochorous species, losses to predation on the soil surface would be potentially extremely high. Predator satiation through massive seed production and deception with empty seed (Chapter 2) was suggested for Passerina. This species showed the largest seed bank and highest seedling recruitment after fire on both slopes at Brandewynkop (Chapter 3) in spite of large losses to seed decay. The two Agathosma species produced relatively moderate numbers of seed with elaiosomes for ant dispersal (Chapter 5). Their seed banks were relatively moderate in size. Muraltia had the lowest seed production, a relatively small seed bank which decreased significantly in size while ageing adult plants died. Yet seed survival in the soil was very high, and post-fire recruitment relatively successful (Chapter 3).

Implications of seed bank unreliability for coexistence

Seed banks of the four species with soil-stored seeds were almost halved after fire, and Muraltia seed banks were almost depleted on the north slope. Under a disturbance regime too frequent for seed bank replenishment, dune fynbos shrub seed banks would be eliminated, hence the success by farmers in altering the state of dune fynbos to grassland through frequent fires and bushcutting.

In conclusion, mature dune fynbos seed banks were relatively small and show no large annual increments in their 13th to 15th years. Studies of seed banks across a successional gradient in the dune landscape indicated that fynbos shrub seeds did not persist in the soil, failing to survive under frequent disturbance beneath grassland, nor under undisturbed conditions beneath thicket (Chapter 6). Limited evidence of seed ageing and loss in germinability over three years was found for one shrub species with soil-stored seed banks (Chapter 2). I infer, therefore, that dune fynbos shrubs must rely mainly on recent years' inputs into the seed bank for post-disturbance recruitment. Seed inputs and losses varied widely from year to year. After any one fire, recruitment of the shrub species with a large available store of germinable seed at the time, would be favoured. This means that fires in different years and seasons would favour recruitment of different proportions of species. In this sense, dune fynbos seed banks may be considered as unreliable in not ensuring direct replacements after disturbance. This contrasts strongly with communities comprising species with persistent or sizeable seed banks which would ensure similar replacements after disturbance. Seed bank unreliability in dune fynbos shrubs provides a mechanism for the coexistence of varying proportions of species over time and might help to explain the maintenance of high species richness in Cape fynbos.

ACKNOWLEDGEMENTS

The technical assistance of C. Douie, F. MacKay, N. Philips and R. Jones is gratefully acknowledged. Invaluable discussions were held with R. M. Cowling, N. Philips, P. Manders and E. Witowski. The study was supported by the Fynbos Biome Programme, Foundation for Research Development of the CSIR, and the University of Cape Town.

REFERENCES

Auld, T. D. (1986). Population dynamics of the shrub Acacia suavolens (Sm.) Willd.: Dispersal and the dynamics of the soil seed bank. Australian Journal of Ecology, 11, 235-54.

Benic, L. & Knox-Davies, P.S. (1983). Anthracnose of Protea compacta caused by Colleotrichum gloeosporoides. Phytophylactica, 15, 109-119.

Bond, P. & Goldblatt, P. (1984). Plants of the Cape Flora: a Descriptive Catalogue. Journal of South African Botany, Suplementary Volume 13. Kirstenbosch, Claremont.

Cavers, P. B. (1983). Seed demography. Canadian Journal of Botany, 61, 3578-90.

Cook, R. (1980). The biology of seeds in the soil. Demography and Evolution in Plant Populations (Ed. by O. T. Solbrig), pp. 107-188. Blackwell, Oxford.

Cowling, R. M. (1984). A syntaxonomic and synecological study in the Humansdorp region of the fynbos biome. Bothalia, 15, 175-227.

Fenner, M. (1987). Seedlings. New Phytologist, 106 (Suppl.), 35-47.

Haig, D. & Westoby, M. (1988). On limits to seed production. American Naturalist, 131, 757-59.

Harper, J. L. (1977). Population biology of plants. Academic Press, London.

Holmes, P. M. (1989). Decay rates in buried alien Acacia seed populations of different density. South African Journal of Botany, 55, 299-303.

Holland, P. G. & Steyn, D. G. (1975). Vegetational responses to latitudinal variations in slope angle and aspect. Journal of Biogeography, 2, 179-83.

Holland, P. G., Steyn, D. G. & Fuggle, R. F. (1977). Habitat occupation by Aloe ferox Mill. (Liliaceae) in relation to topographic variations in direct beam solar radiation income. Journal of Biogeography, 4, 61-72.

Keeley, J. E. (1977). Seed production, seed populations in soil, and seedling production after fire for two congeneric pairs of sprouting and nonsprouting chaparral shrubs. Ecology, 58, 820-29.

Keeley, J. E. (1987). Ten years of change in seed banks of the chaparral shrubs, Arctostaphylos glauca and A. glandulosa. American Midland Naturalist, 117, 446-48.

Keeley, J. E. & Hayes, R. (1976). Differential seed predation on two species of Arctostaphylos (Ericaceae). Oecologia, 24, 71-81.

Keeley, S. C. & Pizzorno, M. (1986). Charred wood stimulated germination of two fire-following herbs of the California chaparral and the role of hemicellulose. American Journal of Botany, 73, 1289-97.

Kruger, F. J. (1984). Effects of fire on vegetation structure and dynamics. Ecological effects of fire in South African Ecosystems Ecological Studies 48. (Ed. by P. de V. Booysen & N. N. Tainton), pp.219-244. Springer-Verlag, Berlin.

Levyns, M.R. (1954). The genus Muraltia. Journal of South African Botany, Supplementary Volume II, 1-247.

Mallik, A. U., Hobbs, R. J. & Legg, C. J. (1984). Seed dynamics in Calluna-Arctostaphylos heath in north-eastern Scotland. Journal of Ecology, 72, 855-71.

Roberts, H. A. (1981). Seed banks in soils. Advances in Applied Biology, 6, 1-55.

Schulze, R. E. (1975). Incoming radiation on sloping terrain: a general model for use in southern Africa. Agrochemophysika, 7, 55-61.

Siegel, S. (1956). Nonparametric Statistics. For the Behavioural Sciences. McGraw-Hill, London.

Thompson, K. (1986). Small-scale heterogeneity in the seed bank of an acidic grassland. Journal of Ecology, 74, 733-38.

Thompson, K. (1987). Seeds and seed banks. New Phytologist (Supplement), 106, 23-34.

Watkinson, A. R. (1978). The demography of a sand dune annual: Vulpia fasciculata II The dynamics of seed populations. Journal of Ecology, 66, 35-44.

Whittaker, R. H. (1975). Communities and Ecosystems. MacMillan Publishing Company, New York.

Willems, J. H. (1988). Soil seed bank and regeneration of a Calluna vulgaris community after forest clearing. Acta Botanica Neerlandica, 37, 313-20.

Zammit, C. A. & Zedler, P. H. (1988). The influence of dominant shrubs, fire, and time since fire on soil seed banks in mixed chaparral. <u>Vegetatio</u>, <u>75</u>, 175-187.

CHAPTER 5

Fate of small seeds in Cape fynbos : granivory and myrmecochory

ABSTRACT

This study was the first investigation of the fate of small seed (1.5-3.5 mm length) of small-leaved, non-sprouting fynbos shrub species which predominate in Cape fynbos. Fresh seeds of three species with elaiosomes and three species lacking elaiosomes were used in a cafeteria experiment sited in dune fynbos in the south eastern Cape. Surveys indicated the presence of granivorous, harvester and seed-dispersing ant taxa as well an extremely dense population of rodents. Results showed almost complete removal from open depots after six days. In ant-accessible depots, seed remnants indicated the occurrence of granivory. No differences were apparent between seed removals by ants and rodents after the first day, but after six days, seed removals by ants of elaiosome-bearing species and species without elaiosomes were significantly higher than by rodents. There was also no significant difference in seed removals by ants between species with and without elaiosomes. A further experiment using seeds of an elaiosome-bearing species showed no significant difference in seed removals by ants between whole seeds and seeds from which the elaiosomes had been separated. This similarity in removals of elaiosome-bearing and non-elaiosome-bearing seed led to the formulation of a new explanation for the high incidence in the Cape flora of species with elaiosome-bearing seeds. Globally there is an association between

nutrient-poor soils and small leaves. Similarly, the infertile soils of the Cape support a preponderance of small-leaved, finely branched sclerophyllous shrubs. I propose that an allometric consequence of fine branching is that fruits produced must be small. These would be highly sought after by small predators, namely ants, in a nutrient-poor system. Burial reduces predation by ants which are surface foragers. In fynbos where seed banks are small and non-persistent, and comprise seeds with unspecialized germination requirements, ant predation would have been a strong selective force for the evolution of myrmecochory. This explanation for the selection of myrmecochory may similarly apply to Australian sclerophyll shrublands.

Nomenclature follows Bond & Goldblatt (1984).

INTRODUCTION

Although myrmecochory or seed dispersal by ants is reported to be widespread in the Cape flora (Bond & Slingsby 1983), studies have focussed mainly on species in the Proteaceae with large seeds (Bond & Slingsby 1983; 1984; Bond & Breytenbach 1985; Breytenbach 1988; Slingsby & Bond 1982; 1985). Studies of dispersal by ants in the small-seeded (2.0-5.0 mg) species have been neglected.

Dispersal by ants is similarly widespread in the analogous nutrient-poor, sclerophyllous vegetation of Australia (Berg, 1975; 1981; Milewski & Bond 1982; Westoby et al. 1982). Various theories have been forwarded to explain the high incidence of myrmecochory (reviewed by Buckley 1982), including escape from predation (e.g. Berg 1981; Slingsby & Bond 1985; Bond & Breytenbach 1985), avoidance of fire (e.g. Berg 1981; Majer & Lamont 1985) and burial in more fertile sites in ant nests (e.g. Culver & Beattie 1983; but see also Rice & Westoby 1986). In the studies of the large-leaved, large-seeded species of the Proteaceae in the Cape, the role of ant-dispersal as a mutualism to escape from rodent predation was well established (Bond & Breytenbach 1985). However, although they are conspicuous as dominants in the Cape landscapes, members of this family form a small proportion of the Cape flora as a whole : 3.8% of some 8500 species (Bond & Goldblatt 1984). Interpretation of the role of myrmecochory in the Cape floral kingdom has been disproportionately influenced by observations of this guild of large-seeded shrubs.

This is the first study of the fate of seed of small-seeded, non-sprouting species, which are dominant in the Cape flora. Of the species selected for study, all belong to genera which are well-represented in the Cape flora (Table 1). Of the three myrmecochorous species, only *Muraltia* has a well developed elaiosome, the other two (*Agathosma* spp.) having relatively small elaiosomes (Fig. 1). The genus *Agathosma* also has ballistic dispersal, a feature often associated with myrmecochory (Berg 1975; Buckley 1982; Bond & Slingsby 1983).

The study aimed to determine the fate of small-sized seed by monitoring in the field, removals from different seed depots, accessible and inaccessible to invertebrates and rodents, i.e. cafeteria experiments. Specifically, the study asked the questions :

(1) after being released from the mother plant, are small seed on the soil surface moved further by fauna ?

(2) are fresh elaiosome-bearing seed of small size removed faster by ants than by rodents (rodent predation-avoidance hypothesis) (see Bond & Breytenbach 1985)?

(3) do ants preferentially remove the elaiosome-bearing seeds of myrmecochorous species over seeds of non-myrmecochorous ones?

(4) what effect does the separation of seed from their elaiosomes have on their removal by ants ?

In the light of these findings, I evaluated the theories explaining the high incidence of small, elaiosome-bearing seeded species in the Cape reported by Bond & Slingsby (1983). From these results and other data on fynbos seed banks, I proposed a new explanation which may similarly apply to myrmecochory in Australian sclerophyll shrublands.

METHODS

Study site

The study was situated at Cape St. Francis in South Coast Dune Fynbos (Cowling 1984) in the coastal dunes of the Humansdorp region (34°02'S;24°47'E). The climate is mild and frost-free, with a range in mean monthly temperatures of 19.9°C in the hottest month (February) and 14.2°C in the coldest (July) (see Chapter 3 for details). Mean annual rainfall is ca. 600 mm with a summer/autumn drought and a winter/spring surplus.

Cafeteria experiment

The study species are dominant shrubs in the dune fynbos community (see Chapter 3). Their characteristics are given in Table 1. In preliminary trials where seed of the study species was placed in petri dishes in the field, seed removals by ants were observed.

The experiment was set up in a study area of ca. 40 X 25 m in mature dune fynbos (13 years post-fire). Separate trials with different seed species were run in October and November 1985 in an attempt to synchronize with the appropriate phenophase (i.e. seed release) for each plant species. A third trial was run in January 1986 with one species only to test for effects of elaiosome separation from seeds on removals. Seed production phenophases are given in Table 1 (this study; Pierce & Cowling 1984). The term, "seed," is used here in place of diaspore. The term, "removal," implies conveyance for one place to another, while "dispersal," implies transportation to a site more favourable for survival and establishment.

Freshly released seeds of the elaiosome-bearing species of *Agathosma apiculata*, *A. stenopetala* and *Muraltia squarrosa* were harvested at each site from bags set up earlier on the morning of the experiment. Seed of the non-elaiosome-bearing species was collected a day or two prior to the experiment. All seed was handled with forceps which prevented possible contamination of non-elaiosome-bearing seeds with elaiosomes. Sites were located haphazardly in the study area: six in October and ten in December. Four treatments were located at each site. Treatment 1 depots excluded invertebrates; Treatment 2 excluded small mammals; Treatment 3 was open to both invertebrates and to rodents; and Treatment 4 was closed to both. Depots comprising petri dishes with the sides coated in Formex, (commercial insect deterrant) excluded invertebrates (as per Bond & Breytenbach 1985). Depots accessible to invertebrates lacked the Formex and were fitted with gently sloping ramps over the petri dish sides to facilitate seed removal. Cages placed over the petri dishes excluded rodents.

To ensure that seed densities in the depots (area of petri dish=64 cm^2) were not unnaturally high, field densities of dispersed seed were determined. These values were determined from estimates of seed production (average of two crops over two years by 13/14 year-old shrubs) from 100 cm^2 of canopy of each shrub species (from Chapter 3). Canopy seed production values, divided by each species' period of reproductive phenophase, yielded dispersed seed densities $week^{-1}$ (see Table 1). Thus, field densities of four species for October were 160 seed 100 cm^{-2} and for two species in December, 126 seed 100 cm^{-2}. The depot seed densities were considerably lower : in each depot, ten seeds of each species were placed. Thus the October trial comprised 40 seed per depot : *A. apiculata*, *Muraltia*, *Felicia* and *Metalasia*; the November trial had 20 seed per depot : *Passerina* and *Agathosma stenopetala*. Both experiments were monitored for each of six days.

The last trial in January tested for differences in invertebrate removals of seed of *Muraltia squarrosa* with and without elaiosomes attached. Here five seeds with elaiosomes and five seeds without were set up in ten depots each under conditions of rodent exclusion (Treatment 2) and monitored for three days. For all trials the weather was warm, and without rain. Non-parametric statistical analyses (Siegel 1956) were used, as seed count data over time were not independent.

Faunal surveys were carried out after completion of the final cafeteria experiment. At each of the ten experimental sites, four pitfall traps with anti-freeze (150 mm diameter dish buried till lip flush to the ground) were randomly set and baited as follows : raw meat; banana and rum; human faeces; and no bait. A further pitfall trap (20 mm diameter) was set up at each site. In addition, a Sherman trap was set up at each of the ten sites early each morning for a total of four days to survey the small mammal component, and an additional 24 traps were randomly placed.

RESULTS

In some depots accessible to rodents only, droppings were observed. In depots accessible to invertebrates only, seed remnants indicated granivory. In some cases, the inside of the flat seed of *Felicia* had been eaten, with just the seed margin remaining. In one invertebrate-accessible depot, two *Muraltia* elaiosomes remained after the seeds had been removed. In an open depot, a *Muraltia* seed without the elaiosome remained, and in another open depot, vice versa. For the purposes of the experiment in determining seed fate, only whole seed were counted as seeds remaining. Detailed observation in pilot studies showed that ants and rodents were responsible for seed removals.

Except for the control depots (Treatment 4) from which no losses were recorded, seeds were removed from all other treatment depots (Figs. 2 & 3). Removals from open depots (Treatment 3) were relatively rapid with almost all seed removed within 2-6 days. Rates of removal by ants were generally significantly higher than by rodents, except in *Agathosma apiculata* (Table 2). After Day 1 results of removals of myrmecochorous and non-myrmecochorous seed types showed no significant differences between ant and rodent removals. However, differences were apparent after Day 6 (Table 2).

The prediction that ants would remove seed of elaiosome-bearing species more rapidly than non-elaiosome-bearing species was not supported. Numbers of seeds remaining after one day for all four species subjected to Treatment 2 (ant accessible) in October were not significantly (NS) different (Kruskal-Wallis one-way analysis of variance by ranks, H = 0.99; p=0.80; NS; n=6 depots X 10 seeds each). Similarly, in December, there was no significant difference in numbers of seeds remaining after the first day of Treatment 2 for Passerina (non-myrmecochorous) and the elaiosome-bearing seeds of Agathosma stenopetala (Mann-Whitney test, U=12; p=0.20; NS, n_1 = 6, n_2 = 6, ties omitted). The comparison of invertebrate removals of Muraltia seed with and without elaiosomes showed no significant differences on Days 1 and 3 (Table 3).

The survey of the invertebrate species indicated the presence of ant species reported to be seed-dispersers, although predators, omnivores and granivores were also identified (Dr A. Prins, 1986, pers. comm.) (Table 4). The small mammal survey recorded only one rodent species, Rhabdomys pumilio (striped field mouse). Trapping counts in 10 traps over four days were four, five, six and four mice respectively, and additional trapping yielded 15 mice in 24 traps. In some cases, traps were sprung seconds after being set. These results indicate extremely high rodent densities (G. Kerley, 1986, pers. comm.).

Table 1. Characteristics of study species.

	Family	No. fynbos spp per genus	Dispersal	Seed prod^{n} period	Seed prod^{n} 100 cm^{-2} canopy wk^{-1}	Seed mass (mg$\pm$SD)
Agathosma apiculata	Rutaceae	130/135	Ant/ ballistic	Aug-Oct	8	4.6$\pm$1.2 (n=38)
Agathosma stenopetala	Rutaceae	"	"	Nov/Dec	26	2.1$\pm$0.2 (n=50)
Felicia echinata	Asteraceae	55/83	Wind	Aug-Oct	94	0.4$\pm$0.5 (n=300)
Metalasia muricata	Asteraceae	32/50	Wind	May/June	56	0.6$\pm$0.2 (n=50)
Muraltia squarrosa	Polygalaceae	106/115	Ant	All yr	2	3.7$\pm$0.7 (n=50)
Passerina vulgaris	Thymelaeaceae	14/18	Other	Nov-Feb	118	1.3$\pm$0.2 (n=47)s

Table 2. Comparisons[a] of seed removals , and numbers of seed remaining in depots accessible to rodents (Treatment 1) and to ants (Treatment 2) after Days 1 and 6. Data are means ± standard deviations.

	No. seed remaining (x±S.D.) Day 1.					Day 6.				
	Rodent access	Ant access	U value	Signif. p		Rodent access	Ant access	U value	Signif. p	
Spp. without elaiosomes										
Metalasia muricata [b]	8.3±1.9	8.3±1.8	16.5	0.41	NS	5.7±2.7	1.7±2.6	5	0.02	*
Felicia echinata [b]	8.7±1.8	8.3±1.9	15.3	0.29	NS	4.7±3.8	1.2±2.4	2	0.004	**
Passerina vulgaris [c]	8.1±3.4	7.7±2.8	41	>0.05	NS	7.5±3.5	3.4±3.4	19	0.01	**
Elaiosome-bearing spp.										
Muraltia squarrosa [b]	8.8±1.6	7.3±2.9	12.5	0.20	NS	5.7±2.1	2.0±2.2	2	0.004	**
Agathosma apiculata [b]	6.8±4.9	8.0±3.9	16.5	0.41	NS	0.2±0.4	1.5±3.6	21	0.05	*
A. stenopetala [c]	7.7±4.1	6.2±2.7	27	>0.05	NS	7.4±4.0	3.2±2.9	8	0.001	***

[a] Mann-Whitney U test, one-tailed,
* = $p \leq 0.05$; ** = $p \leq 0.01$; *** = $p \leq 0.001$

[b] n=6 depots X 10 seed

[c] n=10 depots X 10 seed

Table 3. Seed removals of Muraltia squarrosa from depots accessible to ants only. + = seed with elaiosome; - = seed with elaiosome removed. n=10 depots with 5 seed each.

	Day 1.		Day 3.	
	+	-	+	-
No. seed removed	27	29	41	41
No. seed remaining	23	21	9	9

Table 4. Species of ants collected by baited and pitfall traps set after completion of the cafeteria experiment in January 1986. ^{d} = seed dispersers ; ^{o} = omnivores; ^{p} = predators; ^{g} = granivores (A. Prins, pers. comm; see Results).

	Camponotus sp.1.(near *knysnae*, ?new sp.)
	Camponotus sp.2.
do	*Camponotus niveosetosus*
gp	*Myrmicaria nigra*
	Myrmicaria sp.
p	*Ocymyrmex weitzecheri*
	Pheidole sp.1. (probably *megacephala*)
d	*Anaplolepis steingroeveri*

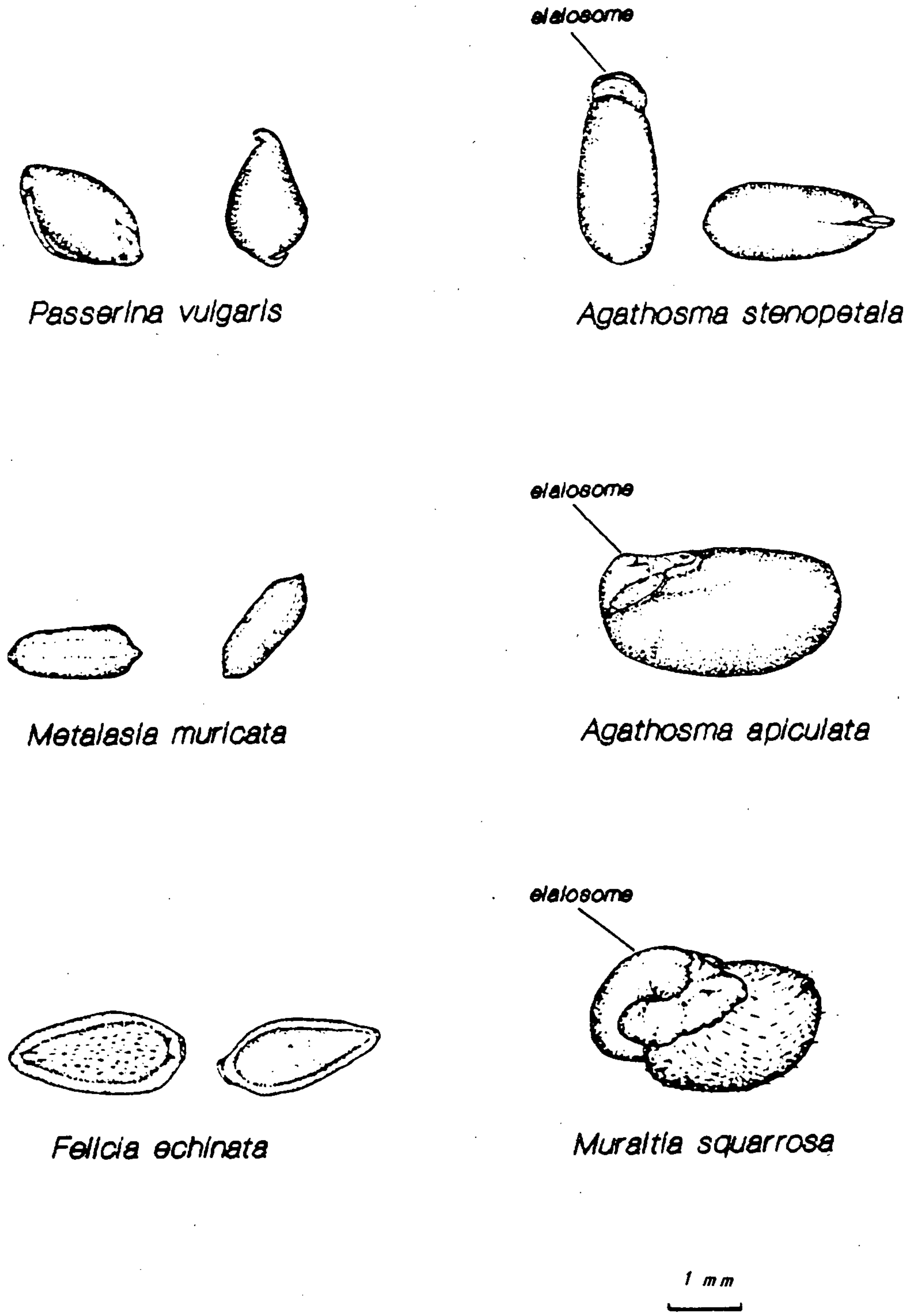


Fig. 1. Seed of the dune fynbos study species.

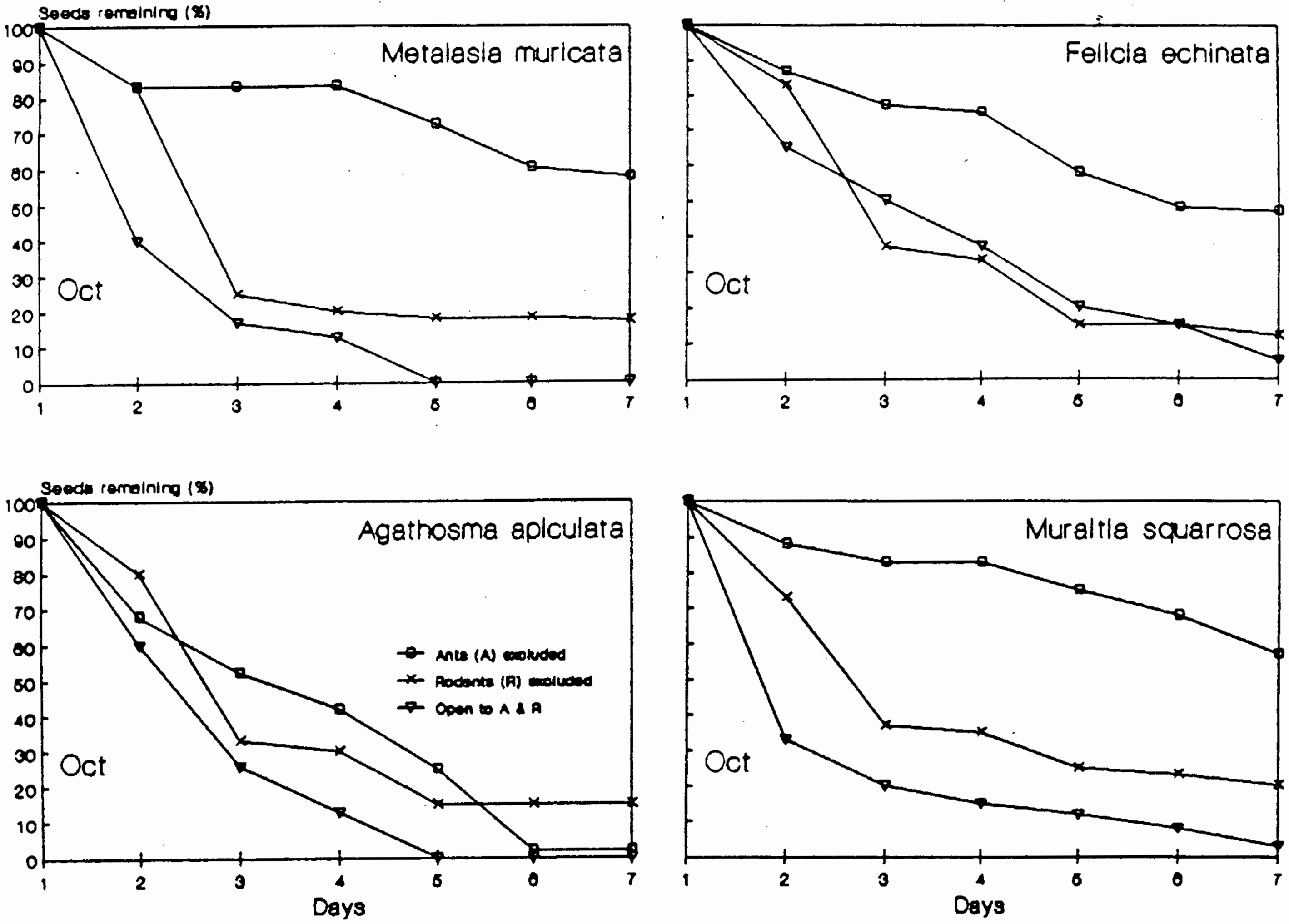


Fig. 2. Seed remaining (%) in cafeteria experiments indicating rates of removal under three treatments on four dune fynbos species in October 1985. n=6 depots X 10 seed each. (Control treatments showed no seed losses.)

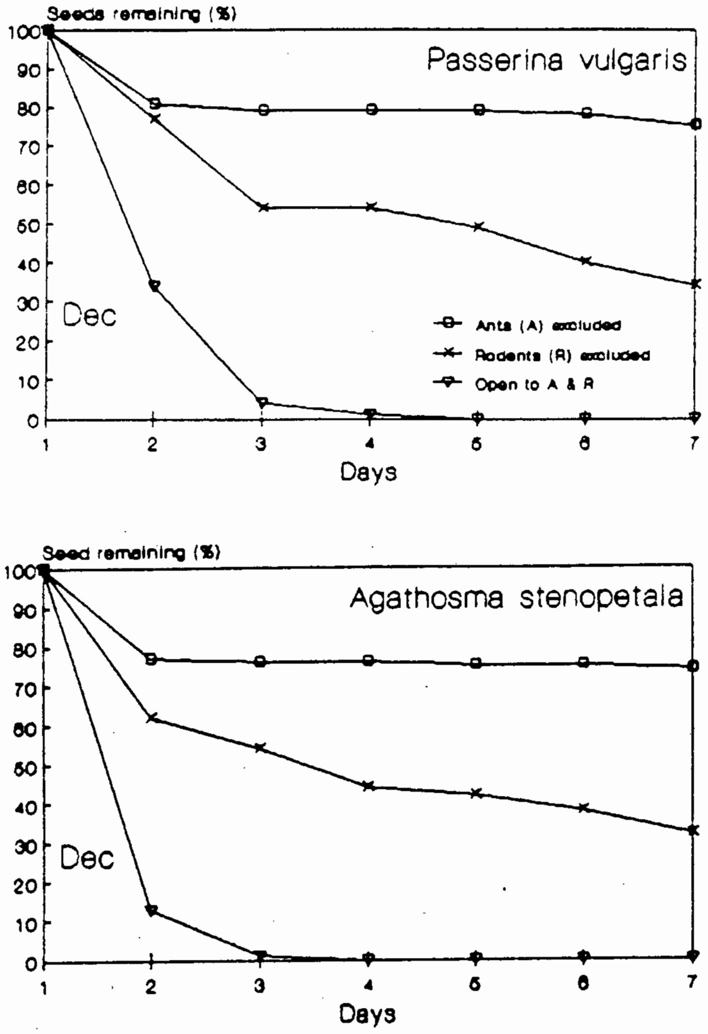


Fig. 3. Seed remaining (%) in cafeteria experiments indicating rates of removal under three treatments on two dune fynbos species in December 1985. n=10 depots X 10 seed each. (Control treatments showed no seed losses.)

DISCUSSION

In general the rapid seed removal rates, with almost all seed disappearing within two to seven days of being exposed in the field, showed that seed is a highly sought-after resource in the dune environment. Seed densities at the depots would not have enhanced removal rates (see Majer 1982) as they were lower than naturally occurring field densities. Results suggest that seasonal effects were larger than any possible density effects of seed caches: the October cafeteria experiment involving 40 seed per dish experienced slower removal rates than did the December trial involving only 20 seed per dish. The faster seed removals in December may reflect generally lower resources at a time when fewer dune species are producing seed (Pierce & Cowling 1984). Alternatively, ant activity may vary with season (Briese 1982), with December being warmer than October. If elaiosome attractiveness is short-lived, more elaiosome-bearing seed would be removed on the first day of exposure. However, amongst the three myrmecochorous species, seed removals by ants and rodents were no different. This refutes the hypothesis of early escape by ant dispersal from predation by rodents (Berg 1981; Bond & Breytenbach 1985), despite very high rodent numbers in the area.

The significantly higher removal of seed by ants than by rodents after six days indicated very high ant activity.

However, it is difficult to interpret removals as dispersal or granivory. Granivory was evident in the ant-accessible depots, and two Muraltia elaiosomes remained after their seeds had been removed. Furthermore, ant removals of elaiosome-bearing species were not significantly different from species lacking elaiosomes. Finally, number of seed removed by ants was not affected by the artificial separation of elaiosomes. In experiments with large-seeded fynbos species, an introduced ant species, the Argentine ant (Iridomyrmex humilis), interfered with dispersal by feeding on seed and outcompeting indigenous seed-dispersing ant species (Bond & Slingsby 1984). However, Argentine ants were absent from the study area.

From the above, I infer that seeds were removed by granivorous as well as by dispersing ants. Seed losses to granivory could have been significant as shown by the high removals of seed of species lacking elaiosomes by ants. This is not the first report of conflicting acts of dispersal and granivory by ants, especially with small seeds (J. Vlok, 1986, pers. comm.; Slingsby & Bond 1982; Bond & Slingsby 1983). However, such findings are often overlooked in the search for support of the existence of plant benefits. Seed harvester ants have been observed taking myrmecochorous seed (Breytenbach 1988). In south western Australian heathlands, Majer (1982) found that two ant species, usually recognized as important seed dispersers, sometimes consume entire seeds. In tropical rain forests, myrmecochory was highly variable in effectiveness, and a reputed seed-dispersing ant species failed to disperse seed (Horwitz & Schemske 1986). In temperate forests, Culver & Beattie (1978) found preliminary evidence that the elaiosome is an attractant not only to ant disperser agents, but also to seed predators.

Myrmecochory may depend upon the ratio of ant size to seed size : a low ratio leads to dispersal; a high ratio to granivory (J. D. Majer, 1983, pers. comm.). In contrast, a case has been reported where two ant species were too small to move seeds, and instead removed the elaiosome _in situ_ without moving the seed (Auld 1986). Hence, myrmecochory can be a somewhat haphazard interaction.

When predation avoidance is discussed as an advantage of myrmecochory in the literature, only rodents and birds are seriously considered as predators (e.g. Westoby _et al_. 1982). However, the most obvious predators of small seeds are ants, yet these are largely ignored. From my results here and findings on the nature of fynbos seed banks (Chapter 4), I propose that the selective forces for myrmecochory in the nutrient-poor fire-prone sclerophyll vegetation in the Cape and in Australia, have been a sequence of factors stemming from low nutrient soils and culminating in ant predation as a selective force. I develop my hypothesis below.

Infertile soils are often associated with small leaves (Loveless 1962; Beadle 1966; Givnish & Vermeij 1976; Cowling & Campbell 1983). Similarly, the infertile soils of the Cape support a preponderance of small-leaved, finely branched sclerophyllous shrubs. By allometry (Corner 1949: Sinnott 1921; Bond & Midgley 1988; Midgley & Bond 1989), reproductive bodies on fine branching would also tend to be small. I propose that on infertile soils bearing small-leaved species, the allometric consequence is small seed. The preponderance of small-leaved shrubs in fynbos would result in an enormous source of small seeds. In a nutrient-poor system, these would provide a valuable resource to necessarily small predators i.e. ants. I disagree with the notion held by Van der Pijl (1972) and Harper (1977) that myrmecochory will not occur where harvester ants are common (see above). Most critical here is the point that ants are strictly surface foragers (see Thompson 1987). Therefore, burial of elaiosome-bearing seeds by ants as dispersal agents would provide an ideal evasion tactic against ant granivory for small seeds. In a review of Australian systems, seeds of 1-2 mg form the preferred size class for ant predation (Campbell (1982). Rodents prefer larger seed (>3 mg, Thompson 1987) and results for small seeds here show that rodents are less important as predators. However, rodent predation of large seeds produced by large-leaved Proteaceae is a significant factor (Bond & Breytenbach 1985).

For plants, the other option for predator evasion is to produce seed too tiny for predation i.e. <<1 mg. In the nutrient poor soils, there could have been an opposing selective pressure to increase seed size to maximize seed nutrients reserves (still within the constraints set by allometry). In some species this would have selected against very tiny seeds as a means of predator evasion. Instead a seed size class vulnerable to ant predation would have evolved, which would have exerted a significant selective force on fynbos species.

A review of granivory by ants shows that the costs to plants can be considerable (Buckley 1982). Under the above-mentioned selective forces, plants stood to gain far more than the ants. They have undergone considerably more adaptive change and are considerably more dependent that the ants (Westoby et al. 1982). Ants may benefit in being provided with certain strict dietary requirements (e.g. lipids) contained in elaiosomes (Beattie 1982). In the case of the large seeds produced by the large-leaved species , there would have been even greater selective pressure for increasing this reward for dispersal agents which are too small to eat and destroy the seed. Cases of almost perfect planting has been recorded where small-sized ants relative to seed size are involved (Berg 1981). Hence the success of the large-seeded myrmecochores, where seed size relative to ant size is great, and rodent evasion is achieved. However, amongst small-seeded species, the process of myrmecochory is still somewhat haphazard, perhaps because of their size class being so critically close to the favourable ratio of ant to seed size .

The unanswered question is raised again: why is myrmecochory limited to the fynbos, and not found in the adjacent non-fynbos vegetation (Breytenbach 1988)? If allometric implications are important why are elaiosome-bearing seeds absent from the similarly small-leaved and small-seeded vegetation of the semi-arid karoo ? I suggest the answer lies in the nature of the interdependence of the plant population and its seed bank. Where interdependence between organisms or communities is loose, co-evolutionary changes are not a significant force (Howe 1984; Briese 1982). Seed predation intensity must be viewed in the context of habitat. For example in a semi-arid system, plant communities show a suite of characteristics which include high seed yield and longevity, large seed banks and complex germination requirements, all in response to a low moisture (rainfall) input which is also variable and unpredictable (Briese 1982). In such a system, there is loose interdependence between the vegetation and ant communities, and ants do not profoundly affect vegetation pattern. Similarly karoo plant species would seem to have resilient seedbanks with generally numerous and tiny seeds (K. Esler, 1989,pers. comm.) which would reduce predation by satiation and evasion by small size. Predation by ants would not be a selective force in such a system. In contrast, fynbos seed banks are relatively small (Chapter 4), are not persistent (Chapter 6), and germination requirements are not particularly complex (Chapter 2). Recruitment after a fire would be dependent primarily on the most recent years' crops (Chapter 4), and could therefore be controlled by predation intensity. Granivory by ants would therefore play an important selective force in the dispersal of small seeds.

Dispersal by ants, when seen in the context of global patterns is not the "unexpected and incomprehensible" phenomenon noted by Berg (1981). In reviewing dispersal, Howe & Smallwood (1982) conclude that in most communities, large proportions of plants are animal dispersed, and that communities poor in animal dispersal are rare (e.g. some deserts and coral islands). As examples, in tropical forests, 50-75% of tree species are animal dispersed; in temperate communities, more than 60% of tree species are animal dispersed. It is therefore highly probable that in fynbos, as in any other plant community, a high proportion of plant species would be animal-dispersed. Just as classes of dispersers are favoured by the alteration of fruit size (Wheelwright & Orians 1982), so ants as a class of small dispersers could have been favoured by allometric constraints.

This cafeteria experiment was conducted on species of Muraltia and in Passerina before the variability in the proportions of "plump" (=full) and empty seeds with concomitant viability had been identified (Chapter 2) . Hence, variable, but random proportions of empty and plump seed, were used in the experiment. Nevertheless, removal was almost complete, suggesting that seed emptiness is not a consideration to the removal agents. There were also equivalent removals of Muraltia seed with and without elaiosomes. (Empty seeds also bear elaiosomes). The overwhelming similarity in pattern of seed removals amongst all the species indicates predator deception (see Chapter 2). The production of variable plump and empty seed of both Muraltia and Passerina was explained as a means of protecting viable seeds through a combination of predator deception and satiation (see Chapter 2). Proportions of viable seed of Muraltia varied through the year but crops in autumn differed from others in showing higher viability and less pronounced dormancy (see Chapter 2). These reproductive traits might serve to sustain possible dispersal agent interest throughout the year from one critical autumn crop to the next. The other study two species without the advantage of an elaiosome, Felicia and

Metalasia, have wind dispersed seeds combined with very high viability and unspecialized germination requirements (Chapter 2).

ACKNOWLEDGEMENTS

I thank G. Kerley for his expertise and field assistance in small rodent trapping; G. J. Breytenbach for advice on invertebrate trapping; and Dr A. Prins, of the South African Museum, for discussion and identification of the ant species. R. Yeaton and R. M. Cowling advised on statistical analyses. W. J. Bond and J. Scott kindly commented on an earlier draft. Funding was provided by the Fynbos Biome Project, Foundation for Research and Development, CSIR and administered by the University of Cape Town.

REFERENCES

Auld, T. D. (1986). Population dynamics of the shrub _Acacia suavolens_ (Sm.) Willd.: Dispersal and the dynamics of the soil seed-bank. _Australian Journal of Ecology_, _11_, 235-254.

Beadle, N. C. W. (1966). Soil phosphate and its role in molding segments of the Australian flora and vegetation, with special reference to xeromorphy and sclerophylly. _Ecology_, _47_, 992-1007.

Beattie, A. J. (1982). Ants and gene dispersal in flowering plants. _Pollination and Evolution_ (Ed. by J. A. Armstrong, J. M. Powell and A.J. Richards),pp.1-8. Royal Botanic Gardens, Sydney.

Berg, R. Y. (1975). Myrmecochorous plants in Australia and their dispersal by ants. _Australian Journal of Botany_, _23_, 475-508.

Berg, R. Y. (1981). The role of ants in seed dispersal in Australian lowland heathland. _Ecosystems of the World. Heathlands and Related Shrublands - Analytical Studies_ (Ed. by R. L. Specht),pp.51-59. Elsevier, New York.

Bond, W. J. & Breytenbach, G. J. (1985). Ants, rodents and seed predation in Proteaceae. South African Journal of Zoology, 20, 150-54.

Bond, P. & Goldblatt, P. (1984). Plants of the Cape Flora. A Descriptive Catalogue. Journal of South African Botany Supplementary Volume, 13. Kirstenbosch, Claremont.

Bond, W. J. & Midgley, J. (1988). Allometry and sexual differences in leaf size. American Naturalist, 131, 901-910.

Bond, W. J. & Slingsby, P. (1983). Seed dispersal by ants in shrublands of the Cape Province and its evolutionary implications. South African Journal of Science, 79, 231-33.

Bond, W. & Slingsby, P. (1984). Collapse of an ant-plant mutualism: the Argentine ant (Iridomyrmex humilis) and myrmecochorous Proteaceae. Ecology, 65, 1031-37.

Briese, D. T. (1982). Relationship between the seed-harvesting ants and the plant community in a semi-arid environment. Ant-plant interactions in Australia. (Ed. by R. C. Buckley), pp.11-25. Junk, The Hague.

Breytenbach, ... overleaf.

Breytenbach, G. J. (1988). Why are myrmecochorous plants limited to fynbos (macchia) vegetation types? South African Forestry Journal, 144, 3-5.

Buckley, R. C.(Ed) (1982). Ant-Plant Interactions in Australia. Junk, The Hague.

Campbell, M. H. (1982). Restricting losses of aerially sown seed due to seed-harvesting ants. Ant-Plant Interactions in Australia (Ed. by R. C. Buckley), pp. 25-30. Junk, The Hague.

Corner, E. J. H. (1949). The durian theory and the origin of the modern tree. Annals of Botany, 13, 367-414.

Cowling, R. M. (1984). A syntaxonomic and synecological study in the Humansdorp region of the Fynbos Biome. Bothalia, 15, 175-227.

Cowling, R. M. & Campbell, B. M. (1983). A comparison of fynbos and non-fynbos coenoclines in the lower Gamtoos River Valley, southeastern Cape, South Africa. Vegetatio, 53, 161-178.

Culver, D. C. & Beattie, A. J. (1978). Myrmecochory in Viola: dynamics of seed-ant interactions in some West Virginia species. Journal of Ecology, 66, 53-72.

Culver, D. C. & Beattie, A. J. (1983). Effects of ant mounds on soil chemistry and vegetation patterns in a Colorado meadow. Ecology, 64, 485-92.

Givnish, T. J. & Vermeij, G. J. (1976). Sizes and shapes of liana leaves. American Naturalist, 110, 743-778.

Harper, J. L. (1977). Population Biology of Plants. Academic Press, London.

Horwitz, C. C. & Schemske, D. W. (1986). Seed dispersal of a neotropical myrmecochore: variation in removal rates and dispersal distance. Biotropica, 18, 319-23.

Howe, H. F. (1984). Constraints on the evolution of mutualisms. The American Naturalist, 123, 764-77.

Howe, H. F. & Smallwood, J. (1982). Ecology of seed dispersal. Annual Review of Ecology and Systematics, 13, 201-28.

Loveless, A. R. (1962). Further evidence to support a nutritional interpretation of sclerophylly. Annals of Botany, 26, 551-561

Majer, J. D. (1982). Ant-plant interactions in the Darling Botanical District of Western Australia. Ant-plant interactions in Australia. (Ed. by R. C. Buckley), pp.45-61.Dr. W. Junk Publishers, The Hague.

Majer, J. D. & Lamont, B. B. (1985). Removal of seed of *Grevillea pteridifolia* (Proteaceae) by ants. Australian Journal of Botany, 33, 611-18.

Midgley, J. & Bond, W. (1989). Leaf size and inflorescence size may be allometrically related traits. Oecologia, 78, 427-29.

Milewski, A. V. & Bond, W. J. (1982). Convergence of myrmecochory in mediterranean Australia and South Africa. Ant-plant interactions in Australia. (Ed. by R. C. Buckley),pp.89-98.Dr. W. Junk Publishers, The Hague.

Pierce, S. M. & Cowling, R. M. (1984). Phenology of fynbos, renosterveld and subtropical thicket in the south eastern Cape. South African Journal of Botany, 3, 1-16.

Rice, B. & Westoby, M. (1986). Evidence against the hypothesis that ant-dispersed seeds reach nutrient-enriched microsites. Ecology, 67, 1270-74.

Siegel, S. (1956). Nonparametric Statistics. For the Behavioural Sciences. McGraw-Hill, London.

Sinnott, E. W. (1921). The relation between body size and organ size in plants. American Naturalist, 640, 385-403.

Slingsby, P. & Bond, W. J. (1982). Of ants and proteas. African Wildlife, 36, 104-107.

Slingsby, P. & Bond, W. J. (1985). The influence of ants on the dispersal distance and seedling recruitment of Leucospermum conocarpodendron (L.) Buek. (Proteaceae). South African Journal of Botany, 51, 30-34.

Thompson, K. (1987). Seeds and seed banks. New Phytologist, 106, 23-34.

Van der Pijl, L. (1972). Principles of Dispersal in Higher Plants. Springer-Verlag, Berlin.

Westoby, M., Rice, B., Shelley, J. M., Haig, D. and Kohen, J. L. (1982). Plant's use of ants for dispersal at West Head New South Wales. Ant-plant interactions in Australia. (Ed. by R. C. Buckley),pp.75-87. Junk, The Hague.

Wheelwright, N. T. & Orians, G.H. (1982). Seed dispersal by animals: contrasts with pollen dispersal, problems of terminology, and constraints on coevolution. American Naturalist, 119, 402-13.

CHAPTER 6

Disturbance regimes as determinants of seed bank size and composition : evidence from grassland, fynbos and thicket on coastal dunes

ABSTRACT

Size and composition of soil-stored seed banks in three dune vegetation types, each subject to different disturbance regimes, were determined from counts of germinants from 50 soil cores from each type. Above-ground estimates of plant species cover in ten X 1 m^{-2} plots were used in determining vegetation/seed bank similarities. There was some support for the hypothesis that the most frequently disturbed community (grassland) would have the largest seed bank (4273 seed m^{-2}); and the least disturbed community (thicket) would have the smallest seed bank (ca. 429 seed m^{2}), if the contribution by a single herb species to the thicket seed bank is ignored. Hypotheses regarding seed bank/vegetation similarities were supported. Highest expected similarity (community coefficient CC=50%) as well as highest correlation in growth form/life-span composition between seed bank and aboveground vegetation were found in the frequently disturbed grassland. As predicted, lowest similarity was found in the undisturbed thicket (CC=13%), with no dominant shrub of tree species present in the seed bank. The fynbos community on the north-facing slope had intermediate-sized seed banks (1683 seed m^{-2}) with intermediate vegetation/seed bank similarity (CC=46%). This slope has initial floristic composition succession following fire. However, beneath the fynbos community on the south-

facing slope, seed banks were larger (4518 seed m^{-2}) but less similar to above-ground vegetation (CC=39%). This community difference was due to aspect-related differences in microclimates: post-fire regeneration on the south slope was initially dominated by many short-lived herb species in addition to longer-lived shrubs of mature fynbos. In the dune landscape, fynbos predominates. In the absence of disturbance, fynbos develops into thicket. Under frequent disturbance, grassland may be derived from fynbos. This successional gradient showed in an ordination (DCA) of the vegetation data but the similar pattern, expected in ordinations of seed bank data, was not found. Fynbos shrub species were absent from seed banks of both grassland and thicket, indicating low persistence. Comparisons with chaparral and Calluna heaths indicated that fynbos seed banks were relatively small. The low persistence and relatively small size of seed banks of the fire-prone fynbos may have implications for species richness in the Cape flora.

Nomenclature according to Bond & Goldblatt (1984).

INTRODUCTION

What conditions favour the accumulation of large seed banks in the soil and what determines the degree of similarity between the seed bank composition and the above-ground vegetation ? Many empirical studies on soil-stored seed banks have been reported from a wide range of habitats e.g. tundra (Roach 1983), tropical rainforests (Hopkins & Graham 1984), European heathland (Granstrom 1988); agricultural grassland (Major & Pyott 1966; Roberts 1981); and desert (Henderson, Redak & Petersen 1988). However, there have been few attempts at providing a cohesive theoretical framework for answering the two questions raised above, and most models have been limited primarily to annuals in temperate environments (Cohen 1966; Harper 1977; Thompson 1978; Thompson & Grime 1979). In this study I developed general hypotheses to explain the determinants of soil-stored seed bank size and composition. These hypotheses were then tested by examining the characteristics of soil-stored seed banks in three vegetation types all occurring in coastal dunes, and each subject to different disturbance regimes.

Thompson (1978) predicted that seed bank size would decline with increasing successional age and decreasing intensity of disturbance. More specifically I predicted that large seed banks would occur in communities subject to recurrent, large-scale disturbances (e.g. fire) where the life-spans of most component species are shorter than the average disturbance interval and where recruitment is confined to the immediate post-disturbance period (cf. Grubb 1988). Small seed banks would accumulate in vegetation such as forest, subject to small-scale disturbances (e.g. gap-phase regeneration - Brokaw 1985) and dominated by species with large fruits with directional vertebrate-dispersal (Howe & Smallwood 1982). Their fruits are prone to high predation levels and are therefore short-lived (Thompson 1987). Small seed banks would therefore be expected (see Hopkins & Graham 1984). Many of these species have seedling banks rather than seed banks (e.g. Vlahos & Bell 1986).

Theory regarding the relationship between seed bank composition and above-ground vegetation has generally been neglected, possibly because the relationship is complex. This complexity is clearly manifest in the large body of theory developed to describe succession (e.g. Pickett, Collins & Armesto 1987; Appendix 1). I predicted highest similarity between seed banks and vegetation in communities where recruitment is tightly coupled to disturbance (Grubb 1988) and where secondary succession follows the initial floristic model (Egler 1954). Conversely, lowest similarity would be expected where vegetation regenerates through a series of compositionally different successional phases after disturbance (e.g. Egler 1954; Connell & Slatyer 1977; Pickett et al. 1987). Low seed bank/vegetation similarity would also be expected in communities with gap-phase regeneration (cf. Brokaw 1985) dominated by long-lived species with large, short-lived seeds, with directional dispersal (Hopkins & Graham 1984).

The dune landscape of the south eastern Cape provides an excellent opportunity for testing hypotheses regarding seed banks and disturbance. It comprises a mosaic of different vegetation types, viz. grassland, fynbos and thicket (Table 1) occurring under the same environmental conditions on deep, well-drained sand (for details see Cowling 1984; Chapter 7). In the absence of grazing and burning, succession proceeds from grassland through fynbos to thicket (Cowling 1984; Chapter 7).

On the basis of the theory developed above, I made predictions regarding the composition and size of the seed bank in the vegetation types studied (Table 1). The grassland, maintained under frequent disturbances of grazing and mowing, would have the largest seed bank. Continuous small-scale disturbances created by grazing, hoof-action, and mole-hills, result in small open patches which would allow the continual recruitment of grassland species from soil-stored seed banks. Therefore I expected a close resemblance between the above- and below-ground composition in this community. The fynbos communities, subjected to less frequent disturbance (fire frequency ca. 10-20 yr), would have smaller seed banks which are less similar to the above-ground vegetation than in the grassland. On a moister south slope, which has a post-fire community of ephemerals not present in the mature vegetation, I expected lower seed bank/vegetation similarity than on the drier north slope which shows more strongly an initial floristic successional pathway (Appendix 1). Lastly, I predicted that the thicket seed bank would be the smallest and show least similarity with the above-ground vegetation. This community is dominated by trees and shrubs with large bird-dispersed fruits (Knight 1988) and is very stable unless threatened by rare, catastrophic fire.

Fynbos is the predominant vegetation type in the dune landscape and can be converted to grassland by frequent (four-year rotation) burning or bushcutting. Fynbos left undisturbed develops into thicket. In view of these processes (Cowling 1984; Chapter 7), I would expect the composition of the underlying seed banks to reflect these same successional gradients. I would expect to find grassland species in fynbos seed banks, and fynbos species in grassland and thicket seed banks.

METHODS

Study site

The study area lies in the coastal dunes in the Humansdorp (34°02'S, 24°47'E) region of the south eastern Cape. Physiographic, climatic, and edaphic details are given in Cowling (1984). The climate is warm temperate with mild temperatures : highest and lowest mean absolute maxima and mimima are 29.7°C (April) and 5.0°C (August) respectively, and a mean annual temperature of 17°C (Anon. 1942). Rain falls throughout the year (ca. 650 mm per annum) although the period from December to February is the driest, compounded by highest evapo-transpirational demands. The stabilized dune ridges run parallel to the direction of the prevailing south westerly winds. Soils are mostly deep, well-drained calcareous sands.

Four study sites (ca. 50 X 50 m), all within a radius of 0.5 km, were located in the dunefields. Each of the three vegetation types was represented, including two sites in fynbos :one on each of the north- and south-facing slopes of a dune valley. Hereafter these are referred to as north and south slopes respectively.

Vegetation and seed bank sampling

In each of the four sites, ten 1 m^2 quadrats were randomly located. In each quadrat the identity and projected canopy cover of all species were determined. Seed banks were sampled in each of the four sites by randomly locating 50 soil cores (50 mm diameter X 50 mm depth). Sampling was done in autumn (March 1987) so that samples reflected the soil seed stores accumulated by the onset of the wet winter season which is optimal for germination. Soil cores were stored in brown paper bags in the laboratory until August of the same year. Each core was then spread in a thin layer on the surface of a pot (150 mm diameter) filled with sterile dune sand (heated at 200°C for 2 h). These 200 pots were placed in an open-sided greenhouse under daily irrigation. The trials were monitored until March 1988. Ambient conditions monitored at an adjacent weather station followed closely temperatures experienced in the study area. Emergent seedlings were identified, counted and removed by uprooting or cutting. Although empty pots were not set up to account for the possible immigration of seed during the trial, no species appeared in the pots which were not recorded in the vegetation, discounting the possibility of contamination.

The problem of adequate sampling for seed banks has been reviewed (Roberts 1981; Forcella 1984; Thompson 1986;

Bigwood & Inouye 1988), and was further exacerbated by the logistics of limited greenhouse space. However, the advice of more, smaller samples (as opposed to fewer, larger samples) (Roberts 1981; Bigwood & Inouye 1988) was heeded. The minimum of 50 samples recommended by Thompson (1986); and a soil depth of 50 mm (Roberts 1981) were used as guidelines here.

All plant species were classified according to growth form/life-span groups of herbs or shrubs of three different life-spans as follows: HS = short-lived (1-3 yr) herbs; HM = medium-lived (4-15 yr) herbs; HL = long-lived (>15 yr) herbs; SS = short-lived (1-5 yr) shrubs; SM = medium-lived (6-30 yr) shrubs; SL = medium-lived (>30 yr) shrubs (Appendix 1). Spearman's rank correlation coefficient (r_s) was used to determine correlation of proportions of growth form/life-span groups between seed banks and vegetation types. Some seed bank samples contained zero seed counts, therefore values from 5 randomly selected replicates were combined and indicated as 10 X 5 combined samples. Differences in scale of sampling disallowed statistical comparisons between vegetation and seed bank samples. Hence the following comparisons were confined to between-vegetation and between-seed bank samples respectively. Species richness (S) was determined as the number of species per unit area. Equitability (H') or evenness was determined by the Shannon-Wiener function; and Simpson's index (C) was used to estimate the degree of dominance in samples (Whittaker 1972, Peet 1974).

As an index of similarity between each vegetation type and its seed bank, Sorenson's (1948) coefficient of community (CC) was used, where CC = $2S_a(S_j+S_k)$ in which S_a is the number of species shared by two samples, S_j is the number in the first and S_k the number in the second sample. In addition, Kendall's rank correlation coefficient (*r*) (Siegel 1956) was used to compare species' ranking in vegetation and seed banks

Detrended correspondence analysis (DCA) (Hill & Gauch 1980; Gauch 1982) was used to assess the floristic relationships along the landscape-level successional gradient for vegetation types and for seed bank samples from the different vegetation types. These analyses (vegetation and seed bank) were performed separately.

RESULTS

Above-ground vegetation

Eight of the ten dominants in the grassland were grasses (Poaceae) (Table 2). Fynbos was dominated by medium-lived, small-leaved shrubs (e.g. Metalasia muricata and Passerina vulgaris) and had a graminoid field layer dominated by Restionaceae (Ischyrolepis spp.). The north slope differed from the south in having as the dominant shrub, a large-leaved, sprouting thicket species, Olea exasperata. The thicket canopy was dominated by Pterocelastrus tricuspidatus with Sideroxylon inerme as the subdominant. Both species have bird-dispersed fruits (Knight 1988). Other thicket dominants were climbers and herbs of the field layer.

Size and composition of seed banks

Grassland and south slope fynbos had the largest seed banks, almost three times larger than those of the north slope fynbos which had the smallest (Table 3). The thicket seed bank was intermediate in size, but showed the highest variation. A single herb species, Lobelia erinus, which had the largest seed bank recorded of any species, comprised 87% of the thicket seed bank. If this species is ignored, the thicket had the smallest seed bank (429 seeds m^{-2}).

Dominant species in the seed banks were mostly present in their corresponding vegetation types, but this tendency decreased from the grassland through the north fynbos and south fynbos, to the thicket. Herbs were dominant in grassland and thicket seed banks but almost no species were common to both. Seeds of shrub species appeared only in the fynbos communities. The short-lived herb, *Vellereophyton vellereum*, was the only species represented in the seed banks of all vegetation types.

There were significant differences in diversity indices for both seed banks and above-ground vegetation among all vegetation types (Table 4). There was a general trend in both vegetation and seed bank diversity (S and H') for values to decline from grassland, through fynbos to thicket. An exception was south fynbos which had the second lowest vegetation diversity and the highest seed bank diversity. Values of equitability (H') and dominance concentration (C) significantly higher for thicket seed banks were significantly lower than for the other types owing to the overwhelming contribution of seeds of the short-lived herb, *Lobelia erinus*. In the above-ground vegetation lowest equitability and highest dominance values were recorded in the south slope fynbos, and in the thicket where a few woody species were dominant (Table 2).

There was a consistent trend for decreasing similarity from grassland through to thicket between the seed banks and the above-ground flora (Table 5). In terms of the proportions of species of different growth form/life-span groups, only the grassland showed a significant correlation between the above-ground vegetation and seed banks (Table 6). In the other three types, there were markedly higher numbers of short-lived herb and shrub species, and generally more herbs than shrubs in the seed banks than in the vegetation.

Ordinations of the vegetation and the seed banks of the four vegetation types displayed different trends (Fig. 1). In the vegetation ordination (Fig.1a), north and south slope fynbos communities were adjacent along the gradient; whilst in the seed bank ordination (Fig.1b), grassland and south slope fynbos were most closely located in the ordination space. These two last-mentioned seed bank communities both had an ephemeral short-lived flora (e.g. Ficinia filiformis, Crassula campestris) which is poorly represented on the north slope (Tables 3 & 6). The thicket community had a distinct flora both above- and below-ground (Fig. 1).

Table 1. Characteristics of vegetation types in study area.

Vegetation type	Formation [a]	Dominant life forms	Disturbance regime
Grassland	Closed grassland	graminoids, herbs	grazing, trampling, mole-hills
Fynbos North slope	Mid-high mid-dense shrubland	small-leaved shrubs, graminoids	fire frequency (10-20 yr)
Fynbos South slope	Mid-high closed shrubland	"	"
Thicket	Low forest/tall closed shrubland	large-leaved shrubs & trees	treefalls/ occasional fires

[a] Nomenclature according to Campbell *et al*. 1981.

Table 2. Cover, frequency and growth form/life-span of ten dominant species in four dune vegetation types. Data are means ± standard deviations. n = 10 X 1 m² samples. Dominant species which are also present in other vegetation types and/or their seed banks, are indicated by v and s respectively. Growth form/life-span classes are defined in text (see also Table 6). Asterisks denote introduced species.

		Grassland		Fynbos North slope		Fynbos South slope		Thicket	
	Growth form	Cover (%)	Freq. (%)	Cover (%)	Freq. (%)	Cover (%)	Freq. (%)	Cover (%)	Freq. (%)
Cynodon dactylon	HL	31 ±24	(100) s						
Arctopus echinatus	HL	26 ±13	(100)						
Sporobolus africanus	HM	13 ±12	(100) s						
Stenotaphrum secundatum	HL	12 ±13	(90) s						
Setaria flabellata	HL	4 ±4	(100)						
Eustachys paspaloides	HL	3 ±10	(20)						
Peucadenum sp.	HS	3 ±3	(90)						
Themeda triandra	HL	3 ±5	(50)						
Senecio hastatus	HS	2 ±1	(100) s						
Erharta calycina	HL	1 ±2	(70) s						
Metalasia muricata	SL			19 ±34	(30) s	34 ±30	(70) s		
Olea exasperata	SL			19 ±11	(90)				
Ischyrolepis eleocharis	HL			16 ±12	(90) s				
Passerina vulgaris	SM			15 ±18	(90) s	17 ±14	(80) s		
Euclea racemosa	SL			8 ±10	(60)				
Imperata cylindrica	HM			4 ±4	(70)	1 ±3	(20)		
Sutera microphylla	SM			3 ±3	(50)				
Indigofera zeyheri	SM			2 ±5	(50)				
Muraltia squarrosa	SM			2 ±3	(50) s				
Cassytha ciliata	HL			2 ±2	(80)				
Ischyrolepis leptocladus	HL				v	86 ±11	(100) s		
Tetraria cuspidata	HL					1 ±3	(20)		
Helichrysum cymosum	SM					1 ±2	(70) s		s
Cymbopogon marginatus	HM				v	1 ±3	(10)		
Helichrysum teretifolium	SM				vs	1 ±1	(70) s		
Asplenium adiantum-nigrum	HL					1 ±1	(50)		v
Carpobrotus fourcadei	HM				v	1 ±1	(40)		
Pterocelastrus tricuspidatus	SL							51 ±29	(100)
Leidesia obtusa	HS							32 ±22	(100)
Sideroxylon inerme	SL							2 ±6	(10)
Cassine peragua	SL							1 ±2	(50)
Senecio quinqueloba	HL							2 ±2	(50)
Erharta erecta	HM							1 ±2	(90) s
Solanum quadrangulare	SL						v	1 ±1	(60)
Stellaria media *	HS						s	1 ±1	(80) s
Secamone alpinii	SL							1 ±1	(80)
Cynanchum obtusifolium	HL							1 ±1	(50)

* Exotic

Table 3. Density, frequency and growth form/life-span of the ten dominant species in the seed banks of four dune vegetation types. Data are means ± standard deviations, n = 10 X 5 combined cores (see text). Dominant species listed which are also present in other seed banks and/or above-ground vegetation types, are indicated by s and v respectively. Growth form/life-span classes are defined in text (see also Table 6). Asterisks denote introduced species.

		Grassland		Fynbos North slope		Fynbos South slope		Thicket	
	Growth form	No.seed m-2	Frequ. (%)	No.seed m-2	Frequ. (%)	No.seed m-2	Frequ. (%)	No.seed m-2	Frequ. (%)
Ficinia filiformis	HM	1244 ±660	(100) v		sv	632 ±410	(100)		
Sporobolus africanus	HM	703 ±267	(100) v						
Avena fatua *	HS	581 ±498	(100) v						
Senecio hastatus	HS	234 ±232	(60) v						
Silene capensis	HS	234 ±237	(80) v				s		
Erharta calycina	HM	193 ±230	(60) v						
Dischisma ciliatum	HS	173 ±262	(70) v						
Crassula campestris	HS	153 ±263	(30) v	81 ±186	(20)	1499 ±425	(100) v		
Senecio inaequidens	HS	142 ±183	(60) v						s
Briza maxima *	HS	102 ±241	(30)						
Sutera campanulata	HS			561 ±368	(100)	183 ±135	(80)		
Passerina vulgaris	SM			173 ±144	(70) v	132 ±151	(50) v		
Metalasia muricata	SL			173 ±245	(60) v	81 ±99	(50) v		
Helichrysum asperum	SS			92 ±154	(40) v		s		
Sonderina tenuis	HS		sv	71 ±65	(60)		s		
Ficinia dunensis	HM		sv	71 ±112	(30)	397 ±259	(90)		
Anthospermum aethiopicum	SS			61 ±81	(40) v		sv		
Muraltia squarrosa	SM			30 ±65	(20) v				
Ischyrolepis eleocharis	HL			30 ±46	(30) v				
Crassula strigosa	HS					489 ±477	(80)		
Manulea parviflora	HS					326 ±202	(90)		
Helichrysum cymosum	SM					173 ±137	(90) v	51 ±68	(40)
Pentaschistis airoides	HS					153 ±172	(60)		
Lobelia erinus	HS							2988 ±3166	(90)
Stellaria media *	HS						s	102 ±111	(50) v
Unidentified herb	H?							82 ±127	(50)
Carpobrotus deliciosus	HM							71 ±91	(50)
Erharta erecta	HM							40 ±67	(30) v
Vellereophyton vellereum	HS		s		sv		sv	20 ±40	(20)
Silene bellidioides	HS							10 ±30	(10)
Senecio inaequidens	HS		sv					10 ±30	(10)
Erigeron capensis *	HS						s	10 ±30	(10)
Total no. seeds m-2 ± S.D.		4273 ± 970		1683 ± 820		4518 ± 953		3417 ± 3083 £	

£ see text for value minus Lobelia

* Exotic

Table 4. Diversity measures for seed banks and vegetation in four dune vegetation types: Total (Tot.) = number of species in combined samples; S = number of species per unit area; H' = Shannon-Wiener index and C = Simpson's index. Data are means ± standard deviations. $n = 10 \times 1\ m^2$ vegetation samples; $n = 10 \times 5$ combined seed bank samples (see text). One-way analysis of variance was used to test for significant differences among sample means; *** = $p \leq 0.001$. Different letters (^{A}, ^{B} etc.) indicate significant differences by Tukey's multiple range test.

	Grassland	Fynbos		Thicket	F-value
		North slope	South slope		
		Seed banks			
Tot.	29	23	32	13	
S	10.5 ± 0.60^{A}	7.10 ± 1.02^{B}	12.0 ± 0.52^{A}	3.80 ± 0.39^{C}	29.6 ***
H'	2.76 ± 0.13^{A}	2.23 ± 0.31^{A}	2.89 ± 0.09^{A}	0.91 ± 0.18^{B}	19.6 ***
C	0.20 ± 0.02^{A}	0.33 ± 0.09^{A}	0.19 ± 0.02^{A}	0.69 ± 0.07^{B}	15.0 ***
		Vegetation			
Tot.	43	35	30	19	
S	25.51 ± 2.11^{A}	11.02 ± 1.24^{B}	9.70 ± 0.45^{B}	7.70 ± 0.70^{B}	39.6 ***
H'	3.04 ± 0.03^{A}	2.29 ± 0.17^{A}	1.33 ± 0.11^{B}	1.39 ± 0.12^{B}	15.0 ***
C	0.22 ± 0.03^{A}	0.29 ± 0.03^{A}	0.49 ± 0.03^{B}	0.50 ± 0.03^{B}	17.6 ***

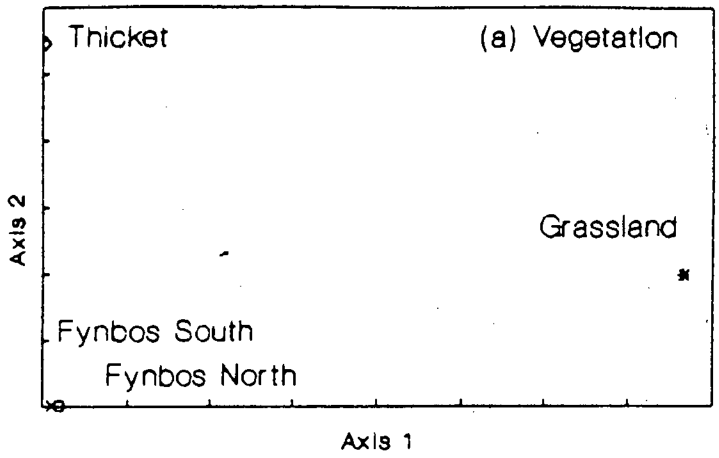
Table 5 . Community coefficient (CC) and Kendall's rank correlation coefficient (r) for comparisons between seed banks and vegetation of four dune vegetation types. n=no. species, * = $p \leq 0.05$; *** = $p \leq 0.001$; NS = not significant.

	Seed banks : Vegetation			
	Grassland	Fynbos		Thicket
		North slope	South slope	
CC	0.50	0.46	0.39	0.13
r	-0.06	-0.16	-0.26	-0.50
(n)	(54)	(44)	(50)	(30)
	NS	*	***	***

Table 6. Rank correlations (Spearman's r_s) of growth form/life-span composition of seed banks (Seed bank) and vegetation (Veg.) of dune vegetation types. Representatives of each growth form expressed as a percentage of the total number of species sampled. n = 10 X 1 m^2 vegetation samples; n = 50 seed bank cores. *=$p \leq 0.05$; NS = not significant.

Growth form/ life-span[a]	Grassland		Fynbos				Thicket	
			North slope		South slope			
	Seed bank	Veg.	Seed bank	Veg.	Seed bank	Veg.	Seed bank	Veg.
Herbs								
HS	52	44	39	6	53	20	69	21
HM	38	26	9	15	13	27	15	11
HL	7	19	4	21	3	10	0	16
Shrubs								
SS	3	5	17	12	13	3	0	0
SM	0	5	26	29	16	17	15	0
SL	0	2	4	18	3	23	0	53
r_s	0.96		-0.40		0.03		-0.02	
	*		NS		NS		NS	

[a] HS = short-lived (1-3 yr) herbs;
HM = medium-lived (4-15 yr) herbs;
HL = long-lived (>15 yr) herbs;
SS = short-lived (1-5 yr) shrubs;
SM = medium-lived (6-30 yr) shrubs;
SL = medium-lived (>30 yr) shrubs



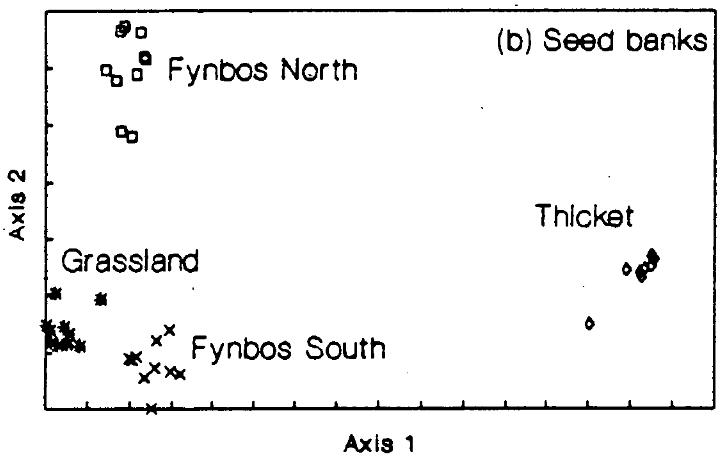


Figure 1. Ordination using detrended correspondence analysis of (a) vegetation and (b) seed banks of four dune vegetation types. In the vegetation ordination, sample points for each vegetation type were highly clustered and were therefore reduced to a single point each in the diagram.

DISCUSSION

Seed bank estimation

Determination by germination may not give an accurate reflection of seed banks, as germination cues supplied in the field e.g. fire, may be lacking (Mallik, Hobbs & Legg 1984). Although germination of dominant fynbos species was apparently unrelated to fire cues (Chapter 2), stimulation by other cues may have been required. Estimates of seed banks by germination were generally lower that those derived from direct, microscopic counts (Chapter 4).

Predictions for size of seed banks

As predicted by Thompson's (1978) disturbance/succession model, seed bank density generally declined from the frequently and heavily disturbed grassland, to the thicket which is subject to very occasional fire and gap-related disturbance. However, there were important deviations from these predictions, related to fynbos seed densities. Thompson's assumption of decreasing nutrient content of soils with increasing successional age does not hold for the study area, as, with increasing vegetation age, dune soils become more nutrient-rich with accumulating organic matter (Cowling 1984). Secondly, disturbance regime characteristics other than frequency are not considered in his scheme. As summed up by Zammit & Zedler (1988), very wide variation in spatial and temporal scale of disturbance, as well as in other factors such as seed production and small-scale variability in seed density, may mask the predicted trend. In this study, differences in disturbance regime included the small-scale disturbances in grassland, the wide-scale perturbation of fire in the fynbos, and the occasional gap-phase regeneration operating in the thicket. A further complicating factor was the exceptionally large contribution of Lobelia erinus to the thicket seed bank size.

The grassland seed bank, predicted to be the largest, was equivalent to the highest seed count recorded in south slope fynbos. The latter seed bank contained seeds of ephemeral pioneer species in addition to the longer-lived mature vegetation types. The thicket seed bank was the smallest as expected if the contribution (ca.87%) of a single herb species is ignored. The north slope fynbos was intermediate in size as predicted for the intermediate frequency of disturbance.

Seed bank/vegetation similarity

The highest similarity between seed bank and vegetation was recorded in the grassland (CC=50%). Growth form/life-span composition between grassland seed bank and vegetation was also very highly correlated, with both sharing a preponderance of perennial grasses and short-lived herbs. Grubb (1988) described the degree of coupling between recruitment and disturbance in perennial grasslands as "variable", with close coupling in dune grasslands but loose coupling in chalk grasslands. The grasslands studied here fitted neither of these types (P. J. Grubb, 1989, pers.comm.). The presence of the short-lived herbs in the grassland seed bank is the result of opportunistic colonization of open patches in the grass canopy due to continual disturbances associated with grazing and mole activities.

As predicted, the north facing fynbos had relatively more species in common with its seed bank than did the south facing fynbos. This agreed with the initial floristic pathway of succession recorded there after a fire (Appendix 1). Although above-ground species diversity did not differ between slopes, the south slope seed banks showed higher species diversity. This was due to a preponderance of many short-lived herb species in addition to the longer-lived shrub species characteristic of mature fynbos apparent in the post-fire succession (Appendix 1). These differences in the seed bank/vegetation relationships were probably due to aspect-related microclimates, with the cooler and moister south-facing aspect allowing the short term establishment of a mesophytic herb community.

The lowest seed bank/vegetation similarity, was found in the thicket (CC = 13%). This was due to a predominance of short-lived herb species and an absence of tree species in the seed bank, a common finding in studies of forests (see references in Vlahos & Bell 1986). The seeds of the short-lived herbs probably persist for very long periods in the soil (cf. Type IV seed bank *sensu* Thompson & Grime 1979). For example, seeds of the cosmopolitan herb, *Stellaria media*, recorded in the thicket soils, can persist up to 600 years (Cook 1980).

Comparisons with other systems

Unfortunately comparisons of seed banks of analogous communities are limited: soil-stored seed banks of Australian temperate heathlands (kwongan), the closest analogue to fynbos, have yet to be studied. The fire-prone *Calluna* heath, weakly analogous to fynbos, has community seed banks of ca. 12148 - 6510 seeds m^{-2} (from Mallik, Hobbs & Legg 1984) while nine year-old chaparral communities have seed banks of ca. 8276 seeds m^{-2} (from Zammit & Zedler 1988). Densities of individual species in chaparral and *Calluna* heath (ca. 2000-3000 seeds m^{-2} in ten year-old stands - Zammit & Zedler 1988) are higher than, or equivalent to, entire fynbos community seed banks :1000-1500 and 3500-5400 seeds m^{-2} for north and south slopes respectively. Therefore, fynbos seed banks were relatively small. Seed characteristics also differed widely. Dominant species of *Arctostaphylos* and *Ceanothus* in chaparral are said to be long-lived (Keeley 1987) although seed longevities are not quoted. Seed banks of *Calluna vulgaris* of ca. 50 years old were still viable (Willems 1988). In contrast, some dune fynbos shrubs showed reduced viability after about three years (Chapter 2). Therefore, seed banks of fynbos shrubs appeared to behave more closely to *Ceanothus greggii*, an unusual species in relation to other chaparral shrubs in failing to accumulate seeds over time, and having post-fire recruitment determined by the vagaries of the previous year's crop (Keeley 1977; Zammit & Zedler 1988).

Landscape-level successional gradient

The seed banks underlying each vegetation type failed to show the same landscape-level successional gradient as the above-ground vegetation. Each seed bank emerged as a discrete community. Furthermore, different trends became apparent in the respective ordinations of vegetation and seed banks. Although the two above-ground fynbos communities had the most similar above-ground floras, in terms of seed bank composition, the south facing fynbos seed bank was more closely related to the grassland seed bank. Both communities shared a preponderance of the same short and medium-lived herbs (e.g. *Crassula campestris*, *Ficinia filiformis*, *Silene capensis*). Reference to the post-fire successional behaviour of these communities (Appendix 1) also cast light on this apparent anomaly. On the south slope, the early colonizing species comprised mainly numerous ephemeral herbs that are probably able to establish and reproduce due to the cooler and moister conditions there (see Chapter 3). Eventually these shorter-lived species die out in mature south fynbos , but not before reproducing and replenishing the seed banks. However, they play an important role early in post-fire succession by outshading seedlings of longer-lived species and thus play a role in determining ultimate community structure (Chapters 3 and 7).

The lack of fynbos shrub species in seed banks of the other vegetation types is a further consequence of the disturbance regime. Shrub species seeds must have been depleted by earlier management practices of frequent (<4 yr) burning and or bushcutting. Such a disturbance regime would eliminate shrubs before reproductive age and seed banks would gradually be depleted by germination and seed ageing (Chapter 2). Intermediate disturbance, as experienced in the fynbos, would allow the persistence of shrub species through a cycle of reproducing adult plants maintaining viable seed banks. Infrequent disturbance (>50 yr) which allows thicket formation, would result in senescence of adult fynbos shrubs, inhibition of germination under the canopy-induced microclimate, and ultimately decay of their seed banks. In this respect dune fynbos shrubs function in a completely different way from their structural analogues occurring in European *Calluna* heath and Californian chaparral. *Calluna vulgaris* is a dominant heathland shrub which produces a very large soil-stored seed bank which can persist some 50 years under succession by forest. After forest removal, these soil stores give rise to *Calluna* seedlings (Willems 1988). In Californian chaparral, species of the dominant genus, *Arctostaphylos*, have long life-spans and most importantly, produce long-lived seeds and considerable seed banks which are dependable in 90 year old stands (Keeley 1977, 1987). *Adenostoma fasciculatum*, another chaparral dominant, showed increasing seed bank size during 80 years of development (Zammit & Zedler 1988).

The important finding in this study was that dune fynbos community seed banks were relatively small. Secondly, seed banks appeared to be relatively short-lived, not persisting in either the earlier successional grassland nor the later thicket phase assuming the successional model outlined earlier (cf. persistence of *Calluna* in forest - Willems 1988). In contrast, communities such as in chaparral, with species with persistent, reliable and sizeable seed banks which ensure community replacement after disturbance, would have lower species diversity. Small and relatively transient soil-stored seed banks in a fire-prone environment might help to explain the very high species diversity in fynbos (Chapter 4).

ACKNOWLEDGEMENTS

I thank K. Wienand for technical assistance. Valuable comments were made by by R. M. Cowling, P. Manders and E. J. Moll. The use of nursery facilities at the Kirstenbosch Botanic Gardens is gratefully acknowledged. This study forms part of the Fynbos Biome Project and was funded by FRD, CSIR, through the University of Cape Town.

REFERENCES

Anon. (1942). Weather on the coast of southern Africa. Part 3. Mossel Bay to East London. Government Printer, Pretoria.

Bond, P. & Goldblatt, P. (1984). Plants of the Cape Flora: a Descriptive Catalogue. Journal of South African Botany Supplementary Volume, 13. Kirstenbosch, Claremont.

Bigwood, D. W. & Inouye, D. W. (1988). Spatial pattern analysis of seed banks: an improved method and optimized sampling. Ecology, 69, 497-507.

Brokaw, N.V.L. (1985). see p.248.

Campbell, B. M., Cowling, R. M., Bond, W. & Kruger, F. J. (1981). Structural characterization of vegetation in the Fynbos Biome. South African National Scientific Programmes Report No. 52. CSIR, Pretoria.

Cohen, D. (1966). Optimizing reproduction in a randomly varying environment. Journal of Theoretical Biology, 12, 119-129.

Cook, R. (1980). The biology of seeds in the soil. Demography and Evolution in Plant Populations. (Ed. by O. T. Solbrig), pp. 107-188. Blackwell, Oxford.

Connell, J. H. & Slatyer, R. O. (1977). Mechanisms of succession in natural communities and their role in community stability and organization. American Naturalist, 111, 119-144.

Cowling, R. M. (1984). A syntaxonomic and synecological study in the Humansdorp region of the fynbos biome. Bothalia, 15, 175-227.

Egler, F. E. (1954). Vegetation science concepts I. Initial floristic composition, a factor in old-field vegetation development. Vegetatio, 4, 412-417.

Forcella, F. (1984). A species-are curve for buried viable seeds. Australian Journal of Agricultural Research, 35, 645-52.

Gauch, H. G. (1982). Multivariate Analysis in Community Ecology. Cambridge University Press, Cambridge.

Granstrom, A. (1988). Seed banks at six open and afforested heathland sites in southern Sweden. Journal of Applied Ecology, 25, 297-306.

Grubb, P. J. (1988). The uncoupling of disturbance and recruitment, two kinds of seed bank, and persistence of plant populations at the regional and local scales. _Annales Zoologici Fennici_, _25_, 23-36.

Harper, J. L. (1977). _The Population Biology of Plants_. Academic Press, London.

Henderson, C. B., Petersen K. E. & Redak, R. A. (1988). Spatial and temporal patterns in the seed bank and vegetation of a desert grassland community. _Journal of Ecology_, _76_, 717-728.

Hill, M. O. & Gauch, H. G. (1980). Detrended correspondence analysis: an improved ordination technique. _Vegetatio_, _42_, 47-58.

Hopkins, M. S. & Graham, A. W. (1984). The role of soil seed banks in regeneration in canopy gaps in Australian tropical lowland rainforest - preliminary field experiments. _The Malaysian Forester_, _47_, 146-158.

Howe, H. F & Smallwood, J. (1982). Ecology of seed dispersal. _Annual Review of Ecology and Systematics_, _13_, 201-28.

Keeley, J. E. (1977). Seed production, seed populations in soil, and seedling production after fire for two congeneric pairs of sprouting and nonsprouting chaparral shrubs. Ecology, 58, 820-829.

Keeley, J. E. (1987). Ten years of change in seed banks of the chaparral shrubs, Arctostaphylos glauca and A. glandulosa. American Midland Naturalist, 117, 446-48.

Knight, R. S. (1988). Aspects of plant dispersal in the southwestern Cape with particular reference to the roles of birds as dispersal agents. Ph.D. thesis, University of Cape Town.

Major, J. & Pyott, W. T. (1966). Buried, viable seeds in two California bunchgrass sites and their bearing on the definition of a flora. Vegetatio, 13, 253-282.

Mallik, A. U. , Hobbs R. J. & Legg, C. J. (1984). Seed dynamics in Calluna-Arctostaphylos heath in north-eastern Scotland. Journal of Ecology, 72, 855-871.

Peet R. K. (1974). The measurement of species diversity. Annual Review of Ecology and Systematics, 5, 285-307.

Pickett, S. T. A., Collins, S. L. & Armesto, J. J. (1987). Models, mechanisms and pathways of succession. Botanical Review, 53, 335-371.

Roach, D. A. (1983). Buried seed and standing vegetation in two adjacent tundra habitats, northern Alaska. Oecologia, 60, 359-364.

Roberts, H. A. (1981). Seed banks in soils. Advances in Applied Biology, 6, 1-55.

Siegel, S. (1956). Nonparametric Statistics for the Behavioural Sciences. McGraw-Hill, Johannesburg.

Sorenson, T. (1948). A method of establishing groups of equal amplitude in plant sociology based on similarity in species content. Biologiske Skrifter - Kongelige Danske Videnskabernes Selskab, 5, 1-34.

Thompson, K. (1978). The occurrence of buried viable seeds in relation to environmental gradients. Journal of Biogeography, 5, 425-430.

Thompson, K. (1986). Small-scale heterogeneity in the seed bank of an acidic grassland. Journal of Ecology, 74, 733-738.

Thompson, K. (1987). Seeds and seed banks. New Phytologist (Supplement), 106, 23-34.

Thompson, K. & Grime, J. P. (1979). Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. Journal of Ecology, 67, 893-921.

Vlahos, S. & Bell, D. T. (1986). Soil seed-bank components of the northern jarrah forest of Western Australia. Australian Journal of Ecology, 11, 171-179.

Whittaker R. H. (1972). Evolution and measurement of species diversity. Taxon, 21, 213-251.

Willems, J. H. (1988). Soil seed bank and regeneration of a Calluna vulgaris community after forest clearing. Acta Botanica Neerlandica, 37, 313-320.

Zammit, C. A. & Zedler, P. H. (1988). The influence of dominant shrubs, fire, and time since fire on soil seed banks in mixed chaparral. Vegetatio, 75, 175-187.

CHAPTER 7

SYNTHESIS

Understanding pattern and process in a coastal dune landscape : a synthesis of fynbos life-history, population, and community studies

ABSTRACT

Individual, life-history and population attributes in response to disturbance were used to explain landscape-level vegetation patterns, and structure of fynbos communities on the coastal dunes in the south eastern Cape. The mosaic and mixture of vegetation types in the dune landscape was attributed to a spatial successional sequence from grassland, through fynbos to thicket. Each vegetation type remains relatively stable under defined disturbance regimes : grassland under continuous grazing and fire/bushcutting on a 2-4 year rotation; fynbos under fire/bushcutting on ca. 12 year rotation; and thicket under occasional fires (frequency >50 yr) and gap disturbance. The responses of the dominant species of the vegetation types to changes in disturbance regimes were described, with particular emphasis on the fynbos. Detailed studies of six fynbos species, all small-leaved, small-seeded, non-resprouting shrubs, indicated much variation in life-history attributes. These life-history attributes explained the spatial and temporal distribution of the selected fynbos species in the seasonally dry and fire-prone dune landscape. Although the study species co-occurred in some sites, each showed slightly different distribution patterns across the dune landscape. Their distribution was a function of each species' life-span and vegetation age. Agathosma apiculata and A. stenopetala

showed some overlap in distribution, with non-overlap due to differences in life-span and microsite preference. Wide dispersal, high germinability and opportunistic colonization of gaps explained the wide distribution of Felicia echinata in the landscape in spite of a short life-span. Muraltia squarrosa occurred mainly in younger fynbos communities, its distribution possibly restricted by the activities of seed dispersing ants under open canopies, and by its shorter (ca.15 yr) lifespan relative to other species. Passerina vulgaris had the widest distribution across the study area. It was able to persist in newly established grasslands by recruitment from soil-stored seed banks, which were large and persistent relative to the other study species. Metalasia muricata, was opportunistic in producing many, wind-dispersed seed with high germinability, but it also had the longest life-span, enabling persistence of the shrub in the early succession into thicket. Variation in life-history attributes such as seed production, germinability, seed predation etc. would result in varying proportions of species regenerating after disturbance, hence explaining the varying dominance of species in the fynbos community.

INTRODUCTION

The key question addressed in this study was: how are fynbos species and communities distributed spatially and temporally in a coastal dune landscape? Fynbos communities in South Coast Dune Fynbos (sensu Cowling 1984) are unlike most Cape fynbos communities, in that, depending on the disturbance regime, they form a mixture and mosaic with grassland and subtropical thicket. This study investigated the determinants of these vegetation types in the landscape. It also considered the landscape-level implications of the life-history traits and population processes of several, non-resprouting shrubs (Table 1) dominant in South Coast Dune Fynbos (Chapters 2-6, Appendix 1).

Central to an understanding of community structure of plant communities are the dynamics of succession (Huston & Smith 1987). In spite of the lack of a single cohesive theory for succession (Pickett, Collins & Armesto 1987; Walker & Chapin 1987) there is wide agreement that life-history attributes are important in understanding plant responses to disturbances (e.g. Drury & Nisbet 1973; Pickett 1976; Connell & Slatyer 1977; Glenn-Lewin 1980; Noble & Slatyer 1980; Peet & Christenen 1980; Horn 1981; Denslow 1985). In fynbos, most life-history studies have concentrated on members of the Proteaceae (e.g. Le Maitre 1988) and the small-leaved, small-seeded, non-resprouting species have been neglected. In vegetation prone to recurrent disturbance, adaptive life-history traits for pre-emptive competition are required to ensure occupation and persistence at an open site. Hence the importance of studying plant adaptations to the occupation of post-disturbance space (Werner 1979).

The study asked the specific questions : what determines the spatial distribution of different vegetation types in the dune landscape and do they exist as stages in a successional gradient from grassland through fynbos to thicket as proposed by Cowling (1984)? How do the dominant, non-resprouting fynbos species co-occur in fynbos communities, and what determines their varying proportions in the landscape? What determines their abundance in the other dune vegetation types of grassland and thicket ? How do these fynbos species respond to fire and the artificial disturbance of bushcutting as practised by graziers to improve grazing ?

METHODS

Study area

The study area is located in the Humansdorp (34°02'S, 24°47'E) region of the south eastern Cape, in the coastal dunefields lying between the Tsitsikamma and Gamtoos Rivers (Fig. 1). The dunes are east-west trending parabolic wind-rift ridges with breached noses, up to 12 km long and rising up to 177 m at the highest point in the west (Tinley 1985).

The climate is mild with an average annual temperature of 17°C at Cape St. Francis, the centre of the study area (see Fig.1 and Chapter 3). Frost is rare, and the highest temperatures are experienced in autumn when "berg" (fohn-like) winds raise temperatures to ca.40°C. Annual rainfall ranges from ca. 900 mm in the west to 500 mm in the east. Rain can fall at any time of the year, but the summer/autumn periods are the driest. Details are given elsewhere of the physiography and geology (Cowling 1984) and of the climate (Chapter 3).

Sampling

Data were re-analysed from an earlier study (Cowling 1984) in which forty-six plots (10X10 m) were located in the study area to include the full range of vegetation of the dune coastline between the Tsitsikamma and Gamtoos Rivers (Fig. 1). In each plot, projected canopy cover of each species was estimated as a percentage. Also recorded were biotic factors including post-disturbance vegetation age, litter, and site variables of soil depth, rock cover (%), rainfall (mm yr^{-1}), and altitude. Radiant flux density (J m^{-2} day^{-1}) at each site was determined as a function of degree of slope and aspect for 34°S (see Schulze 1975). Selected data are given in Table 2. From the soil cores sampled at each of the 46 plots, nineteen were randomly selected for chemical analysis (Cowling 1984).

In order to identify successional and environmental factors as determinants of landscape-level vegetation patterns, the data were subjected to detrended correspondence analysis (DCA - Hill & Gauch 1980). The plots on the ordination diagram were identified as belonging to different communities which had been classified by two-way indicator species analysis (Hill 1979) in Cowling (1984). For each plot, species were categorized into four classes of growth form: graminoids (grasses); small-leaved shrubs (leptophyll and smaller); large-leaved shrubs (nanophyll and larger); and other (herbs, reed-like Restionaceae etc.). The percentage of projected canopy cover contributed by each growth form was then determined.

The resulting ordination scores for plots for the first and second axes were correlated (Spearman's rank $\underline{r_s}$) with biotic (vegetation age, litter) and environmental data (rock cover, annual rainfall, altitude) for each plot.

Although Wartenberg, Ferson & Rohlf (1987) have advised against the use of DCA, Peet *et al*. (1988) convincingly argued that, in spite of imperfections, it is an efficient tool for summarizing community variation relative to underlying gradients.

Soil nutrient data (pH, Na, K, Ca, Mg, exchangeable cations, oxidizable carbon, N, P) were grouped into vegetation types according to the classification of plots as described above. Significant differences amongst vegetation types were tested by the Kruskal-Wallis one-way analysis of variance by ranks due to unequal numbers of replicates.

The six species selected for study are dominants in the fynbos, which predominates in the dune landscape. Further, they are members of important genera well-represented in the Cape Flora (see Table 1). The study species' presence was superimposed on the plots in the ordination diagram to show their occurrence in the landscape. In addition the cover-abundance values of the study species recorded in the plots were tabulated.

RESULTS

The communities identified in the two-way indicator analysis (see Table 2; from Cowling 1984) did not separate out as distinct communities, but were ordered across the two-dimensional ordination space (Fig.2). The vegetation types of grassland, fynbos, fynbos/thicket and thicket were apparent in the proportion of growth forms (ie. the projected canopy cover of grasses, small-leaved shrubs, large-leaved shrub/trees) within each plot (Fig. 2). The plots were ordered in the ordination space in a continuum from grassland through fynbos to thicket along the first ordination axis. This first ordination axis was strongly negatively correlated with both post-disturbance vegetation age and litter (Table 3). Both the first and second axes were positively correlated with annual rainfall. (Values of vegetation age, rock cover, litter cover, annual rainfall, radiant density flux and altitude are given in Table 2).

Analysis of the study species' presence from the plot data showed that, although they co-occurred in some plots, each species showed a particular pattern of distribution across the landscape (Fig. 3). *Passerina* had the widest distribution, being the only species to extend into the grassland plots. Its extension into dune fynbos/thicket plots was shared with *Metalasia* and to a lesser extent, *Felicia* and *Agathosma apiculata*. The most restricted species found mainly in the younger fynbos community were *Agathosma stenopetala* and *Muraltia*.

Analysis for differences in nutrient status of soils from the different vegetation types were not significantly different except for levels of Na, K and Mg, although sum of exchangeable cations (S-value) showed no differences (Table 4).

Table 1. Characteristics of the study species.

Species [a]	Family	No.spp.[b] in Cape flora	Distribution[b]	Shrub height (m)	Shrub longevity (yr)	Pollin- ation	Dispersal	Seed [d] prodn	Seed mass (mg) (x±SE)
Agathosma apiculata	Rutaceae	135	Riversdale to Port Elizabeth	0.8	25	Insect	Ballistic and myrmecochory	May-Oct	4.6±0.2 (n=38)
Agathosma stenopetala	Rutaceae	135	Humansdorp to Port Elizabeth	0.6	20	Insect	Ballistic and myrmecochory	Sep-Dec	2.1±0.03 (n=50)
Felicia echinata	Asteraceae	83	Mossel Bay to Port Alfred	0.1	5	Insect	Wind	May-Sep	0.4±0.03 (n=300)
Metalasia muricata	Asteraceae	50	Cape to Drakensberg	2.3	>30	Insect	Wind	May-Jul	0.6±0.03 (n=50)
Muraltia squarrosa	Polygalaceae	115	Mossel Bay to Port Elizabeth	0.8	14	Insect/[c] self	Myrmecochory	All year	3.7±0.1 (n=50)
Passerina vulgaris	Thymelaeaceae	18	Cape to Drakensberg	1.5	14	Wind	Unspecialized	Oct-Feb	1.3±0.03 (n=47)

[a] Nomenclature after Bond & Goldblatt (1984).
[b] From Bond & Goldblatt (1984).
[c] Levyns (1954).
[d] Pierce & Cowling (1984) and this study.

Table 2. South eastern Cape dune communities, constancy values of dominant species, and environmental variables. Communities derived from a classification (Cowling 1984) of 46 10X10 m plots by means of two-way indicator species analysis (Hill 1979) (from Cowling 1984). Environmental data are means ± standard deviations. Frequency on 1-5 scale: 1=1-20%; 2=21-40%; 3=41-60%; 4=61-80%; 5=>81%.

	Dune Grassland	Dune Fynbos	Dune Fynbos/ Thicket	Dune Thicket
Community structural formation [a]	Closed grassland	Mid-high mid-dense shrubland	Mid-high closed shrubland	Low forest/ tall closed shrubland
Dominant species				
Stenotaphrum secundatum	5	1	1	-
Themeda triandra	5	2	-	-
Cynodon dactylon	5	2	1	-
Ischyrolepis eleocharis [b]	3	5	4	-
Felicia echinata	2	4	4	-
Tetraria cuspidata	2	4	2	-
Passerina vulgaris	3	4	4	-
Euclea racemosa	2	4	5	-
Anthospermum aethiopicum	4	4	3	-
Agathosma stenopetala	-	4	1	-
Muraltia squarrosa	-	4	2	-
Olea exasperata	-	2	5	3
Agathosma apiculata	-	1	3	-
Maytenus procumbens	-	-	5	-
Sideroxylon inerme	-	-	-	5
Pterocelastrus tricuspidatus	-	-	-	5
Cassine aethiopica	-	-	-	5
Scutia myrtina	-	-	-	4
Environmental variables	(n=4)	(n=13)	(n=12)	(n=17)
Soil depth (m)	>1	>1	>1	>1
Post-disturbance vegetation age (yr)	2±0	7±3	8±5	45±9 [c]
Rock cover (%)	0	4±6	3±5	0.02±0.04
Litter cover (%)	17±14	18±18	37±22	66±21
Rainfall (mm yr^{-1}) [d]	722±85	686±85	662±26	611±110
Radiant density flux (10^6 J m^{-2} day^{-1}) [e]	11.4±0.3	9.8±2.7	11.3±2.8	10.0±2.6
Altitude (m)	43±25	36±29	23±14	26±17

[a] Structural classification according to Campbell *et al.* (1981)

[b] Formerly *Restio eleocharis*

[c] Many plots had not been burnt for more than 50 years. This age was arbitrarily taken as the maximum.

[d] From 1:250 000 mean annual rainfall maps

[e] Radiation loads at 34°S at midwinter for different combinations of slope angle and aspect (see Schulze 1975).

Table 3. Correlation analysis (Spearman's rank $\underline{r_s}$) of ordination axis values with environmental variables using . n=46; *=$p \leq 0.05$; **=$p \leq 0.01$; ***$p \leq 0.001$; NS= not significant. See Table 1 for means of environmental data for each community.

Environmental variable	Axis 1 $\underline{r_s}$	Sig.	Axis 2 $\underline{r_s}$	Sig.
Veg age	-0.88	***	-0.02	NS
Rock cover	0.09	NS	0.12	NS
Litter cover	-0.62	***	0.10	NS
Annual rainfall	0.43	**	0.31	*
Radiant density flux	0.16	NS	-0.27	NS
Altitude	0.20	NS	0.38	**

Table 4. Soil nutrient data from plots in south eastern Cape (Humansdorp) dune communities. Data (means ± standard deviations) are from Cowling (1984). Differences tested by Kruskal-Wallis one-way analysis of variance by ranks (*H*) ; *=$p \leq 0.05$; NS = not significant.

		Exchangeable cations[a]							
	pH	Na (ppm)	K (ppm)	Ca (ppm)	Mg (ppm)	S-[b] value (meq)	Oxidizable[c] carbon (%)	Total[d] nitrogen (%)	Available[e] phosphorus (ppm)
Grassland (n=3)	7.0±1.2	79±43	114±17	2408±1208	267± 59	14±6	6±1	0.246±0.071	19± 5
Fynbos (n=6)	7.4±0.6	45±19	50±19	2168±765	105± 50	11±4	3±1	0.123±0.063	17±13
Fynbos/ thicket (n=4)	7.5±0.2	74±34	89±69	2454±615	192±140	14±4	7±5	0.250±0.171	34±21
Thicket (n=6)	7.2±0.5	113±43	103±63	2300±1045	436±218	16±4	7±3	0.243±0.116	19± 6
H	2.3	9.1	8.4	0.6	9.7	3.4	5.7	6.0	1.4
Sig.	NS	*	*	NS	*	NS	NS	NS	NS

[a] Determined in 1 N NH_4

[b] Sum of exchangeable cations

[c] Walkley-Black method

[d] Kjeldahl

[e] Modified Olsen (alkali extraction, pH 8)

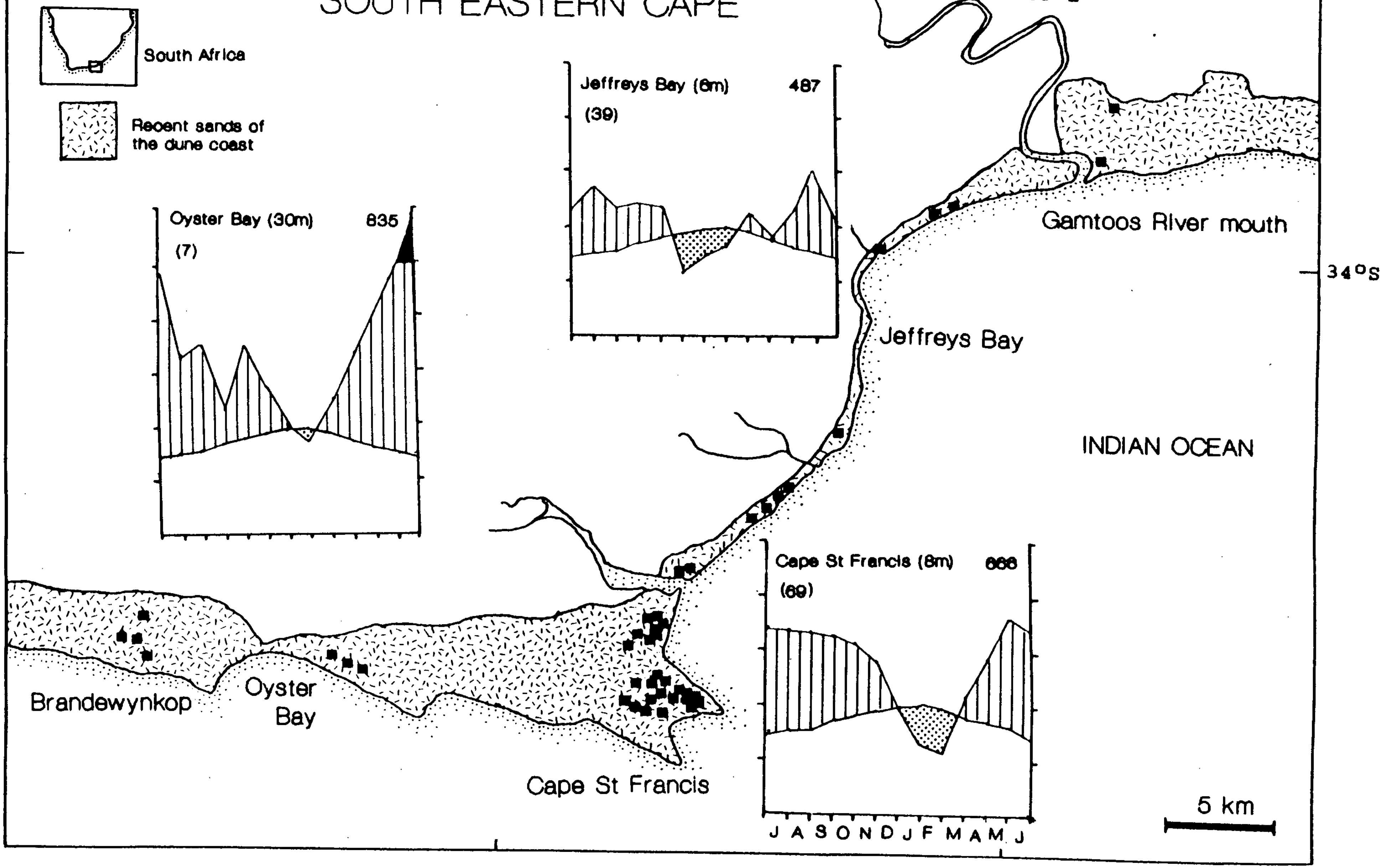


Fig. 1. Map of study area showing location of plots in the study area, and climate data for the area.

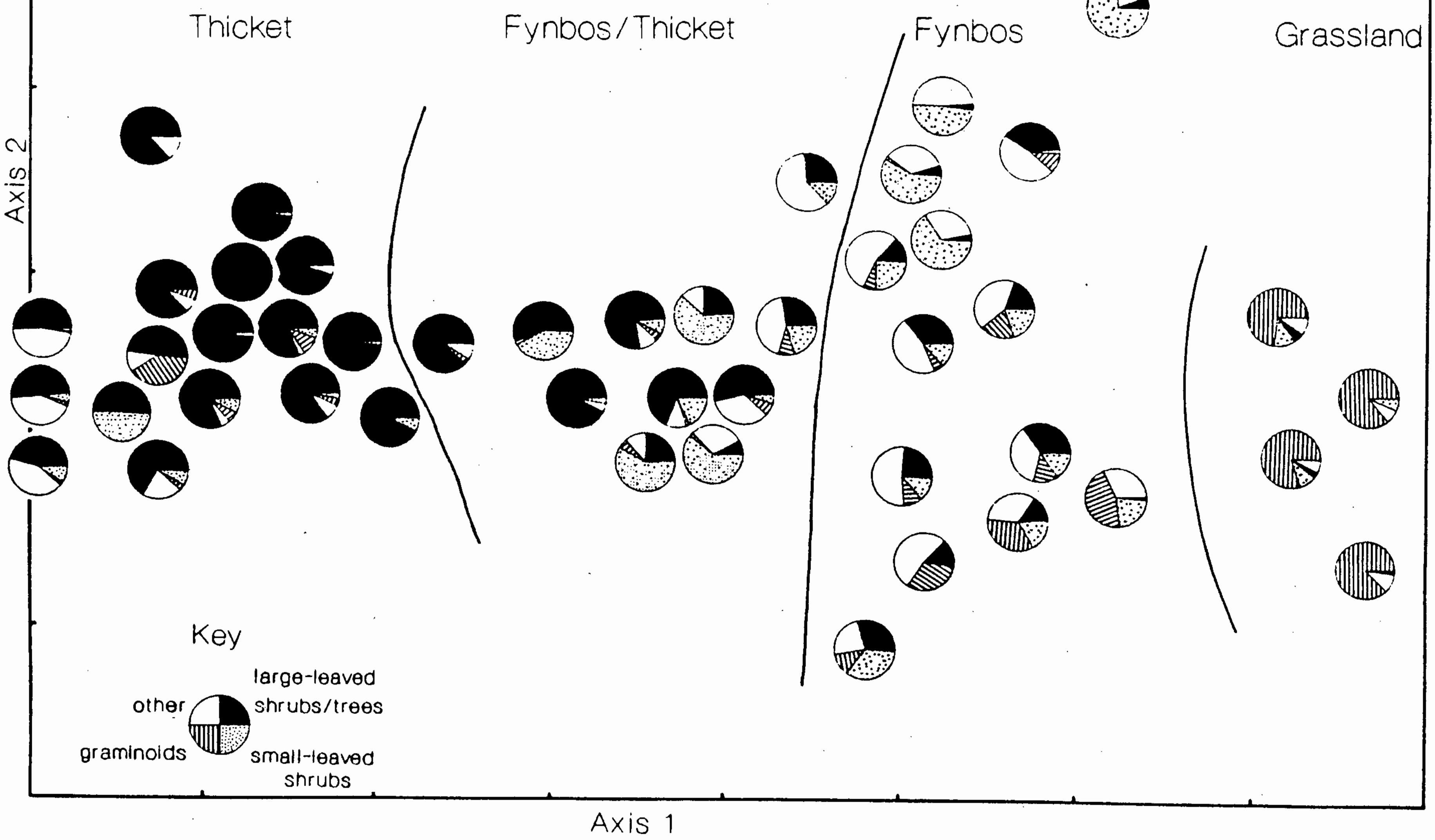


Fig. 2. Ordination diagram of plots in different communities identified in Cowling (1984). Proportions of growth forms: grasses, small-leaved shrubs and large-leaved shrubs/trees indicated for each plot. Large proportions of growth form class "other" are due to a preponderance of succulents in the three furthermost Thicket plots, and a preponderance of reed-like members of the Restionaceae in the Fynbos plots.

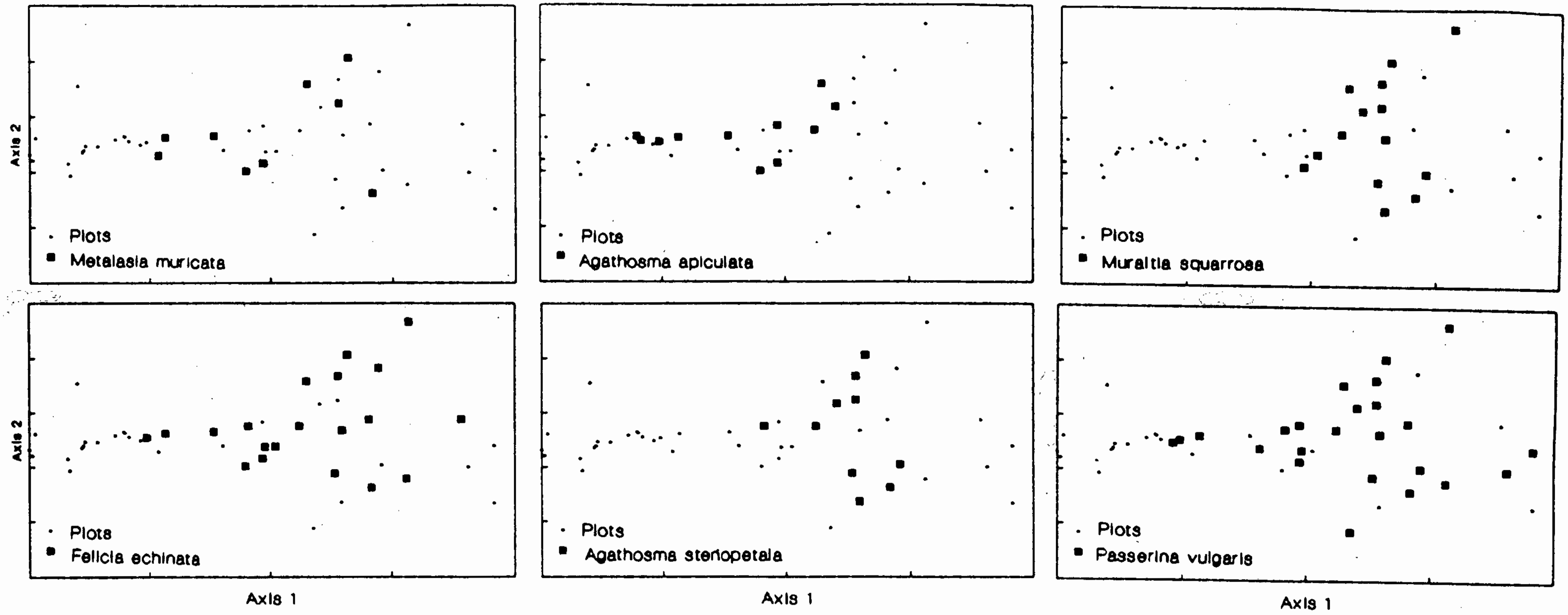


Fig. 3. Presence of study species recorded in plots represented in the ordination diagram (see Fig.2.).

DISCUSSION

In the discussion below, I describe the landscape-level pattern of grassland, fynbos and thicket and their responses to changes in disturbance through the responses of the dominant component species, with particular emphasis on the fynbos vegetation. The explanation for dune vegetation dynamics was thus moulded in part on models based on the individual (Huston & Smith 1987); life-histories (Noble & Slatyer 1980) and population levels (Peet & Christenson 1980).

Landscape pattern

The major finding was that the the dune vegetation mosaic of grassland, fynbos and thicket was not determined by abiotic factors. Instead, landscape-level pattern was attributed to different stages in a succession process. The evidence for this was provided by post-disturbance vegetation age explaining most variation along the first ordination axis. In parallel with vegetation age, (assuming litter to be related to vegetation age), the first ordination axis correlation with litter cover further suggests that dune succession at the landscape-level follows the classical Clementsian or relay floristic pathway (Egler 1954; Drury & Nisbet 1973) of succession. Although rainfall was positively correlated with both axes (Table 3) (suggesting drier sites with thicket and wetter sites with grassland), rainfall values varied only slightly amongst communities (Table 2). Also, grasslands in general were undersampled, especially in the drier east, which may have affected results.

The study indicated that the dune landscape consists of a successional gradient of grassland, through fynbos to thicket, each of which remains relatively stable under defined disturbance regimes. It was revealed that changes in these disturbance regimes (such as increased frequency of fire in the fynbos) could result in changes from one vegetation state to another because of the response of component species to the new biotic and abiotic conditions. Species were competitively displaced depending on their life-history attributes and physiological properties (Pickett 1976; Peet & Christenson 1980; Huston & Smith 1987). Although succession is a temporal phenomenon, much evidence for successional changes comes from spatial sequences of vegetation on adjacent sites, and successional theory should explain both temporal and spatial patterns (Drury & Nisbet 1973).

At the landscape level, in the absence of disturbance, succession proceeds by different mechanisms along the classical Clementsian pathway with inhibition and facilitation (Connell & Slatyer 1977), and with species replacing others as a function of their life-history strategies. Grass species would be out-shaded by fynbos shrub species (Cowling 1983) (inhibition), and over time, these shrubs senesce (Chapter 3) (life-history). In the shade provided by the mature shrubs, the shade-requiring thicket species would germinate (unpubl. data, S.M.P.) (facilitation), and ultimately replace the fynbos. In contrast, succession after fire in the fynbos communities followed the initial floristic composition model (Egler 1954), although on the south-facing slope, the short-lived colonizing herbs out-shaded the fynbos shrub seedlings, indicating inhibition (Chapter 3; Appendix 1).

The importance of identifying patches in space and phases in time on the basis of relative species abundances and their correlations with other variables such as litter was first recognized by Watt (1947). He emphasized that an understanding of landscapes required an understanding of the relationships between phases, such as different patches providing seed sources for the sequences of phases, and how different phases induce microclimatic changes which alter suitability of sites to other species. He called this pattern and process.

Grassland

The grassland cover state is maintained by continuous grazing and by either burning or bushcutting on a short rotation (two to four years). This frequency of disturbance prevents any fynbos shrubs from reaching reproductive age and contributing to the deteriorating soil-stored seed bank (Chapters 4 and 6). Grassland, with an admixture of particular fynbos shrubs, can persist in certain sites in the absence of frequent fire and bushcutting. These sites are always in dune valleys where a ferrihumic hardpan causes seasonal waterlogging which prevents the invasion of most shrubs (Cowling 1984). These patches would have provided the noda for the spread of grassland species into areas subjected to more frequent fire and bushcutting regimes. Ultimately, under a continued regime of frequent disturbance, the fynbos shrubs dependent on soil-stored seeds would be completely eliminated (Chapter 6). This is due to the relatively small and short-lived nature of fynbos shrub seed banks (Chapter 4 and 6). Hence the reported effectiveness of bushcutting as a management practice in the Humansdorp dunes (Smith 1967). For most effective management of grassland, I predict that disturbance (fire or bushcutting) in early spring would favour the growth of grasses (Pierce & Cowling 1984) and removal of cover would favour growth of C4 grasses in particular (Cowling 1983). The fynbos seedlings which were able to germinate in spite of unfavourable conditions would be outcompeted, especially as they would have had insufficient time to develop adequate root systems to survive the summer drought, especially in the face of competition with grasses. Similar processes probably occur in the grasslands of the eastern Cape where overgrazing and the absence of fire have resulted in the transition from the grassland state to that of fynbos comprising shrub species of *Passerina* spp., *Erica* sp., and *Cliffortia* sp.(Trollope 1970). There, fynbos is eradicated by a program of frequent (every two years) burning in spring.

Thicket

In the absence of fire or bushcutting for an extended but indeterminate period, fynbos develops into thicket on all sites except on seasonally waterlogged sites. Preliminary data indicate that dominant thicket species of *Sideroxylon inerme* and *Chionanthus foveolatus* showed higher germination success under shaded than direct sunlight conditions (unpubl. data, S.M.P.). Once established, the thicket or forest is stable. It may be subject to occasional gap-phase disturbance (Brokaw 1985) through treefalls or damage by large herbivores. Species would recruit from bird-dispersed seed (Tinley 1985). Thicket species are apparently fire-resistant and succumb only under exceptional circumstances of disastrous fires under "berg" wind conditions ((hot,dry mountain winds). Even so, most thicket species are vigorous resprouters. Investigation of seed banks under well established thicket were devoid of species of the other vegetation types, their seeds having long since decayed under the canopy-induced, stable microclimate unsuitable for fynbos shrub germination (Chapter 2).

Fynbos

As there is very little inter-fire regeneration, a fire frequency compatible with fynbos species life-history traits is needed for the maintenance of fynbos (Chapter 3). In fynbos left undisturbed for longer than ca. 15 years, dominant species senesce (Chapter 3). There is a concomitant decrease in seed production (Chapter 4), and a closing of the canopy which inhibits fynbos species germination (Chapters 2 and 3), but which facilitates chance entry of thicket species by bird dispersal. Preliminary data (R. M. Cowling and S.M.P.) on thicket seedling numbers in 60 X 1 m^2 quadrats indicated an abundance of thicket seedlings establishing under Metalasia shrubs (162 total), but a scarcity under other fynbos shrubs (3 total). This indicates that Metalasia, the longest living fynbos shrub to establish immediately after fire, in acting as a bird perch and a "nurse plant" to thicket species seedlings, may be a keystone species in dune vegetation dynamics. Thicket species are vigorous resprouters so that, once having gained a foothold in fynbos, they are able to form numerous ramets from sympodial lateral growth (Tinley 1985) e.g. *Euclea racemosa*, *Rhus laevigata*, *Olea exasperata* and *Rapanea gilliana*. Once these thicket species have invaded fynbos, they in turn provide perches for birds (Tinley 1985) and thus accelerate the spread of thicket. These processes help to explain the admixture of thicket species in fynbos communities, and also the fynbos/thicket mixed communities.

Seed banks of fynbos community species including the dominant species, did not persist under thicket (unlike *Calluna* heath species under forest - Willems 1988), nor under grassland (Chapter 6). The seed banks of dominant fynbos shrub species were relatively small under mature fynbos stands, and failed to show significant accumulations at mature age (Chapter 4). Therefore, it was inferred that fynbos species were dependent on recent years' inputs which can vary by orders of magnitude from year to year (Chapter 4). In addition, after release and prior to burial (either passively or by ants), losses to predation by rodents and possibly to invertebrates were very rapid and very high (Chapter 5). Once buried, seeds of fynbos species suffered fairly severe losses (up to 50%) to decay and unsuccessful germination (Chapter 4). The losses from fynbos seed banks through inter-fire germination are apparently anomalous amongst obligate reseeding species. In contrast, a more efficient adaptation in fire-prone vegetation was described in a model for survival of herbs in chaparral (Keeley & Keeley 1989). Two possible mechanisms were proposed. The first, inhibition of seedling germination under mature chaparral, was unsupported due to lack of evidence of abiotic inhibition. (Alternating temperatures, however, as a possible germination cue do not appear to have been investigated). The second mechanism, that of reducing seedling survival, would, through evolutionary time have developed through selection for dormancy mechanisms to minimize seed germination through periods of low survival probability. (Alternatively, for chaparral species lacking these dormancy mechanism, and which establish in gaps, germination may be prevented by allelopathic inhibition.) The models do not appear to hold for dune fynbos shrubs. The reason might be the relatively unspecialized germination requirement of widely fluctuating diurnal temperatures (Chapter 2). In a fire-prone system, fire-related stimuli would appear to be a better adaptation, but the study species showed no particular response to heat nor to charred wood solutions as found in chaparral (Keeley 1984). A fire-induced cue such as a heat pulse would have served just as well as alternating diurnal temperatures, and not led to appparently wasteful depletion of seed banks by inter-fire germination (Chapter 4).

In many respects the vegetation pattern of the dune landscape aptly fits the model of succession proposed by

Pickett (1976) - "the dynamic view of landscapes as mosaics of successional habitats, generated by random or periodic disturbance". The patches of different successional stage are dynamic and move around the landscape depending on the disturbance regime. Time and type of disturbance dictate size of patches, and in turn, their size, age, and distance from the next patch determine speed of development, maximum population sizes and and species richness. A patch supports species with appropriate adaptations, and when the level of adaptation of species present exceeds that of arriving propagules, climax is attained. The position of a species in the successional gradient is limited and determined by the evolutionary strategy of life span, time of reproduction, and reproductive output. This leads to the question of how the individual study species fit into the landscape.

Study species

Both *Felicia echinata* and *Metalasia muricata* occur widely across the landscape (Fig. 3). *Felicia* is a short-lived species (ca. 6 years) with early reproduction at 18 months. It has a high annual seed production (1300-10 000 seed per individual) with extremely high germinability under relatively unspecialized requirements. Low seed survival in six months' soil storage (ca. 55%) result in negligible belowground seed banks (Chapters 2, 3 and 4). In all, it behaves like a opportunistic species, regenerating after disturbance and colonizing new sites through wind-dispersal, and senescing and dying early in the community (Chapter 3). However, it was the only species to colonize, albeit in very low numbers, the small gaps created in dense mature fynbos (Chapter 3). Hence this explains its ability to retain a presence in older fynbos/thicket plots (Fig. 3). Metalasia, although similar in producing many seeds per year (1200-34 000 seeds per individual), which are highly germinable and wind-dispersed, and lacking substantial underground seed banks, differs in having a longer juvenile period (ca. 4 years) and a considerably longer life-span (>30 years) (Chapters 2, 3 and 4). Few seedlings appear to establish by the first year after a fire. However, survival on a percentage basis is high relative to the other study species (ca. 50% on N slope) and its growth rate is one of the fastest (Chapter 3). Inter-fire recruitment in small gaps in mature fynbos was not recorded, possibly due to this species having a light-requirement for germination (Chapter 2). As mentioned earlier, this species is a keystone species in dune vegetation dynamics in providing bird perches above the densely shaded conditions conducive to germination and establishment of thicket species.

The congeners, Agathosma apiculata and A. stenopetala, co-occur in young fynbos communities in the dune landscape. A. stenopetala is limited to younger communities (Fig. 3) and favours cooler south-facing aspects (data from Cowling 1984). The two species differ in a number of ways - *A. stenopetala* is smaller and shorter-lived (ca. 20 years). Annual seed production per unit canopy area is higher than for its congener, but when expressed per individual, the difference in seed production (775-2900 seed) is less marked (*A. apiculata* with 900-4000 seed per individual) (Chapter 4). *A. stenopetala* flowers later in the later part of spring (Pierce & Cowling 1984). *A. apiculata* is longer lived (ca. 25 years). In this way the two species provide an example of niche differentiation, particularly in terms of regeneration (Grubb 1977; Pierce 1984). Both species are able to recruit after disturbance from moderately sized soil-stored seed banks (Chapter 3 and 4), although *A. stenopetala* has higher seed survival (17-50%) after six months' soil storage than *A. apiculata* (7-30%). In both species, the elaiosome-bearing seeds are not as efficient as might be predicted (cf. Bond & Slingsby 1983) in ensuring ant dispersal (pers. obs. and Chapter 5). Their germination requirements of alternating diurnal temperatures in the low range of 10°/20°C appears to be a drought-avoiding strategy (*sensu* Angevine & Chabot 1979). This ensures germination at the onset of the first winter rains, and the establishment of adequate root systems for survival through the summer drought (Chapter 2).

Muraltia squarrosa would appear to be the most specialized of the study species in a number of ways. It has the lowest seed production (21-169 seeds per individual shrub), the smallest of the soil-stored seed banks (Chapter 4), yet the highest seed survival after six months' burial (ca. 96%). This may explain the substantial recruitment of seedlings after disturbance (Chapter 3). Seeds showed dormancy in the first year, and thereafter variable germination among different annual crops (Chapter 2). The anomalous lack of dormancy and complete germination success of seeds from an autumn crop suggests germination to be finely tuned to the wet winters and dry summers of the south eastern Cape (Chapter 2). This species had the best developed elaiosome of the study species (Fig.1 in Chapter 5). From a cost-benefit point of view, the high proportion of empty, though elaiosome-bearing seed produced throughout the year in a relatively nutrient-poor environment, might be considered wasteful. However, the empty seeds may serve to maintain disperser interest throughout the year (Chapter 5). Despite apparent costs, the elaiosome may be advantageous as, in spite of very low seed production, post-fire recruitment was comparable with the other species (Chapter 3). This species distribution in the landscape could be restricted to younger or more open (and thus warmer) fynbos communities by sun-seeking ants (Yeaton & Bond 1989).

Passerina vulgaris showed the widest distribution across the landscape, extending further into the grassland than any other of the study species (Fig. 3). Seeds of this species were not found in the grassland seed bank as the site sampled had long been maintained in the grassland state (Chapter 6). Passerina was, by far, the most successful species to recruit after fire (Chapter 3). Annual seed production was high (2500-26 000 seed per individual) and seed bank densities were the highest of the study species (Chapter 4). From these data, and high numbers of dormant seed assumed form its tardy germination (Chapter 2), this species appears to be the "weediest" of the study species in being reliant on relatively large and persistent seed banks. This explains its appearance as one of the last fynbos species to be eliminated under a grassland management programme of frequent disturbance.

Coexistence of species

The small and non-persistent nature of seed banks of fynbos species is critical in fire-prone communities dominated by species dependent on soil-stored seed banks for post-fire regeneration. Such seed banks would not ensure population stability of species after disturbance (Chapter 4). Almost all life-history traits of the dune fynbos species - varying seed germinability in each crop (Chapter 2); varying seed production (Chapter 4), high seed predation (Chapter 5);

relatively small and non-persistent seed banks (Chapters 6 and 4) - would result in varying proportions of species recruitment after each fire. This might depend mainly on accumulated germinable seed banks at the time of disturbance, and this would vary according to community age, and season, and the unpredictable vagaries responsible for variation in crop germinability and seed predation levels. This lends support to the idea of Christenson (1985) that due to variation in post-fire environments with resultant variation in community from fire to fire, the "optimal fire regime" is a meaningless concept. Through this varying recruitment, the model of "shifting clouds of abundance" of different species, all competing for post-disturbance space, might apply (Grubb 1986). This would explain the pattern of varying abundances of fynbos dominants found on different dune ridges. This variation in the biotic component would add to the model of variability in fire regimes used to explain coexistence and high diversity in fynbos communities (Cowling 1987).

ACKNOWLEDGEMENTS

I thank R. M. Cowling for making his data available to me for re-analysis, and for comments by both him and E. J. Moll.

REFERENCES

Angevine, M. W. & Chabot, B. F. (1979). Seed germination syndromes in higher plants. Topics in Plant Population Biology (Ed. by O. T. Solbrig, S. Jain, G. B. Johnson and P. H. Raven),pp. 188-206. Columbia University Press, New York.

Bond, W. J. & Slingsby, P.(1983). Seed dispersal by ants in shrublands of the Cape Province and its evolutionary implications. South African Journal of Science, 79, 231-33.

Brokaw, N. V. L. (1985). Treefalls, regrowth and community structure in tropical forsts. The Ecology of Natural Disturbance and Patch Dynamics. (Ed. by T. A. Pickett and P. S. White), pp. 53-69. Academic Press, New York.

Campbell, B. M., Cowling, R. M., Bond, W. & Kruger, F. J. (1981). Structural characterization of vegetation in the Fynbos Biome. South African National Scientific Programmes Report No. 52. CSIR, Pretoria.

Christensen, N. L. (1985). Shrubland fire regimes and their evolutionary consequences. The Ecology of Natural Disturbance and Patch Dynamics. (Ed. by S. T. A. Pickett & P. S. White), pp. 85-100. Academic Press, New York.

Connell, J. H. & Slatyer, R. O. (1977). Mechanisms of succession in natural communities and their role in community stability and organization. American Naturalist, 111, 1119-1144.

Cowling, R. M. (1983). The occurrence of C_3 and C_4 grasses in fynbos and allied shrublands in the south-eastern Cape, South Africa. Oecologia 58, 121-127.

Cowling, R. M. (1984). A syntaxonomic and synecological study in the Humansdorp region of the Fynbos Biome. Bothalia, 15, 175-227.

Cowling, R. M. (1987). Fire and its role in coexistence and speciation in Gondwanan shrublands. South African Journal of Science, 83, 106-112.

Denslow, J. S. (1985). Disturbance-mediated coexistence of species. The Ecology of Natural Disturbance and Patch Dynamics. (Ed. by S. T. A. Pickett & P. S. White), pp. 307-323. Academic Press, New York.

Drury, W. H. & Nisbet, I. C. H. (1973). Succession. Journal of the Arnold Arboretum, 54, 331-368.

Egler, F. E. (1954). Vegetation science concepts. I. Initial floristic composition, a factor in old-field vegetation development. Vegetatio, 4, 412-417.

Glenn-Lewin, D. C. (1980). The individualistic nature of plant community development. Vegetatio, 43, 141-46.

Grubb, P. J. (1977). The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biological Review, 52, 107-145.

Grubb, P. J. (1986). Problems posed by sparse and patchily distributed species in species-rich plant communities. Community Ecology (Ed. by J. Diamond and T. J. Case),pp.207-225. Harper & Row Publishers, New York.

Hill, M. O. (1979). TWINSPAN - A FORTRAN programme for arranging multivariate data in two-way tables by classification of individuals and attributes. Ithaca, New York: Section of Ecology and Systematics, Cornell University.

Hill, M. O. & Gauch, H. G. Jr. (1980). Detrended correspondence analysis : an improved ordination technique. Vegetatio, 42, 47-58.

Horn, H. S. (1981). Some causes of variety in patterns of secondary succession. Forest Succession: Concepts and Appplication. (Ed. by D. C. West, H. H. Shugart and D. B. Botkin), pp.24-35.Springer-Verlag, New York.

Huston, M. & Smith, T. (1987). Plant succession: life history and competition. American Naturalist 130, 168-198.

Keeley, J. E. (1984). Factors affecting germination of chaparral seeds. Bulletin of Southern Californian Academy of Science, 83, 113-120.

Keeley, J. E. & Keeley, S. C. (1989). Allelopathy and the fire-induced herb cycle. The Californian Chaparral. Paradigms Re-examined. (Ed. by S. C. Keely), pp. 65-72. Natural History Museum, Los Angeles.

Le Maitre, D. C. (1988). Effects of season of burn on the regeneration of two Proteaceae with soil-stored seed. South African Journal of Botany, 54, 575-80.

Noble, I. R. & Slatyer, R. O. (1980). The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. Vegetatio, 43, 5-21.

4. Pickett, S. T.A., Collins, S. L. & Armesto, J. J. (1987). Models, mechanisms and pathways of succession. Botanical Review, 53, 335-371.

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

5. Peet, R. K. & Christenson, N. L. (1980). Succession, a population process. Vegetatio, 43, 131-140.

6. Peet, R. K., Knox, R. G., Case, J. S. & Allen, R. B. (1988). Putting things in order: the advantages of detrended correspondence analysis. American Naturalist, 131, 924-934.

3. Pickett, S. T. A. (1976). Succession : an evolutionary interpretation. American Naturalist, 110, 107-119.

2. Pierce, S. M. & Cowling, R. M. (1984). Phenology of fynbos, renosterveld and subtropical thicket in the south eastern Cape. South African Journal of Botany, 3, 1-16.

Schulze, R. E. (1975). Incoming radiation on sloping terrain: a general model for use in southern Africa. Agrochemohysika, 7, 55-61.

Smith, H. J. (1967). Ondersoek na die bestuur en benutting van die skynsfynbosveldtipe in die Humansdorp grondbewaringdistrik. Department of Agriculture Technical Services, Eastern Cape Region, Dohne.

Tinley, K. L. (1985). Coastal Dunes of South Africa. South African National Scientific Programmes Report No. 109. CSIR, Pretoria.

Trollope, W. S. W.(1970). A consideration of macchia (fynbos) encroachment in South Africa and an investigation into methods of macchia eradication in the Amatole mountains. MSc. thesis, University of Natal.

Walker, L. R. & Chapin, F. S. (1987). Interactions among processes controlling successional change. Oikos 50, 131-35.

Wartenberg, D., Ferson, S. & Rohlf, F. J. (1987). Putting things in order: a critique of detrended correspondence analysis. American Naturalist, 129, 434-448.

Watt, A. S. (1947). Pattern and process in the plant community. Journal of Ecology, 35, 1-22.

Willems, J. H. (1988). Soil seed bank and regeneration of a *Calluna vulgaris* community after forest clearing. Acta Botanica Neerlandica, 37, 313-320.

Werner, P. (1979). Competition and coexistence of similar species. Topics in Plant Population Biology (Ed. by O. T. Solbrig, S. Jain, G. B. Johnson and P. H. Raven), pp. 287-310. Columbia University Press, New York.

Yeaton, R. I. & Bond, W. J. (1989). Competition between two shrub aspecies: directed dispersal by ants promotes coexistence. American Naturalist (in press).

CHAPTER 8

CONCLUSIONS

CONCLUSIONS

For this chapter I extracted the major findings of the thesis and listed them briefly below. These include the major findings from the preceding chapters, as well as conclusions drawn from the thesis as a whole.

In order to enhance the usefulness of this study beyond its theoretical contribution, I also attempted to give practical guidelines for future research. Hence, I discussed the study's limitations and major problems encountered during its progress. I have included some recommendations, with the wish that future researchers in this field might also benefit from my experiences.

Major findings

1. The type of hierarchical approach used in this study, which concentrated on the population, community and landscape levels of organization, has been criticized by O'Neill et al. (1986) as naive, and flawed in ignoring the role of ecosystem processes (e.g. nutrient cycling). However, as a pioneer study it served its purpose in providing an understanding of the processes maintaining the

dune communities and their pattern at the landscape-level resulting from successional processes.

2. The varying proportions of fynbos species populations in communities across the dune landscape can possibly be explained as a result of the variation in time of numbers of germinable seed available for regeneration after disturbance. Seed banks under 13-15 year-old communities generally showed no change in size over three years. However, wide fluctuations were revealed in: seed production; germinability of annual seed production; slight dormancy; predation and dispersal; and decay in the soil. These would be important determinants of variation in seed available for recruitment over time. The interaction of all these factors would affect the level of success of each species in surviving different disturbances. Similar vulnerability to variations in fire regimes (i.e. season of burn) has been identified in studies of recruitment of two Proteaceae with large seeds stored in the soil (Le Maitre 1988). In Proteaceae with canopy-stored seeds, annual variations in seed reserves similarly expose species to variable post-fire recruitment and even local extinctions under different fire regimes (Bond 1984; 1985; Bond, Vlok & Viviers 1984; Le Maitre 1987).

3. Soil-stored seed banks of selected dune fynbos shrubs were shown to be small and not persistent relative to other

fire-prone shrublands e.g. Calluna heath (Mallik, Hobbs & Legg 1984) and chaparral (Keeley 1977). These characteristics of the seed banks would not always favour plant species population stability after disturbance. This "unreliability" might help to explain coexistence of shrub species in fynbos in adding to the model of varying clouds of abundance with each fire event (Grubb 1986; Cowling 1987).

4. Germination of selected dune fynbos shrubs was not directly cued to fire nor highly specialized as expected. Dormancy was not strongly developed, and germination success was generally high (ca. 80%). (Zedler & Zammit (1989) also found little demographic evidence of fire-selected plant strategies in chaparral.) However, germination of the study species was indirectly cued to disturbance in responding to widely fluctuating diurnal temperatures which would be experienced at soil surface after removal of the insulating effects of vegetation cover (Chapters 2 and 3).

5. The study contributed to the generally neglected body of theory regarding disturbance and soil-stored seed banks, developed almost exclusively by Thompson (1978) and Grubb (1988). It was the first study of its kind in fynbos. The study elaborated on existing ideas on the effects of disturbance frequency on seed bank size, by considering other aspects of the disturbance regime, as well as life-

history attributes of the plant species, and successional pathways in determining the relationship between seed bank composition and its above-ground vegetation.

6. The study showed that no single model of succession applied in the dune landscape, and that different successional pathways and mechanisms (cf. Connell & Slatyer 1977; Noble & Slatyer 1977; Connell, Noble & Slatyer 1987; Huston & Smith 1987; Pickett, Collins & Armesto 1987; Walker & Chapin 1987) operate at different temporal and spatial scales. At the landscape-level, the different vegetation types were identified as successional sequences in space, as a form of gradient along which species are displaced (Pickett 1976). Different life-histories and life-spans (including seed bank duration) of dominant species were important factors in determining patterns of succession (Egler 1954). With the development of the grassland under a frequent disturbance regime, recruitment of fynbos shrubs would be inhibited (sensu Connell & Slatyer 1977) by vegetative growth of dominant grasses. Under the mechanism of facilitation (sensu Connell & Slatyer 1977) the shade-requiring thicket shrubs would germinate and establish under mature and ageing fynbos shrubs. At the community-level, after fire, fynbos followed mainly the initial floristic composition pathway (Egler 1954). However, on the cooler south-facing slope, the dominance of early colonizing

ephemeral herbs resulted in inhibition (sensu Connell & Slatyer 1977) of dune fynbos shrub seedlings.

7. Investigation of the fate of seeds of fynbos shrub species after release indicated that myrmecochory, or seed dispersal and burial by ants, may not be as efficient for small elaiosome-bearing seeds (24 mg) as for larger-seeded Proteaceae species (Bond & Slingsby 1983). The limitation may be a critical ratio of seed:ant size. This suggests that survival of some small-seeded species is not heavily dependent on burial of seed by ants. If so, predictions regarding the deleterious effects of the introduced Argentine ant (Iridomyrmex humilis) on fynbos shrub recruitment may not be as extensive in the Cape flora as predicted (Bond & Slingsby 1984).

8. The study's findings led to speculation regarding the high incidence of species with elaiosome-bearing seed in the Cape fynbos. The nutrient-poor soils of the Cape support a preponderance of small-leaved, finely branched shrubs. I suggest that the allometric consequence (cf. Corner 1949) of fine branching is small reproductive bodies or seeds. These would be highly sought after by similarly small predators, such as ants. Burial of seeds would ensure escape as ants are surface foragers (Thompson 1987). In species dependent on somewhat unreliable seed numbers, ant predation might have been a strong selective force in

the evolution of elaiosome-bearing seeds. The potential success of the strategy might be constrained by the critical seed:ant size ratio.

9. The wide range in individual life-history attributes found in only six species of the same group of small-leaved, non-resprouting shrubs indicated that plant groups, classified according to characteristics such as growth form (cf. Cody 1986) and vital attributes (Noble & Slatyer 1977), should be used with circumspection.

10. Finally the study, provided an understanding of the communities' structure and functioning on the basis of the life-history attributes of important species in response to different disturbance regimes. This understanding will allow managers to promote and maintain the different communities as desired in the dune landscape. In broad terms, grassland may be maintained under continous grazing and burning or bushcutting in spring on a four year rotation. Fynbos maintenance would require autumn burns on a ca. 12 year frequency. Thicket development would require the exclusion of fire for long periods (>50 yr). Thicket maintenance would require occasional gap formations which may have been more frequent in earlier times under more intense use by large herbivores.

Limitations and recommendations.

Much of this empirically-based thesis has been of an exploratory and descriptive nature, with statistical inferences being drawn where appropriate. Theory testing, however, was limited, and in general the thesis was a pioneer study which allowed hypotheses to be developed as the research progressed. As Loehle (1987) stated "Efficient hypothesis testing is often not possible when theories are in an immature state, as is the case in much of ecology".

A major constraint was the inadequate seed supply due to the laborious methods needed for sorting. Nevertheless, experimental design should have accommodated the retrieval of buried seeds (in bags) over increasing periods of time so that seed decay rates could have been determined. Seed should also have been buried for periods greater than one year, and up to five years, with others left for ten, fifteen and twenty years etc. to determine actual longevity of soil stored seeds. Originally the study was aimed primarily to determine seasonal effects of spring and autumn fires. However, due to logistic problems, the landowner was unable to initiate a spring burn, which precluded this important aspect of the study. Similar constraints prevented the replication of treatments such as burning and bushcutting, raising the problems of pseudoreplication (Hurlbert 1984) but reasonably countered by Hawkins (1986).

The lack of replication obviated direct comparisons and so results have been reported mainly in terms of observations. The difficulties in attributing differences, when there are confounding temporal and spatial problems, have been recognized (Zedler & Zammit 1989).

Experiments to determine the fate of small seeds could have been improved. A clearer idea of whether seed removals led to granivory or safe burial, would have been achieved if the removal agents could have been carefully observed and identified. Even so, a clear answer would have been unlikely as ant behaviour is not necessarily species specific. Seed bank accumulation patterns could have been better determined by sampling under fynbos communities of a range of increasing ages e.g. 4, 8, 12, 16 years old. However, difficulties in finding comparable, yet different aged stands precluded this. Investigation of seed banks of intermediate vegetation types e.g. grassland/fynbos, fynbos/thicket would have given greater insights into successional processes. Gaps in the mature fynbos should have been much larger than those in the study to provide a more rigorous determination of inter-fire recruitment. I recognize as unfortunate the premature termination of the study of succession in fynbos communities after disturbance (Appendix 1). Continuation of formal monitoring for four years would have yielded valuable insights into the development of community structure.

In achieving some understanding of species and community dynamics in response to disturbance, this project showed the value of the approach used. This involved studies of interactions (seed inputs to and losses from seed banks) at population-, community- and landscape-levels. This approach has recently been strongly recommended for future studies in chaparral (Zedler & Zammit 1989) although much more ground work has already been completed there (e.g. Keeley 1977; see also Keeley 1989). However, the desired goal of a predictive model for managing fynbos communities for maximum species diversity (Kruger 1983) based on a knowledge of seed bank dynamics was not fully realized. While Christensen (1985) suggests that the concept of an optimal fire (regime) is meaningless, Denslow (1985) proposes that the historical disturbance pattern should be the regime that maximises species diversity. These two apparently opposing ideas are not incompatible. It might be expedient to accept the notion of variability and limited predictability in communities, and manage systems within the limits of historical disturbance regimes.

Finally, the findings here of the variability in seed bank potential offer a novel explanation for existing fynbos community patterns. I propose that these findings for dune fynbos communities provide the basis for a new approach to the functioning of the more widespread lowland and mountain fynbos communities on the acid sands of the Cape Region.

REFERENCES

Bond, W. J. (1984). Fire survival of Cape Proteaceae - influence of fire season and seed predators. Vegetatio, 56, 65-74.

Bond, W. J. (1985). Canopy-stored seed reserves (serotiny) in Cape Proteaceae. South African Journal of Botany, 51, 181-86.

Bond, W. J. & Slingsby, P. (1983). Seed dispersal by ants in shrublands of the Cape Province and its evolutionary implications. South African Journal of Science, 79, 231-33.

Bond, W. & Slingsby, P. (1984). Collapse of an ant-plant mutualism: the Argentine ant (*Iridomyrmex humilis*) and myrmecochorous Proteaceae. Ecology, 65, 1031-37.

Bond, W. J., Vlok, J. & Viviers, M. (1984). Variation in seedling recruitmment of Cape Proteaceae after fire. Journal of Ecology, 72, 209-21.

Christensen, N. L. (1985). Shrubland fire regimes and their evolutionary consequences. The Ecology of Natural Disturbance and Patch Dynamics. (Ed. by S. T. A. Pickett and P. S. White), pp. 85-100. Academic Press, New York.

Cody, M. L. (1986). Structural Niches in Plant Communities. Community Ecology. (Ed. by J. Diamond and T. J. Case), pp. 381-405. Harper & Row, New York.

Connell, J. H., Noble, I. R. & Slatyer, R. O. (1987). On the mechanisms producing successional change. Oikos, 50, 136-37.

Connell, J. H. & Slatyer, R. O. (1977). Mechanisms of succession in natural communities and their role in community stability and organization. American Naturalist, 111, 119-144.

Corner, E. J. H. (1949). The durian theory and the origin of the modern tree. Annals of Botany, 13, 367-414.

Cowling, R. M. (1987). Fire and its role in coexistence and speciation in Gondwanan shrublands. South African Journal of Science, 83, 106-112.

Denslow, J. S. (1985). Disturbance-mediated coexistence of species. The Ecology of Natural Disturbance and Patch Dynamics. (Ed. by S. T. A. Pickett and P. S. White), pp.307-323. Academic Press, New York.

Egler, F. E. (1954). Vegetation science concepts I. Initial floristic composition, a factor in old-field vegetation development. Vegetatio, 4, 412-417.

Grubb, P. J. (1986). Problems posed by sparse and patchily distributed species in species-rich plant communities. Community Ecology. (Ed. by J. Diamond and T. J. Case), pp. 207-226. Harper & Row, New York.

Grubb, P. J. (1988). The uncoupling of disturbance and recruitment, two kinds of seed bank, and persistence of plant populations at the regional and local scales. Annales Zoologici Fennici, 25, 23-36.

Hawkins, C. P. (1986). Pseudo-understanding of pseudoreplication: a cautionary note. Bulletin of the Ecological Society of America, 67, 184-85.

Hurlbert, S. H. (1984). Pseudoreplication and the design of ecological field experiments. Ecological Monographs, 54, 187-211.

Huston, M. & Smith, T. (1987). Plant succession: life history and competition. American Naturalist, 130, 168-98.

Keeley, J. E. (1977). Seed production, seed populations in soil, and seedling production after fire for two congeneric pairs of sprouting and non-sprouting chaparral shrubs. Ecology, 58, 820-29.

Keeley, S. C. (1989). The California chaparral. Paradigms Reexamined. Natural History Museum of Los Angeles County, Science Series No. 34. Los Angeles.

Kruger, F. J. (1983). Plant community diversity and dynamics in relation to fire. Mediterranean-type Ecosystems. The Role of Nutrients. (Ed. by F. J. Kruger, D. T. Mitchell and J. U. M. Jarvis), pp. 446-72. Springer-Verlag, Berlin.

Le Maitre, D. C. (1987). Dynamics of canopy-stored seed in relation to fire. Disturbance and the dynamics of fynbos biome communities. (Ed. by R. M. Cowling, D. C. Le Maitre, B. McKenzie, R. P. Prys-Jones and B. W. van Wilgen), pp.24-45. South African Scientific Programmes Report No. 135. CSIR, Pretoria.

Le Maitre, D. C. (1988). Effects of season of burn on the regeneration of two Proteaceae with soil-stored seed. South African Journal of Botany, 54, 575-80.

Loehle, C. (1987). Hypothesis testing in ecology: psychological aspects and the importance of theory maturation. Quarterly Review of Biology, 62, 397-409.

Mallik A. U., Hobbs, R. J. & Legg, C. J. (1984). Seed dynamics in Calluna-Arctostaphylos heath in north-eastern Scotland. Journal of Ecology, 72, 855-871.

Noble, I. R. & Slatyer, R. O. (1977). Post fire succession of plants in Mediterranean ecosystems. Proceedings of the Symposium on the Environmental Consequences of Fire and Fuel Management in Mediterranean Ecosystems. (Ed. by H. A. Mooney and C. E. Conrad), pp. 27-36. USDA Forest Service General Technical Report WO-3, Washington, DC.

O'Neill, R. V., De Angelis, D. L., Waide, J. B. & Allen, T. F. M. (1986). A Hierarchical Concept of Ecosystems. Princeton University Press, New Jersey.

Pickett, S. T. A. (1976). Succession: an evolutionary interpretation. American Naturalist, 110, 107-119.

Pickett, S. T. A., Collins, S. L. & Armesto, J. J. (1987). Models, mechanisms and pathways of succession. Botanical Review, 53, 335-71.

Thompson, K. (1978). The occurrence of buried viable seeds in relation to environmental gradients. Journal of Biogeography, 5, 425-430.

Thompson, K. (1987). Seeds and seed banks. New Phytologist, 106, 23-34.

Walker, L. R. & Chapin, F. S. (1987). Interactions among processes controlling successional change. Oikos, 50, 131-35.

Zedler, P. H. & Zammit, C. A. (1989). A population-based critique of concepts of change in the chaparral. The California Chaparral. Paradigms Reexamined. (Ed.by S. C. Keeley, pp. 73-83). Natural History Museum of Los Angeles County, Science Series No. 34. Los Angeles.

Additional Discussion in response to R L Specht's comments.

Theory pertaining to the structure and functioning of overstorey/understorey communities are not applicable to the communities studied here as they lack this type of structure. Also, the shrub species studied in detail tend to form a canopy of fairly even height, with negligible overlapping of canopies.

1. Dune fynbos, as described in this study, fits the definition of fynbos (*sensu* Campbell 1981) in having a high cover of restioids (>10%) and a high cover of non-ericaceous ericoids (e.g. *Passerina*, *Metalasia*, *Phylica*) and an occasional high cover of Ericaceae (e.g. *Erica chloroloma*). More specifically, dune fynbos is included in Asteraceous fynbos because of its high non-ericaceous ericoid shrub cover and, relative to other fynbos series, its low restioid and sedge cover, and high constancy of stem spinescence (Campbell 1981). Cowling et al. (1988) recognize dune Asteraceous fynbos as a subseries which is characterized by an absence of proteoids and a high cover of nannophyllous and microphyllous shrubs of sub-tropical affinity (e.g. *Rhus*, *Olea* etc.).

2. The thesis concentrated on secondary succession after disturbance of vegetated dunes (see Appendix 1 title), and made no reference to primary succession on unvegetated

dunes. The ecophysiological implications of the microhabitats on unstable, unvegetated dunes are not comparable with those on stable, vegetated dune microhabitats.

3. Seed storage variability is the result of many influences, including seed production and wind dispersal, and this variability was accounted for in the study by the random location of high numbers of replicate samples. Furthermore, the dunes run parallel to the prevailing easterly and westerly winds, and consequently the winds funnel directly up and down the dune valleys. Hence, windward and leeward effects are not of relevance here.

4. The measurement of such ecophysiological characters as leaf specific areas, water content, nitrate reductase activity and chlorophyll content, fell beyond the scope of this study which used an ecological approach with measures of populations, communities and germination characteristics.

REFERENCES

Campbell, B. M. (1981). A classification of the mountain vegetation of the fynbos biome. Memoirs of the Botanical Survey of South Africa No. 50. BRI, Department of Agriculture and Water Supply, Pretoria.

Cowling, R. M., Campbell, B. M.,Mustart, P., McDonald, D., Jarman, M. L. & Moll, E. J. (1988). Vegetation classification in a floristically complex area: The Agulhas Plain. South African Journal of Botany, 54,290-300.

APPENDIX 1

Vegetatio 76: 131–139 (1988)
© Kluwer Academic Publishers, Dordrecht – Printed in the Netherlands

Secondary succession in coastal dune fynbos: variation due to site and disturbance

R. M. Cowling & Shirley M. Pierce
Botany Department, University of Cape Town, Rondebosch, 7700, South Africa

Accepted 16.5.1988

Keywords: Aspect, Bushcutting, Fire, Ordination, South eastern Cape

Abstract

Succession after fire and bushcutting in coastal dune fynbos was monitored for two and a half years and comparisons were made with adjacent, mature (13 year-old) fynbos. Sixty-two to 68% of pre-disturbance species, including all the dominants, were found in the successional communities 1.5 yr after disturbance: the patterns thus fitted the initial floristic composition model. On the more mesic south facing slope, post-fire succession differed from the north-facing (burnt) and bushcut sites in that ordinations showed a clear separation between the mature and successional communities. This difference was due to the post-fire abundance on the south-facing slope site of short- and medium-lived species not present in the mature fynbos. One and a half years after disturbance, species richness and equitability had increased relative to mature vegetation. This increase was greatest for the south facing slope where short- and medium-lived species and juveniles of pre-disturbance dominants co-occurred. In general, successional patterns were consistent with those described for other fynbos and fire-prone mediterranean shrublands.

Nomenclature: P. Bond & P. Goldblatt (1984). Plants of the Cape Flora. A descriptive catalogue. Jl. S. Afr. Bot. Suppl. Vol. 13.

Introduction

The continued interest in ecological succession (Gray *et al.* 1987; Pickett *et al.* 1987) has spawned a plethora of models, mechanisms and pathways to explain and describe successional patterns. There have been several attempts to develop general theories of succession invoking processes at different levels of organization e.g. ecosystem (Odum 1969), population (Peet & Christensen 1980) and individual (Huston & Smith 1987). However, it appears that successional patterns are governed by a diversity of processes, often acting in concert, and that no single model sufficiently describes the mechanisms of succession for any one community (Connell & Slatyer 1977; Noble & Slatyer 1980; Connell *et al.* 1987; Walker & Chapin 1987; Pickett *et al.* 1987).

In the fire-prone Cape fynbos shrublands (Kruger 1979), it is generally argued that secondary succession involves initial floristic composition model (*cf.* Kruger 1977). We investigated early secondary successional patterns in fynbos on calcareous coastal dunes in the south eastern Cape. We used multivariate methods to compare results after different disturbances (fire and bushcutting) and on different sites (adjacent north and south facing slopes) in order to evaluate the applicability of current successional models.

Study area

The study area is located on the coastal dunes in the Humansdorp (34°02′S, 24°47′E) region of the south eastern Cape. Details on the physiography, climate, soils and vegetation are given in Cowling (1984). The climate is mild (mean annual temperature of 17 °C) and frost-free. Annual rainfall ranges from 500 – 800 mm. Rain can fall at any time of the year, but the summer months (December – February) are always driest. The vegetation comprises an admixture and mosaic of Cape fynbos and subtropical thicket. The study sites were located in fynbos which is predominant in the dune landscape and has been subject to natural fires every 10 – 20 years. Dune fynbos is distinguished from other fynbos types in lacking Proteaceae and in the general occurrence of subtropical shrubs (e.g. *Euclea, Maytenus, Rhus* etc). According to Campbell's (1985) scheme for the mountain vegetation of the fynbos biome, dune fynbos would be a form of Asteraceous Fynbos. Dune fynbos occurs over a wide range of habitats including dune ridges where the soils are deep, well-drained, alkaline sands and also shallow sands overlying calcrete.

Methods

Two sites were chosen for the study, one at Brandewynkop (ca 800 mm yr^{-1}) and the other at Cape St Francis (ca 650 mm yr^{-1}). The former site comprised the north and south facing slopes of a valley formed between two parallel dune ridges. Hereafter the slopes are referred to as north and south slopes respectively, with the term 'facing' omitted. Soils and vegetation on both slopes were markedly uniform. The south slope was dominated by *Ischyrolepis leptoclados, Metalasia muricata* and *Passerina vulgaris* while dominants on the north slope included *Olea exasperata, Metalasia muricata, Passerina vulgaris* and *Ischyrolepis eleocharis.* Both slopes are subjected to light grazing by cattle and were burnt in 1972. A portion of both slopes was burnt again in March 1984. We established homogenous 50 × 50 m sites on either side of the 1984 fire boundary in burnt and unburnt vegetation on both the north and south slopes. In October 1985 we located ten 1 m^2 plots randomly in all four sites and estimated the projective canopy cover of each species included in the plots. We repeated the procedure for the same plots in the burnt sites in October 1986.

A similar approach was adopted at the Cape St Francis site. Here a uniform patch of fynbos, dominated by *Agathosma apiculata, Metalasia muricata* and *Ischyrolepis leptoclados* was bushcut in May 1985. The vegetation was last burnt in 1972. Ten 1 m^2 plots were located randomly on either side of the bushcut boundary. Data were collected in mature and bushcut vegetation in February 1986 and repeated for permanent plots in the latter area in October 1986.

At both bushcut and burnt sites it was assumed that mature vegetation represented a stage in the development of the successional communities. For logistic reasons it was not possible to have replicate treatments nor could plots be interspersed in disturbed and undisturbed sites. However, in applying inferential statistics (*t* tests), we assumed that the tests were not simply for differences in plot location. We used DCA to ordinate the site-time data (mature and post-disturbance plots) from both sites in order to reveal successional patterns (e.g., Austin 1977). We ordinated the post-disturbance data (permanent plots) separately in order to display more clearly the time trajectories of the replicate sites in the compositional space of the ordination.

All species encountered in the community study were classified according to growth form/longevity and post-disturbance regeneration mode. The growth form/longevity group refers to herbs and shrubs of three different longevities as follows: HS = short-lived (1 – 3 yr) herbs; HM = medium-lived (4 – 15 yr) herbs; HL = long-lived (>15 yr) herbs; SS = short-lived (1 – 5 yr) shrubs; SM = medium-lived (6 – 30 yr) shrubs and SL = long-lived (> 30 yr) shrubs. We compared the relative cover of the growth form/longevity and regeneration groups for mature and successional plots. Comparisons were made of total species richness and equitability (Shannon-Wiener function) (Whittaker 1972) as well as richness of growth form/longevity and regeneration groups between the mature and successional plots.

Results

Ordination of the Brandewynkop site data showed distinct compositional differences between the mature and the post-fire plots on the south slope, but no clear separation on the north slope (Fig. 1a). All of the dominants in mature fynbos on both slopes were re-established 2.5 yr after the fire (Table 1). Seventy-one and 64% of species present in the mature fynbos were recorded 1.5 yr post-fire on the south and north slopes respectively. Of the species not present in the mature fynbos, more were dominant (i.e. >5% cover) 2.5 yr post-fire on the south slope (e.g. *Ficinia filiformis, Aspalathus spinosa, Helichrysum argenteum, Felicia echinata*) than on the north slope (*Themeda triandra*).

The analysis of the trajectories resulting from the ordination of the post-fire plot-time data indicated little directional change on either the south or the north slopes in the year between sampling dates (Fig. 1b). There was a greater compositional change in some of the south slope plots.

Mature fynbos and bushcut plots from the Cape St Francis site did not separate into discrete groups in the ordination field (Fig. 2a). One permanent successional plot was excluded from the analysis as an outlier since it was dominated by a single sprouting species (*Disparago ericoides*) not found in any of the other plots. Generally the 10 month-old plots grouped closer to the mature plots than the 1.4 yr ones (Fig. 2b). As was the case after fire, all of the pre-bushcut dominants were re-established 1.4 yr after disturbance, yet at this stage only one of the four covered >5% (Table 1). Sixty-eight percent of the species recorded in the undisturbed fynbos was noted in the 1.4 yr bushcut plots. Although some of the replicate plots showed parallel and similar trajectories, there was strong evidence of plot-specific trends and weak overall directionality (Fig. 2b).

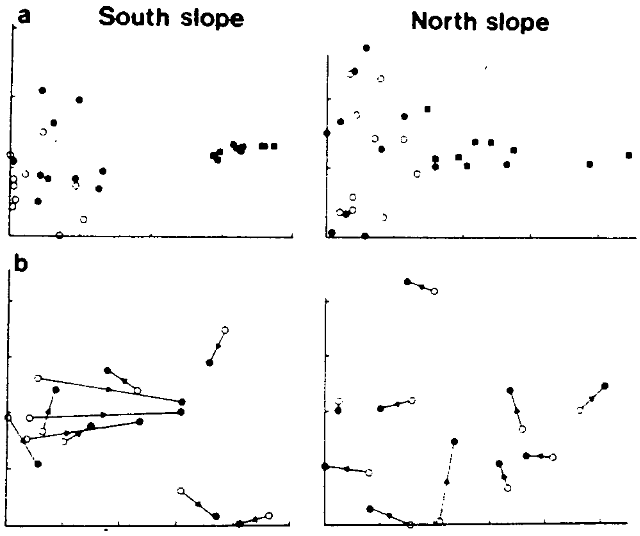


Fig. 1. Ordination using detrended correspondence analysis of (a) 1.5 (○) and 2.5 (●) yr post-fire and mature (■) plots at Brandewynkop and (b) of post-fire plots only, with time trajectories shown as lines linking permanent plots observed 1.5 and 2.5 yr after the fire.

On both the north and the south slopes species richness was markedly higher 2.5 yr after fire than in mature fynbos (Fig. 3a). This fire-induced increase in species richness was 1.4 times higher on the south than the north slope. Equitability was only half as high in mature fynbos on the south as on the north slope. Like richness, equitability on the south slope was markedly higher in the 1.5 yr-old site than in mature fynbos and continued to increase during the following year to a level similar to the north slope. On the north slope, the trend in equitability mirrored that for species richness. Both slopes showed broadly similar changes in projected canopy cover after fire, although values were always higher, and recovery faster, on the south than the north slope.

Ten months after bushcutting, species richness was lower than in undisturbed fynbos, yet after 1.4 yr, richness increased two-fold (Fig. 3b). Post-bushcut equitability values were marginally higher than mature fynbos. The extent of cover re-establishment 1.4 yr after bushcutting was broadly similar to post-fire recovery.

In mature vegetation on the north slope at Brandewynkop, long-lived shrubs (SL, e.g. *Olea exasperata*) comprised nearly half the cover with medium-lived shrubs (SM, e.g. *Passerina vulgaris*) and long-lived herbs (HL, e.g. *Ischyrolepis eleocharis*) contributing equally to the remainder (Table 2). A broadly similar pattern existed in mature vegetation on the south slope although there was a significantly greater cover of HL species (e.g. *Ischyrolepis leptoclados*) and correspondingly lower cover of SM

Table 1. Growth form/longevity, fire response, percentage cover, and frequency (%) of dominant species (>5% cover) in mature and post-disturbance dune fynbos communities. See text for explanation of abbreviations. Species dominant in mature vegetation but also present in post-disturbance fynbos indicated by +. NS = non sprouter, S = sprouter.

	Growth form/ longevity	Fire response	Brandwynkop						Cape St. Francis		
			S. slope			N. slope					
			Mature	Post-fire		Mature	Post-fire		Mature	Post-bushcut	
			13 yr	1.5 yr	2.5 yr	13 yr	1.5 yr	2.5 yr	13 yr	0.8 yr	1.4 yr
Ischyrolepis leptoclados	HL	NS	84.5 (100)	6.4 (100)	15.1	6.0 (20)			12.8 (90)	+	+
Metalasia muricata	SL	NS	34.0 (80)	+	+	18.5 (30)	+	+	18.2 (30)	+	+
Passerina vulgaris	SM	NS	16.7 (90)	+	+	15.3 (90)	+	6.0 (90)			
Ficinia filiformis	HM	NS		30.3 (90)	14.6 (90)						
Anthospermum aethiopicum	SM	NS		16.1 (90)	18.0 (100)						
Aspalathus spinosa	SM	NS		11.6 (50)	11.7 (50)						
Helichrysum argenteum	SS	NS		5.1 (100)	11.0 (100)						
Felicia echinata	SS	NS			10.1 (100)						
Ficinia ramosissima	HL	S			7.2 (90)						
Olea exasperata	SL	S				18.5 (90)	+	+	6.6 (90)	+	6.8 (80)
Ischyrolepis eleocharis	HL	S				16.4 (90)	9.7 (100)	9.1 (100)			
Euclea racemosa	HM	S				8.2 (60)	8.1 (70)	12.7 (70)			
Themeda triandra	HM	S					11.2 (50)	10.9 (60)			
Eustachys paspaloides	HM	S					5.6 (50)				
Agathosma apiculata	SM	NS							30.0 (100)	+	+
Tetragonia fruticosa	HS	NS									29.5 (50)
Tephrosia capensis	HM	NS									5.3 (40)

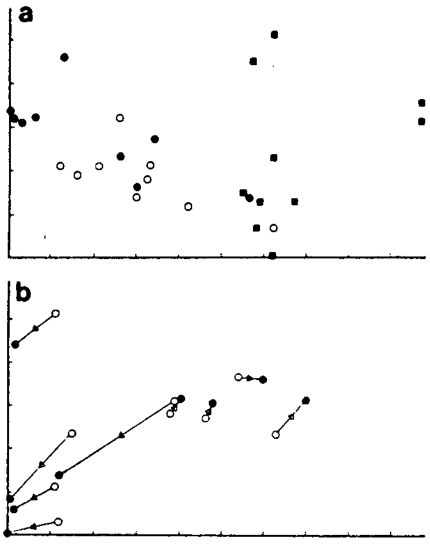


Fig. 2. Ordination using detrended correspondence analysis of (a) 0.8 (○) and 1.4 (●) yr post-bushcut and mature (■) plots at Cape St Francis and (b) of bushcut plots only, with time trajectories shown as lines linking permanent plots observed 0.8 and 1.4 yr after bushcutting.

(e.g. *Passerina vulgaris*) and SL (*Metalasia muricata*) species. Burning resulted in significant increases in the relative cover of shorter- and medium-lived herbs and shrubs on both slopes, although these changes were more marked on the south than the north slope. On the latter slope, the most striking change was a significant increase in the relative cover of medium-lived herbs (HM, e.g. *Themeda triandra*). On the south slope, fire resulted in significant changes in all longevity groups as the longer-lived

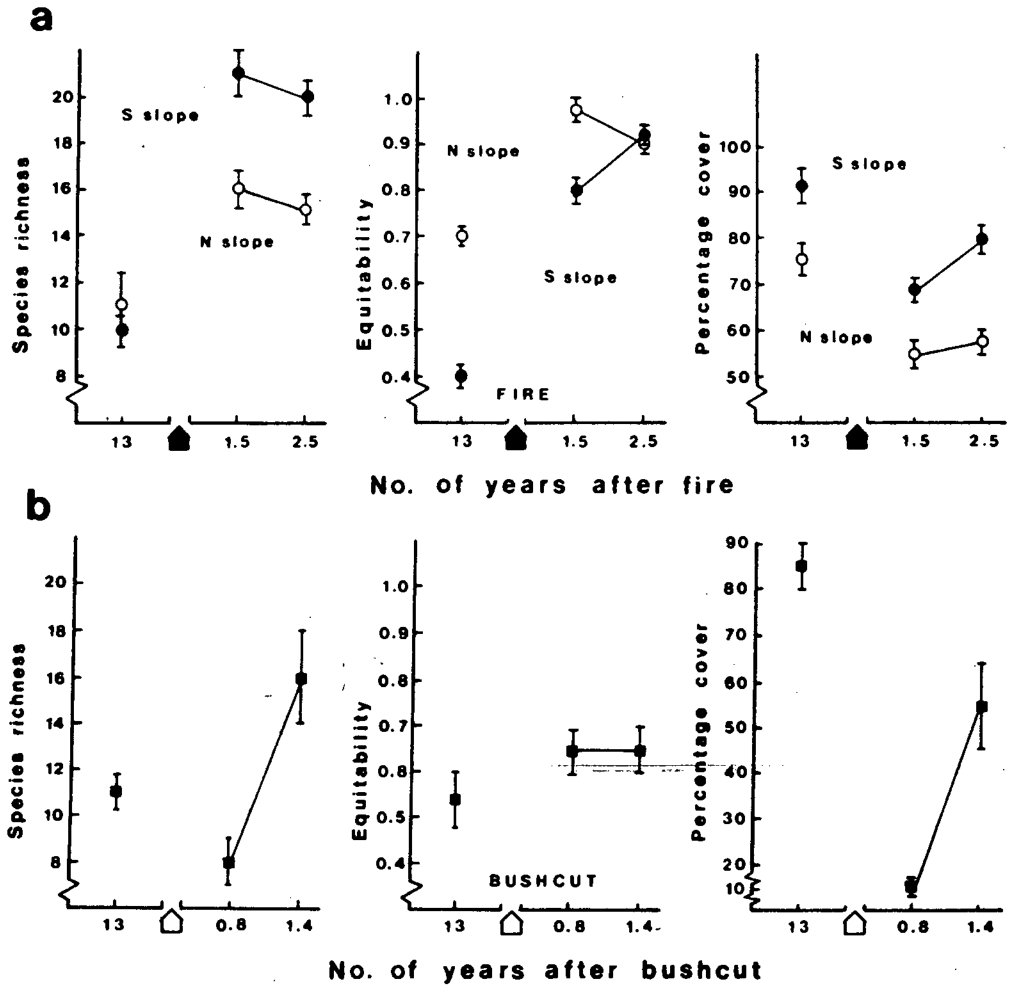


Fig. 3. Mean richness, equitability (Shannon-Wiener function) and projected canopy cover in 1 m² plots in mature and post-disturbance fynbos at (a) Brandewynkop and (b) Cape St. Francis. Vertical bars are SE.

Table 2. Mean relative percentage cover and species richness (±SE) in ten 1 m^2 plots in mature and burnt dune fynbos on different aspects. Significance assessed by t tests using arcsin transformed data where appropriate.

		Relative percentage cover				Species richness			
		Mature (13 yr)		Burnt (1.5 yr)		Mature (13 yr)		Burnt (1.5 yr)	
		North	South	North	South	North	South	North	South
Herbs									
Short-lived	HS	0.4 ± 0.3	0^{a}	0.5 ± 0.2	7.8 ± 1.5	0.3 ± 0.2^{b}	1.6 ± 0.4^{a}	1.6 ± 0.2^{b}	7.6 ± 0.5
Medium-lived	HM	4.2 ± 1.3^{a}	0.7 ± 0.2^{a}	41.4 ± 4.3	38.4 ± 6.5	1.0 ± 0.2^{a}	1.2 ± 0.5	4.7 ± 0.4^{b}	2.7 ± 0.5
Long-lived	HL	24.2 ± 3.9^{b}	61.9 ± 3.1^{a}	12.9 ± 1.3	11.1 ± 3.5	2.4 ± 0.2^{a}	1.7 ± 0.2	1.3 ± 0.2^{b}	2.5 ± 0.3
Shrubs									
Short-lived	SS	0.3 ± 0.2	0^{a}	1.5 ± 0.6^{b}	11.1 ± 1.9	0.7 ± 0.3	0	1.0 ± 0.2^{b}	2.4 ± 0.2
Medium-lived	SM	25.6 ± 6.3	14.3 ± 3.8^{a}	30.6 ± 2.8	30.3 ± 4.1	4.3 ± 0.6	3.1 ± 0.4	5.9 ± 0.4^{b}	4.3 ± 0.3
Long-lived	SL	45.1 ± 5.5^{a}	22.4 ± 5.4^{a}	13.3 ± 4.3	0.9 ± 0.2	2.3 ± 0.3	1.9 ± 0.5	1.5 ± 0.3	1.2 ± 0.3
Herbs									
Sprouters	H-SP	20.8 ± 4.4^{ab}	1.5 ± 0.8	51.2 ± 4.5^{b}	8.0 ± 4.0	2.2 ± 0.3^{a}	1.5 ± 0.5	6.2 ± 0.5^{b}	2.3 ± 0.7
Non-sprouters	H-NS	7.3 ± 3.6^{ab}	61.9 ± 3.3	0.6 ± 0.2^{b}	50.0 ± 5.8	1.3 ± 0.2	2.9 ± 0.4^{a}	1.2 ± 0.3^{b}	10.3 ± 0.7
Shrubs									
Sprouters	S-SP	32.6 ± 5.6^{b}	0.5 ± 0.5	19.1 ± 5.0^{b}	0.6 ± 0.3	2.2 ± 0.2^{b}	0.9 ± 0.3	2.4 ± 0.4^{b}	0.8 ± 0.3
Non-sprouters	S-NS	38.4 ± 7.0	36.2 ± 3.1	29.1 ± 3.9	41.0 ± 5.1	5.3 ± 0.8	4.2 ± 0.5^{a}	6.2 ± 0.4	7.7 ± 0.4

[a] Significantly different ($P<0.01$) from burnt site on same aspect.

[b] Significantly different ($P<0.01$) from same aged site on different aspect.

taxa were replaced with shorter lived species including annuals (HS, *Dischisma cilliatum, Cineraria* sp.), graminoids (HM, *Ficinia filiformis*) and shrubs (SM, *Aspalathus spinosa, Helichrysum argenteum*) which were absent from the pre-fire fynbos.

The most marked differences in species richness within the longevity groups were between burnt north and south slope communities, the latter having significantly higher numbers of HS and SS species (Table 2). The dramatic increase in species richness of the 1.5 yr south slope fynbos relative to the mature vegetation, was largely due to the post-fire establishment of numerous HS taxa.

Both sprouting herbs (e.g. *Ischyrolepis eleocharis*) and shrubs (e.g. *Olea exasperata*) contributed significantly more to the canopy cover on the north than the south slope in both mature and burnt vegetation (Table 2). Generally, sprouters were very poorly represented on the south slope both in terms of cover and richness. On the north slope, a significant increase in the cover of only the herbaceous sprouting component relative to the unburnt vegetation was apparent.

In terms of longevity groups the structure of the mature fynbos at Cape St Francis was similar to the north slope vegetation at Brandewynkop (Table 3). However, bushcutting resulted in a very different regeneration response to fire – a large increase in the relative cover of HS species, (e.g. *Tetragonia fruticosa, Zygophyllum uitenhagense*), few of which were recorded in the mature fynbos at Cape St Francis or at any of the Brandewynkop sites. These taxa accounted for the post-disturbance increase in species richness (Table 3; Fig. 3).

Bushcutting resulted in a significant increase in the cover and richness of both sprouting and non-sprouting herbs but a significant decline in the relative cover of non-sprouting shrubs (Table 3).

Table 3. Mean relative percentage cover and species richness (± SE) in mature and bushcut dune fynbos. Significance assessed by *t* tests using arcsin transformed data where appropriate.

		Relative percentage cover		Species richness	
		Mature (13 yr)	Bushcut (1.4 yr)	Mature 13 yr)	Bushcut (1.4 yr)
Herbs					
Short-lived	HS	0.1 ± 0.1[a]	41.1 ± 9.7	0.1 ± 0.1[a]	6.3 ± 0.7
Medium-lived	HM	0.2 ± 0.1[a]	2.2 ± 0.8	0.2 ± 0.1	1.0 ± 0.2
Long-lived	HL	14.0 ± 4.6	9.1 ± 4.8	2.0 ± 0.3	1.1 ± 0.3
Shrubs					
Short-lived	SS	0	0.8 ± 0.4	0 [a]	0.8 ± 0.3
Medium-lived	SM	36.8 ± 8.5[a]	22.9 ± 9.7	3.3 ± 0.4	3.3 ± 0.6
Long-lived	SL	49.1 ± 8.7	24.1 ± 6.7	5.5 ± 0.4	3.6 ± 0.5
Herbs					
Sprouters	H-SP	1.6 ± 0.6[a]	10.7 ± 3.9	1.0 ± 0.3[a]	3.6 ± 0.8
Non-sprouters	H-NS	12.6 ± 4.8[a]	41.6 ± 9.7	1.3 ± 0.2[a]	4.8 ± 0.6
Shrubs					
Sprouters	S-SP	31.5 ± 7.2	33.4 ± 9.2	5.2 ± 0.5[a]	3.1 ± 0.4
Non-sprouters	S-NS	54.5 ± 8.6[a]	14.2 ± 5.7	3.6 ± 0.4	4.6 ± 0.8

[a] Significantly different ($P<0.01$) from bushcut site.

Discussion

At all sites more than half the species present in the mature fynbos, including all the dominants, had re-established 1.5 years after disturbance. The multivariate analyses showed no clear separation in the ordination space between mature and post-fire communities on the north slope, nor between the mature and post-bushcut communities at Cape St Francis. These results are consistent with Egler's (1954) initial floristic composition pathway. However, despite the post-fire re-establishment of all the dominant species on the south slope, mature and successional communities showed a clear separation in the ordination space. Unlike the post-disturbance communities at the other sites, the post-fire south slope plots had a high cover of short-lived species. This phenomenon is not uncommon in more mesic fynbos communities (Kruger & Bigalke 1984) and other fire-prone mediterranean-type shrublands (Hanes 1971; Trabaud & Lepart 1980). At the bushcut site, there was a significantly high cover of post-disturbance ephemeral species 1.4 yr after bushcutting, (but not at 10 months), which would explain the greater distance of the former from the mature plots in the ordination field.

The different successional patterns evident at the three fynbos sites are the result of different successional processes due to different disturbances and site conditions (Pickett & White 1985; Walker & Chapin 1987). The north slope soils, which experience higher evapo-transpirational demand (Cowling 1984), are probably too dry to support a high biomass of mesophytic short-lived species. On the more mesic south slope, the high post-fire cover of short-lived species could, as a result of interference competition, result in the mortality of seedlings of longer-lived shrubs (S. M. Pierce & R. M. Cowling, unpubl.). These processes could cause differences in the mortality of seedlings of longer-lived shrubs on the south and north slopes. This inhibitory process (Connell & Slatyer 1977) resulting from the interaction of individual plants (Huston & Smith 1987), would vary spatially as a result of differential establishment of species in different longevity/growth form groups, and temporally in association with stochastic soil moisture fluctuations (*cf.* van der Maarel *et al.* 1985).

The post-disturbance pulse in richness at all sites is consistent with data from a variety of fire-prone mediterranean-type shrublands (Hanes 1971; Trabaud & Lepart 1980; Gill & Groves 1981; Westman 1981; Kruger & Bigalke 1984; Westman & O'Leary 1986; Hoffman *et al.* 1987). Not only are there a greater number of species but equitability is also high. Conditions after disturbance are suitable for the coexistence of short-lived species and longer-lived fynbos shrubs regenerating from wind-borne and soil-stored seeds (Pierce 1987) and resprouting thicket species.

Dune fynbos differs from most other fynbos communities in that it includes a component of sprouting subtropical thicket shrubs (*Euclea, Olea, Rhus* etc.) which establish from bird-dispersed propagules in between disturbances. These species are biologically similar to the obligate resprouters in chaparral (e.g. *Heteromeles arbutifolia, Quercus dumosa, Rhamnus* spp.) (Keeley 1986). Like their chaparral counterparts, established individuals are highly resilient to a range of fire regimes, and, as they are long-lived, will eventually gain dominance after extended fire-free periods. In chaparral, these species are most common on mesic sites (Keeley 1986). In mature fynbos on the north slope, we recorded a significantly higher cover of sprouting shrubs (largely *Olea exasperata* and *Euclea racemosa*) than on the south slope (Table 2). The above-mentioned species recruit numerous ramets after fire from sympodial lateral growth (Tinley 1985) and are possibly the most fire-resilient species in the dune landscape. Their high cover on the north slope does not necessarily refute the general tendency for thicket development to be most rapid on mesic sites. It probably reflects a history of frequent burning which has favoured these species which produce ramets, but which has hindered the establishment of seedlings of other thicket species.

In general, however, secondary successional patterns in dune fynbos were similar to those recorded in other fynbos communities in the re-establishment of pre-disturbance dominants (Kruger & Bigalke 1984). The post-disturbance compositional turnover is largely the result of differential longevity as biomass recovers and competition for resources increases (Egler 1954; Peet & Christensen 1980). Differential establishment of species after disturbance may result in changing dominance patterns (Van Wilgen & Kruger 1981; Bond 1984; Cowling 1987). A predictive understanding of the variation in post-disturbance recruitment patterns in dune fynbos must await the results of studies on seedbank composition and dynamics, germination cues and mortality trends (Pierce & Cowling in prep.).

Acknowledgements

We thank Penny Mustart, Carolyn Hoffman and Nicole Goedhart for technical assistance. G. Davis, R. Knight and B. M. Campbell commented on an earlier draft. This study was funded by the CSIR's Foundation for Research Development and forms part of the Fynbos Biome Project.

References

Austin, M. P. 1977. Use of ordination and other multivariate descriptive methods to study succession. Vegetatio 35: 165–175.

Bond, W. J. 1984. Fire survival in Cape Proteaceae – influence of fire season and seed predators. Vegetatio 54: 65–74.

Campbell, B. M. 1985. A classification of the mountain vegetation of the fynbos biome. Mem. Bot. Surv. South Africa 50: 1–121.

Connell, J. H. & Slatyer, R. O. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. Am. Nat. 111: 119–144.

Connell, J. H., Noble, I. R. & Slatyer R. O. 1987. On the mechanisms producing successional change. Oikos 50: 136–137.

Cowling, R. M. 1984. A syntaxonomic and synecological study in the Humansdorp region of the fynbos biome. Bothalia 15: 175–227.

Cowling, R. M. 1987. Fire and its role in coexistence and speciation in Gondwanan shrublands. S. Afr. J. Sci. 83: 106–112.

Egler, F. E. 1954. Vegetation science concepts I. Initial floristic composition, a factor in old-field vegetation development. Vegetatio 4: 412–417.

Gray, A. J., Crawley, M. J. & Edwards, P. J. (eds). 1987. Colonization, succession and stability. Blackwell Scientific Publications, Oxford.

Gill, A. M. & Groves, R. H. 1981. Fire regimes in heathlands and their plant ecological effects. In: Specht, R. L. (ed.), Ecosystems of the World 9B. Heathlands and related shrublands, pp. 61 – 84. Elsevier, Amsterdam.

Hanes, T. 1971. Succession after fire in the chaparral of southern California. Ecol. Monogr. 41: 27 – 42.

Hoffman, M. T., Moll, E. J. & Boucher, C. 1987. Post-fire succession at Pella, a South African lowland fynbos site. S. Afr. J. Bot. 53: 370 – 374.

Huston, M. & Smith, T. 1987. Plant succession: life history and competition. Am. Nat. 130: 168 – 198.

Keeley, J. E. 1986. Resilience of mediterranean shrub communities to fires. In: Dell, B., Hopkins, A. J. M. & Lamont, B. B. (eds), Resilience in mediterranean-type ecosystems, pp. 95 – 112. Junk, The Hague.

Kruger, F. J. 1977. Ecology of Cape fynbos in relation to fire. In: Mooney, H. A. & Conrad, C. E. (techn. coords), Proceedings of the environmental consequences of fire and fuel management in mediterranean ecosystems, pp. 75 – 84. USDA Forest Services General Technical Report WO-3, Washington DC.

Kruger, F. J. 1979. South African heathlands. In: Specht, R. L. (ed.), Ecosystems of the World, 9A. Heathlands and related shrublands, pp. 19 – 80. Elsevier, Amsterdam.

Kruger, F. J. & Bigalke, R. C. 1984. Fire in fynbos. In: Booysen, P. V. de & Tainton, N. M. (eds), Ecological effects of fire in South African ecosystems, pp. 67 – 114. Springer-Verlag, Berlin.

Noble, I. R. & Slatyer, R. O. 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. Vegetatio 43: 5 – 21.

Odum, E. P. 1969. The strategy of ecosystem development. Science 164: 262 – 270.

Peet, R. K. & Christensen, N. L. 1980. Succession: a population process. Vegetatio 43: 131 – 140.

Pickett, S. T. A. & White, P. S. (eds) 1985. The ecology of natural disturbance and patch dynamics. Academic Press, New York.

Pickett, S. T. A., Collins S. L. & Armesto, J. J. 1987. Models, mechanisms and pathways of succession. Bot Rev. 53: 335 – 371.

Pierce, S. M. 1987. Dynamics of soil-stored seed banks in relation to disturbance. In: Cowling, R. M. *et al.* (eds), Disturbance and the dynamics of fynbos biome communities, pp. 46 – 55. S. Afr. Nat. Sci. Prog. Rep. No. 135. CSIR, Pretoria.

Tinley, K. L. 1985. Coastal dunes of South Africa. S. Afr. Nat. Sci. Prog. Rep. 109. CSIR, Pretoria.

Trabaud, L. & Lepart, J. 1980. Diversity and stability in garrigue ecosystems after fire. Vegetatio 43: 49 – 57.

Van Wilgen, B. W. & Kruger, F. J. 1981. Observations on the effects of fire in mountain fynbos at Zachariashoek, Paarl. Jl. S. Afr. Bot. 47: 195 – 211.

van der Maarel, E., de Cock, N. & de Wildt, E. 1985. Population dynamics of some major woody species in relation to long-term succession on the dunes of Voorne. Vegetatio 61: 209 – 219.

Walker, L. R. & Chapin, F. S. 1987. Interactions among processes controlling successional change. Oikos 50: 131 – 135.

Westman, W. E. 1981. Diversity relations and succession in Californian coastal sage scrub. Ecology 62: 170 – 184.

Westman, W. E. & O'Leary, J. F. 1986. Measures of resilience: the response of a coastal sage scrub to fire. Vegetatio 65: 179 – 189.

Whittaker, R. H. 1972. Evolution and measurement of species diversity. Taxon 21: 213 – 251.