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COASTAL DUNE ECOLOGY AND MANAGEMENT IN THE EASTERN CAPE

THESIS

Submitted in fulfilment of the requirements for the Degree of
DOCTOR OF PHILOSOPHY
of Rhodes University

by

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December 1992

TABLE OF CONTENTS

CHAPTER THREE : EVIDENCE FOR A CLEMENTSIAN VIEW OF SUCCESSION IN THE DUNEFIELDS AT MTUNZINI, NATAL

CHAPTER FOUR : SUCCESSION ON COASTAL DUNES AND DUNE SLACKS AT KLEINEMONDE. II. SUPPORTIVE EVIDENCE FOR THE CONCEPTUAL MODEL

CHAPTER FIVE : RECREATIONAL USE OF THREE URBAN BEACHES AT EAST LONDON, AND EFFECTS ON COASTAL DUNE VEGETATION

CHAPTER SIX : THE EFFECTS OF HUMAN TRAMPLING AND OFF-ROAD VEHICLES ON DUNE VEGETATION AT GREAT FISH POINT, EASTERN CAPE

CHAPTER SEVEN : A REVIEW OF COASTAL DUNE STABILIZATION IN THE CAPE PROVINCE OF SOUTH AFRICA

CHAPTER EIGHT : A SURVEY OF COASTAL DUNE STABILIZATION IN SOUTH AFRICA: QUANTIFICATION AND EVALUATION

PREFACE

South Africa is blessed with a varied and exceedingly attractive coastline, and it is not uncommon to be alone on an expansive stretch of undeveloped beach, with no signs of human habitation or influences. Unfortunately this rewarding and fulfilling experience is becoming less obtainable as population numbers increase and the need for similar experiences grow. The demand on our coastal resources is increasing at an alarming rate and we need to determine maximum utilization levels before we kill the goose that lays the golden egg. It is also important that the ecological needs of coastal ecosystems are considered, since the social and economic value of the coastline is dependent on healthy ecological processes. To help achieve these goals, fundamental and applied ecological studies were undertaken along the Eastern Cape coastline, defined as the area from Cape St Francis in the west to the Kei River in the east.

Each Chapter is presented in the format of a paper, with its own introduction, methods, results, discussion and conclusion. This approach has been necessary due to the range of topics and varied approaches adopted for each. Chapter Two has been published in Monographs of Systematic Botany, Missouri Botanical Gardens as part of the proceedings of the 1985 AETFAT conference in St. Louis, Missouri, where I gave an oral presentation. Chapter Seven has been published in Landscape and Urban Planning. Chapter Six was presented at the Dune's 89 conference in Swakopmund, Namibia, and Chapter Eight was presented at the 70th Annual Ecological Society of America conference in Minneapolis in 1985, and portions of this chapter and Chapter Five have been published in two articles in Veld & Flora.

REFERENCES TO THESE PAPERS:

AVIS, A.M. 1985. Coastal Management and Dune Stabilization. Veld & Flora 71(2): 34-37.

AVIS, A.M. 1986. Some basic guidelines for managing and preserving our coastline. Veld & Flora 72(2): 51-55.

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Information from most of the other chapters have been presented at local conferences.

This work would not have been possible without the support and encouragement of many people. I am particularly indebted to my supervisor, colleague and friend, Professor Roy Lubke. It was his enthusiasm and support that kindled my interest in ecology, and his encouragement during the process of producing this thesis is greatly appreciated. I sincerely hope I have produced something to be proud of. I would also like to thank Professor Norman Pammenter of the University of Natal, Durban who worked with Roy and I at Mtunzini. It was deemed necessary to compare the Eastern Cape coastal dunes with the model system of Mtunzini, and Norman's knowledge of this area and useful comments on Chapter Three are greatly appreciated. Dr Pablo Weisser of the National Botanical Institute is warmly thanked for supplying

maps and copies of unpublished manuscripts relating to the Mtunzini dunefield. I am grateful for the stimulation received from discussions with Dr Patrick Hesp on the geomorphological aspects of coastal dune systems. My colleagues at the Department of Botany are thanked for their support and encouragement, particularly during these past few months. The numerous students and colleagues, particularly Andrea Sinclair and Berndt Sonnenberg, who assisted with field work and data analysis from time to time are also thanked.

The financial support of the Foundation for Research Development, who awarded an MSc and later a PhD bursary during my period of full time study are acknowledged. The Department of Botany, Rhodes University is thanked for the award of a Graduate Assistant Bursary and for providing equipment and facilities. The Flora Conservation Committee of the Botanical Society of Southern Africa are gratefully acknowledged for awarding me their Flora Conservation Scholarship for two consecutive years. Research funds were made available by the Rhodes University Joint Research Committee; and the Municipality of the City of East London are thanked for providing funds to cover the research undertaken in Chapter Five. The co-operative attitude of the Directorate of Forestry, and in particular the Eastern Cape Regional Directorate is appreciated.

The production of this thesis has only been possible through the dedication and support of many people. The late Heather Kew, who typed much of the first draft, is posthumously thanked for her support over so many years. She is sadly missed, but not forgotten. Sue Drake, who's incommensurable dedication is largely responsible for the quality of the final production, deserves a gold medal. Claire Cameron is also thanked for assisting with some of the tables and final layout. John Keulder, Oakley West and Debbie Brody of the Carto Unit, Department of Geography, are thanked for final production of most of the figures, and Belinda Haggard for drafting most of the figures in Chapters 3, 4 and 8.

I am most grateful to my parents for their support over so many years, and for providing me with the opportunity to study for such an extended period.

Finally, a sincere, warm and affectionate thank you to my wife, Cheryl, for her love, support and encouragement over many years.

Although I am aware that this work only represents a single grain of sand in the dune of knowledge, may I humbly hope it rests upon the crest.

ABSTRACT

The importance of understanding the ecological functioning of coastal dune systems is emphasized as being fundamental to the correct management of the dune landscape. Dune vegetation along the Eastern Cape coastline, from Cape St Francis in the west to Kei Mouth in the east was described in terms of the distribution and phytochorological affinities of the taxa. At a regional scale species distribution was strongly influenced by both the climate, particularly rainfall, and the phytochorological affinities of the taxa. Seven communities were defined using TWINSPAN, and the interrelationships between these communities in any one area appeared to be linked to a successional gradient. Dune Slacks are thought to play a key role in this successional sequence, and a temporal study of this community led to a conceptual model of plant succession in these dunefields. Climate, particularly rainfall and wind, are major factors influencing plant succession. Wind-borne sand causes the slacks to migrate in an easterly direction under the influence of the predominantly westerly winds, although easterly winds, mainly in summer months may reverse these trends. Autogenic changes appeared to be important in this succession, and a comparative study of a good example of a primary succession at Mtunzini in Natal was undertaken to elucidate the main mechanism of change. Eight communities that were identified here were concluded to be distributed along a gradient of increasing age, with successional changes predictable, linear and directional. Species were grouped in distinct zones along the continuum and edaphic changes (decrease in soil pH, increase in organic matter and exchangeable bases) were related to the community based changes in species composition. The mechanism of change supported the facilitation model of plant succession which is a modification of the original Clementsian concept. Similar results were found in the Eastern Cape, but due to the harsh environment, multiple pathways of succession exist. Data from this study lent support to the model of plant succession developed earlier, and confirmed that the dune slacks played an important role in this facilitation by acting as centres of diversity. The foredunes were found to have an indirect role in protecting these slacks from salt spray and sand movement.

The central theme of the management studies was to investigate the ecological consequences of recreational pressure within the dune environment. Current levels of beach utilization at East London were lower than other beaches in South Africa, but a general trend of increasing utilization due to socio-political changes can be expected. The suitability of questionnaire surveys to assess aspects such as the adequacy of facilities, perceptual carrying capacity and the beach users opinion of natural vegetation and preference for particular beaches was demonstrated. The dune vegetation was found to be sensitive to human trampling, but at current levels, the ecological carrying capacity will not be exceeded since results of the aerial census counts and questionnaire survey revealed that few people entered sensitive zones such as the coastal forest. More detailed long term studies on the susceptibility of dune vegetation to both trampling and off-road vehicle impacts revealed a low resilience of dune plant communities to these effects. Although susceptibility differed between the three communities tested, generally the greatest amount of damage occurred after the first few passages, and vehicles caused a more significant decrease in height when compared to trampling. Recovery rates were slow and low levels of repeated damage were sufficient to retard or prevent the recovery of the plants. Stricter control of vehicle use on beaches is therefore required, and in high use zones the ecological carrying capacity should be increased by providing access tracks if possible, or if not possible, by restricting access.

A historical account of the process of dune stabilization showed that although first initiated in 1845, indigenous species were only used in the past three decades. The use of alien species has resulted in problems such as a reduction in the ecological integrity and aesthetic appeal of coastal systems. The techniques applied in the stabilization of drift sands with indigenous vegetation have been successful, as revealed by a quantitative survey of 17 sites in the Eastern Cape. Sites were grouped by multivariate analysis on the basis of their species composition, and variability between sites was dependent on the types of species planted. Selection of suitable species is therefore important and is discussed with respect to their natural distribution along the coast. The long term objective of stabilization should be the creation of functional, diverse, aesthetic ecosystems, since the intrinsic and economic value of the dune landscape for tourism lies therein. However, detailed studies should be undertaken prior to implementing a manipulative process such as dune stabilization, since ecological processes may be disrupted. An understanding of such processes is therefore important if one wishes to effectively manage the dune landscape.

CHAPTER SUMMARIES

INTRODUCTION

The main objectives of this thesis are to investigate the dynamics of dune vegetation in the Eastern Cape, and elucidate the main pathways of succession; and secondly, to assess the resilience of dune vegetation to recreational pressure, and its suitability for dune stabilization. It is argued that there is a need for an ecological approach to dune management, and in light of this relevant concepts in vegetation science and successional theory are reviewed. The philosophical approach to this thesis follows the Judeo-Christian ethic of environmental accountability, which is important in view of the dynamic and sensitive nature of the coastline. For this reason, it is suggested that an ecological approach to dune management makes sound utilitarian sense. The application of these concepts in the following chapters follow two lines of approach, namely ecological studies of a fundamental type, and applied ecological studies of a management nature.

CHAPTER ONE

The Eastern Cape region, between Cape St Francis and Kei Mouth, has long been recognized as a transition zone where major phytochoria of southern Africa converge. A multivariate analysis of the coastal vegetation from a survey of 152 relevés at 62 sites revealed the nature of the seven communities recognized by TWINSPAN. The distribution of species was strongly influenced by both the climate and phytochorological affinities of the taxa. Cape species decreased from west to east, and Tongoland/Pondoland species, mainly woody trees and shrubs, decrease from east to west, as a consequence of changing rainfall patterns. TWINSPAN initially divided the data set into five communities, but after re-analysis of subsets of the data, a further two woody communities were recognized. The Dune Pioneer community dominated by herbs and grasses with a typically low species diversity was separated into three sub-communities on the basis of diagnostic species. Dune Slacks were more diverse and luxuriant, and the four sub-communities appeared to be related to a soil moisture gradient. The Rocky Cliff communities were either dominated by forbs or woody species which were severely wind pruned. Bushpocket communities were floristically similar to the Dune Scrub, but occurred as isolated patches of vegetation in more extensive dunefields. Dune Scrub was common west of the Kowie River, and Dune Thicket towards the east in the higher rainfall areas. Further west Dune Scrub formed a mosaic with fynbos which eventually replaces it. Two fynbos communities were recognised, the Scrub Fynbos with a predominance of shrubs, and the Dune Fynbos dominated by herbs and restios. Ordination suggested a successional gradient from Dune Slack to Dune Thicket, with increases in community complexity, species diversity and physiognomy occurring in any one area.

CHAPTER TWO

A temporal study of plant community change in a dune slack at Kleinemonde from 1981 to 1985, and observations on foredune communities together with interpretive climatic data provided further insight into dune plant succession. *Scaevola plumieri*, along with a few other species are pioneers of the foredunes. In wet slacks, the sedge *Scirpus nodosus* invades by means of wind borne seeds; whereas in the drier margins, *Arctotheca populifolia* and *Sporobolus virginicus* are the major pioneers. Once *S. nodosus* becomes established, *Juncus kraussii* appears, suggesting that slacks dominated by this rush are older and drier. In the last two years a few shrubs characteristic of older slacks and Dune Scrub such as *Rhus crenata* were recorded, and they have continued to increase in abundance. Climatic factors, especially rainfall and wind, appear to be the major factors affecting natural plant succession in the ecosystem. A decline in rainfall and available soil moisture in 1984 and 1985 resulted in a decline in plant abundance in the slacks as dry wind-borne sand buried the vegetation. The slack vegetation appears to migrate in an easterly direction as the predominant westerly winds move large amounts of sand and bury the plants on the western side of the slacks. A conceptual model of plant succession in the dunefields is presented, but it is acknowledged that unless higher rainfall conditions return, succession to the climax Dune Thicket will not be attained.

CHAPTER THREE

Classical and contemporary theories of succession are reviewed and evaluated in the light of a quantitative vegetation survey of an area of dunefield on the Zululand coastline of South Africa, which presents a good example of primary succession and could be compared with the situation in the Eastern Cape. Vegetation and soil parameters (pH, conductivity, percentage organic matter, K, Na, Mg, Ca, P) were sampled in thirty-four 10 by 10 m relevés located along 3 transects and the data sets classified using TWINSPAN and ordinated using DECORANA. Plant diversity and importance values of life forms of selected species were calculated and illustrated along the successional gradient and eight plant communities were classified and described. Ordination revealed that these communities were distributed along a gradient of increasing distance from the sea, and increasing age of the dunes as estimated from dating the parallel dune ridges identified on sequential aerial photographs of known age. The communities along this chronosequence were Pioneer, Enriched Pioneer, Open Dune Scrub, Closed Dune Scrub, Bushclumps, Bushclump/Forest Margin Transition, Forest Margin and Forest. These communities showed a general increase in species diversity, species richness, mean number of species per relevé, stature, biomass and total mean cover per relevé. Herbs were initially the dominant life form, but grasses became dominant in the transitional communities. Later in the successional sequence, shrubs, ferns and trees became more abundant, but in the forest a more even distribution of life forms was noted. The importance value curves showed that species were not evenly distributed along a gradient but were grouped in distinct zones along the continuum, an observation supported by the ordinations generated using DECORANA. Soil properties changed along the chronosequence. A decrease in pH and increase in % organic matter and exchangeable bases with increasing age was noted. Generally, the data tend to support the community-unit concept of vegetation ecology, and the mechanism of change supports the facilitation model.

CHAPTER FOUR

Chapter Two led to the development of a model of plant succession in Eastern Cape dunefields, which was tested by quantitative studies in this chapter. Thirty-six relevés of vegetation in the dunefields were quantitatively sampled, and multivariate analysis revealed distinct plant communities along a gradient of increasing distance (age) from the sea, namely from Pioneer to Young Slack, Old Slack, Bushclump, Thicket Margin and Dune Thicket communities. Classification of soil samples recorded at each relevé isolated a number of groups which could be related to the plant communities, and the ordination revealed a gradient of increasing distance from the sea related to soil development. With age, species richness, cover, diversity, number of life forms and structural complexity of the communities all increased. Individual species became larger and more complex, with dominance changing from grasses and herbs on the foredunes to shrubs and trees in the Dune Thicket. An increase in soil organic matter, exchangeable bases (Ca, Mg, Na, K), phosphate and conductivity and a decrease in soil pH from foredune to thicket was noted. It is argued that these distinct communities represent directional changes along a successional sequence as proposed in the earlier model, and that the mode of transition between them relies heavily on autogenic changes. The dune slacks play an important role in this facilitation by acting as centres of diversity within the sparsely vegetated dunefield, and the foredunes in protecting these dune slacks from salt spray and sand movement.

CHAPTER FIVE

The recreational use of coastal dune systems and beaches impacts negatively on the ecological functioning of these systems, and information on their carrying capacity is useful. Data were gathered for three beaches in the coastal city of East London, to determine current levels of utilization, by means of aerial census counts on peak days in December 1984, and January 1986 and 1989. A questionnaire survey was aimed at assessing the popularity of the beaches and adequacy of facilities, and experimental studies were undertaken to assess the tolerance of natural vegetation to human trampling. Although levels of utilization are lower than other beaches in South Africa and abroad, a trend of increasing use was noted, this mainly being the result of socio-political changes. From the questionnaire survey it was evident that the Nahoon Beach was most popular, mainly because people were attracted to its natural and undeveloped character. It was felt that this area and the Nahoon River should not be developed commercially, whereas at the Eastern Beach more facilities could be provided. The emphasis should therefore be on resource protection at the Nahoon Beach, whereas the Eastern Beach should be developed into a more intensive use zone. Nevertheless, there was a need for a beach café, picnic spots and improved ablution facilities at all three beaches. The perceptual carrying capacity had not been reached at any of the beaches, and results suggest that overcrowding will only occur at densities of between 6 to 9m^2/person. However, the surrounding vegetation was found to be very sensitive to human trampling, particularly the Dune Scrub and Forest communities at the Nahoon Beach. The forest layer at the Eastern Beach was less sensitive, owing to the more level topography and the greater abundance of grasses. The protection of these communities is important due to their ecological and intrinsic value, but fortunately results showed that few people entered the coastal forest.

CHAPTER SIX

Studies abroad have shown that coastal vegetation is very susceptible to off-road vehicle (ORV) and human trampling effects, but prior to this study, no data were available in South Africa. An experimental study was initiated to quantitatively measure the sensitivity of vegetation to these effects, to monitor the recovery rates and to assess whether dune communities would tolerate low levels of disturbance over extended periods of time. Three dune communities dominated by single species were chosen, namely, the pioneer shrub *Scaevola plumieri*, the pioneer grass *Sporobolus virginicus* and the fine leaved thymeleaceous shrub *Passerina rigida*. In experimental plots these communities were exposed to measured amounts of trampling and ORV effects on a single day. Results were expressed as a percentage decrease in plant height and cover, which was measured after each successive passage, and recovery rates were monitored for an 18 month period. In order to assess long term effects additional sample plots were repeatedly exposed to damage which caused a 10, 20 and 35% decrease in height. Significance was tested using a pairwise analysis of variance, which showed that height of *P. rigida* decreased significantly after only one passage and one pass of an ORV. *S. virginicus* was most resistant to trampling, but *Scaevola plumieri* was more susceptible to trampling than ORV's, possibly due to its growth habit. The greatest amount of damage always occurred after the first few passages, and it was concluded that dune vegetation in South Africa has a low resistance to trampling and ORV's when compared to similar coastal plant communities studied elsewhere. Rates of recovery were also slow, and although *Sporobolus virginicus* recovered best from both trampling and ORV impacts, none of the species fully recovered after 18 months. There was also no real difference in the rates of recovery following a trampling or ORV episode, and height of *Passerina rigida* continued to decline for the duration of the study. Although levels of repeated damage were low when equated to number of passages or vehicle passes per month, they were sufficient to retard or prevent the recovery of the various communities. This effect was least pronounced for *Sporobolus virginicus*, which would tolerate low levels of trampling or ORV passages, but most dramatic for *Passerina rigida*, which could not withstand any disturbance at all. The main effect on the substrate was to loosen rather than compact the loose sand, which would result in increased sand movement. Implications for management include stricter control of vehicle use on beaches, and in high use zones, human impact management plans should be implemented to increase the ecological carrying capacities of the natural systems, and specific recommendations are made in this regard.

CHAPTER SEVEN

An historical account of the process of dune stabilization is presented. In South Africa, organized dune stabilization began in 1845 in the Western Cape with the introduction of Australian *Acacia* species which were regarded as the most useful plants for this process. Initially, seed was sown directly onto the sand, but in 1875 this was modified by spreading city refuse over the bare sand to temporarily stabilize the sands before seeding with Port Jackson Wattle and a few other species. This proved uneconomical because of the need to construct a railway line, and in 1896 a French technique was introduced. A foredune was formed at the source of the drift sand by constructing barriers with wooden poles or Marram grass. The area behind this was then thatched with brushwood or seeded with grass before introducing alien woody species. Later the area was simply covered with seed-bearing *Acacia* branches. In the late 1940's it was realised that the ability of alien species to oust indigenous species posed a threat to the natural vegetation. However, it was not until 1974 that their use was curtailed. The present policy is to only stabilise areas when absolutely necessary, using indigenous species. An artificial foredune is no longer constructed, but brushwood packing prior to seeding is still undertaken. Indigenous seedlings, grown in nurseries are also planted under the brushwood and successful stabilization takes at least five years. Harmful effects which arise from the use of alien species are discussed and include the ability of species to produce impenetrable thickets and suppress the growth of indigenous vegetation, the increase in the periodicity of fires, the draining of soil water resources and loss of cultivated land. The problem associated with stabilizing large sand drifts is the net loss of sand from beaches. Dune stabilization is an important management tool in the coastal zone, but there is a need for greater awareness of the problems associated with both stabilization using alien species and with poorly planned development.

CHAPTER EIGHT

The success of the dune reclamation programmes of the Directorate of Forestry and the use of indigenous vegetation for dune stabilization was quantitatively assessed. A total of 17 stabilization sites ranging from Sunday's River mouth in the west to Kei River mouth in the east were sampled to assess the species composition and abundance of vegetation in each site. These data were analyzed by TWINSPAN and DECORANA, and the total mean percentage cover and density, diversity and importance values of all species calculated and used to describe each site. Relevant documents of the Directorate of Forestry, outlining the activities undertaken at each site were also perused to assess the amount of work undertaken and the plant species and techniques that were used. TWINSPAN grouped sites found in similar localities, mainly on the basis of their species composition. Ordination of the data showed that the variability between sites was not related to the natural distribution of the indigenous vegetation, but was dependent on the types of species planted at the different stabilization sites. The importance of temporarily stabilizing the dune surface and the factors influencing species selection and establishment were reviewed. It is felt that more emphasis should be placed on creating diverse, functional, self perpetuating ecosystems since the aesthetic appeal of coastal areas has an important economic benefit in terms of increased tourism to sites of natural beauty. Indigenous species most suited to dune stabilization are discussed with respect to their natural distribution along the Eastern Cape coastline.

CONCLUDING CHAPTER

Coastal dune vegetation in the Eastern Cape is diverse and influenced by the variable climate and chorological complexity of the region. The low and erratic rainfall is also responsible for the maintenance of mobile dune systems along this stretch of the coastline, and together with wind, it exerts a strong influence on the establishment and growth of plants at a local scale. Salt spray and edaphic factors were found to be of secondary importance in the complete successional sequence, but within dune slacks, soil moisture affected species composition. Communities were found to be linked along a gradient of increasing complexity, and changes in species composition were independently linked to changes in

edaphic properties. Autogenic processes were very important in the successional sequence, and a comparative study of a primary successional sequence in Natal showed that the facilitation model was the main mechanism of change. Foredunes played an indirect role in this facilitation, and dune slacks were important nuclei which could be invaded by more mesic species thus leading to a climax woody plant community of Dune Thicket or Fynbos.

Management studies suggested that current levels of beach use did not exceed the physical, perceptual and ecological carrying capacity of three urban beaches. From the questionnaire surveys, useful information ranging from the adequacy of existing facilities and the beach users opinion of areas of ecological importance were obtained, and such information could be used to solve the problem of whether to increase access to sensitive areas or to preserve them. This is important since the dune vegetation was found to be very sensitive to both trampling and vehicle impacts. A long term study revealed that this vegetation had no carrying capacity for ORV's and a very low capacity for human trampling. Uncontrolled use of dune systems would require dune stabilization, and although it was found that techniques using indigenous vegetation were suitable, the need for many of the costly and manipulative stabilization programmes was questioned. It is therefore concluded that ecological processes must be considered when managing the coastal dune environment.

LIST OF FIGURES

CHAPTER ONE

CHAPTER TWO

CHAPTER THREE

CHAPTER FOUR

CHAPTER FIVE

CHAPTER SIX

CHAPTER SEVEN

CHAPTER EIGHT

LIST OF TABLES

CHAPTER ONE

CHAPTER TWO

CHAPTER THREE

CHAPTER FOUR

CHAPTER FIVE

CHAPTER SIX

CHAPTER SEVEN

CHAPTER EIGHT

LIST OF PLATES

CHAPTER ONE

CHAPTER TWO

CHAPTER THREE

CHAPTER FOUR

CHAPTER FIVE

CHAPTER SIX

CHAPTER SEVEN

CHAPTER EIGHT

LIST OF APPENDICES

GENERAL INTRODUCTION

This thesis has two main objectives. Firstly, to investigate the dynamics of dune vegetation in the Eastern Cape, and elucidate the main pathways of succession; and secondly, to assess the resilience of dune vegetation to recreational pressure, and its suitability for dune stabilization. The fundamental studies undertaken to fulfil the first objective, and the more applied research to meet the second, have as their unifying goal the need for sound ecological principles to be incorporated into management decisions which will affect the sensitive and dynamic coastal zone. The need for an ecological approach to dune management will be presented here, followed by a review of relevant concepts in vegetation science and successional theory. Finally, the philosophical approach underpinning this thesis, and the structure and outline of subsequent chapters will be explained.

THE NEED FOR AN ECOLOGICAL APPROACH TO DUNE MANAGEMENT

Coastal dune systems are highly diverse and variable environments, combining outstanding scenic variation and beauty with a wealth of animal and plant life. Due to their location at the interface between land and sea, they present an attractive area for human activities. They are often multifunctional systems of great importance to society, offering utility functions such as coastal defence, recreation, nature conservation, housing and wilderness areas. However, since the dune landscape is extremely complex and varied in space and time, a dynamic approach towards management is required (Wanders 1989). Such an approach requires a clear understanding of the ecological processes active in the dune environment (van der Meulen *et al.* 1989), and in 1974 Clark emphasized the importance of adopting an ecological approach to coastal zone management. He believed that the fundamental goal of management was to ensure "best achievable ecosystem function", and derived eleven principles from ecology to underlie major management functions. Aspects such as ecosystem integrity, linkages between ecosystems, energy flow and storage were considered important by Clark. Also, since many of man's projects backfire through the ecosystem, the ecological effects of specific projects or actions should be assessed.

Within the coastal zone, as defined by the Council for the Environment (1989) to only include actual coastal feature such as lagoons, dunes and beaches, it is critical for management to take into account the dynamic nature and vulnerability of these various systems to numerous forms of disturbance; for example, temporal and spatial scales relating to dune building (Ranwell 1979). Most often a dune area will serve several functions, from nature conservation to high intensity recreational use, and the manager must determine if these various uses are in conflict with one another. More importantly, he needs to know the natural characteristics of the dune landscape, and the important ecological processes acting on the system, to determine if current functions or uses conflict with these ecological processes. For information to be useful to the manager, it should show ecological relationships and developments within the dune landscape, and their causes, for example, plant succession. For this reason research needs to be extended to the ecological impacts of human activities such as trampling and off-road vehicles, since all utility functions will influence the dune environment, and must therefore be counteracted (Wanders 1989).

However, the natural dune landscape is dynamic and spatial patterns are changeable, making the main aim of environmental management - to promote beneficial and counteract deleterious human impacts (Westoff 1989) - difficult to achieve. To maintain the delicate and precarious balance between too much and too little, dune management must not be static but aimed at guiding changes and processes by focusing on the basic components of the landscape (Wanders 1989). It is also important to accommodate for natural fluctuations within the system, but to do so the coastal manager has to be able to determine whether a particular event (e.g. blowout dune development) could be considered a natural event. If so, no remedial action would be required, but if not, remedial or manipulative actions, such as dune stabilization, would need to be undertaken. The action to be taken is therefore dependent on a particular set of criteria, not the least of which is the ecological processes acting on that system.

Earlier dune management philosophy throughout the world has been conservative and meddlesome. The best example of this is from North Amercia, where widescale and expensive shoreline stabilization and beach protection measures rely on engineering structures or nourishment schemes to "protect" barrier islands and shorelines. Not only are they expensive, but they are also not very effective. Canis *et al.* (1985) feel that a better solution is to design to live with the flexible coastal environment, and not to fight nature with a line of defences. It is important to cater for natural erosion events, since no erosion problem will exist until a structure is built on a shoreline. Dunes should also be protected, since their removal reduces the sand supply used by the beach to adjust its profile during storms (Canis *et al.* 1985). Detailed studies should be undertaken if one wishes to adopt a hard structural approach to coastal management (Buckley 1980), since very often shoreline engineering destroys the beaches it was intended to save (Canis *et al.* 1985). Ecological engineering approaches, such as dune stabilization programmes, can also result in problems of downdrift beach erosion, discussed in Chapter Seven. For these reasons, extensive dune stabilization programmes, such as those undertaken in the first half of this century are no longer initiated in South Africa (Cobby 1988).

In Europe, where the rainfall is high and the climate more favourable for plant growth, interference with dune communities has had the opposite effect. Here, changes in vegetation dynamics leads to the development of higher successional closed scrub communities at the expense of pioneer communities (Westoff 1989). A re-examination of concepts such as constancy and spatial variation (De Raeve 1989) has resulted in a trend towards a more dynamic approach to dune management in Europe (Wanders 1989; van der Meulen *et al.* 1989), and calls for a similar approach to be adopted in North America (Canis *et al.* 1985). Although there have been some changes in attitude to dune management, it would be wise to adopt the same general philosophy in South Africa.

According to Usher (1978) the management of coastal areas is often concerned with the management or control of seral communities, due to the presence of active successional processes. This has been a major problem in Europe and particularly the Netherlands, where grazing and mowing have been applied as management tools (Westoff 1989). Usher believes that three questions need to be considered to effectively manage coastal areas, viz:

1) At what stage in ecological succession is the land that is to be managed?
2) What are the dynamics of the present species diversity - are some species expected to become locally extinct, or are others overdue in their colonization?
3) What are the chances of a catastrophe?

Part One of this thesis attempts to answer the first two questions. However, it is not only desirable to have data on the ecology of various systems. Sociological and socio-ecological information dealing with the importance and value of particular areas and the relationship between man and his natural environment, also needs to be gathered (Usher 1978). Chapter Five attempts to do this for a specific site within the study area. This is particularly relevant as much conflict in planning and management study results from disparities between different perceptions of problems (Clarke 1976 in Ranwell 1979). This results in a primary conflict in coastal zone management, as recognised by Vogt (1979) and discussed in more detail in Chapter Five; namely the conflict between increased access and protection of the resource base. McCarthy (1976 in Ranwell 1979) lists the following as other common problems relating to management within the coastal zone :

1) The conflict between economic and environmental needs. For example, the recreational attractions of the coast may be potentially damaging to the environment.
2) Establishing common ground between administrators and ecologists, since administrative boundaries do not recognise ecological boundaries, and *vice versa*.
3) Gathering and handling large amounts of scientific and planning data, arising from the dynamic nature of the system and variety of functions.
4) Translating results into field action is beset with difficulties arising from legal problems relating to ownerships and the fact that management action in one area (for example, dune stabilization) may have deleterious effects in another (Ranwell 1979).

Ranwell (1979) suggests that by recognizing three levels of operation, some of the above problems can be overcome. At the individual site level management would be aimed at restoration and protection, to preserve the resource base and increase its utility. For example, evidence of erosion may lead to pressure for a management strategy aimed at stabilization, which could be costly and unnecessary, as discussed in Chapters Seven and Eight. It would therefore be wiser to first assess the ecological carrying capacity of natural systems to recreation pressure, as undertaken in Chapters Five and Six, before opening these areas up to increased utilization. In other words, to look before you leap. At the regional level, extensive surveys such as that undertaken in Chapter One, provide inventory information so that future changes can be measured. Regional ecological surveys indicate deficiencies and further research requirements, but should be more process orientated to determine how coastal systems work (Ranwell 1979). Studies should therefore focus on cause and effect, so that predictive or conceptual models can be generated for wider application, as undertaken in Chapters Two to Four. The third level of operation recognised by Ranwell (1979), the national level, falls outside the bounds of this thesis. However, the formulation of national policies on coastal zone management should be moulded around basic ecological principles, as first mooted by Clark (1974) and discussed earlier. It is fortunate that the recently published policy for coastal zone management in South Africa (Council for the Environment 1989 & 1991) has emphasized the importance of ecological processes, but sadly these policies have not yet been legislated, and therefore remain as guidelines.

The value of an understanding of the processes involved in plant succession within the dune landscape, as discussed above, led to detailed studies aimed at elucidating dominant pathways and mechanisms of succession. It is therefore necessary at this stage to review current concepts and theories.

CONCEPTS IN VEGETATION SCIENCE AND SUCCESSIONAL THEORIES

The early work of Cowles (1899) on Lake Michigan sand dune vegetation stimulated Clements to formulate his philosophical and comprehensive theories concerning plant succession (Clements 1916). This work was supported by Tansley and other European ecologists, although they challenged the view of the plant association as "an organic entity" (Sheail 1987). However, Gleason (1926) felt that the key to understanding succession was migration, and that "every species of plant was a law unto itself". He put forward these views in a classical paper entitled "The individualistic concept of the plant association", which played a major role in formulating and consolidating new theories of plant succession (Egler 1954; Whittaker 1953; 1967; 1975). However, at the time Gleason's work was not favourably received, and was ridiculed by Nicholls at the 1926 International Conference on Plant Science at Ithaca, condemning him to spend the next 10 years as "an ecological outlaw" (Sheail 1987).

Although the community-unit and individualistic concepts have been widely debated (see McIntosh 1967 & Dansereau *et al.* 1968), work based on Gleason's original concept converted the majority of American community ecologists towards his reductionist approach to community organization (Shipley & Keddy 1987). It is therefore germane to explain these two early theories in more detail, and to discuss some relevant contemporary theories which developed from Clements' and Gleason's early work.

Clements (1916) considered the climax formation to be an organic entity and viewed succession as a process of development whereby "such an organism ... arises, grows, matures and dies". The community of animals and plants develop during time and ultimately achieve a state of balance with the physical environment, after which no further changes occur (Cox *et al.* 1978). An integral part of this concept was the existence of only one climax formation for each major climatic region, the so-called climatic climax.

The initial course is the formation of a new habitat from an uncolonized area (primary succession) or the change of an existing one following a disturbance (secondary succession). The species themselves modify the physical environment by the additions of litter, alterations to light intensity, enhancement of soil development and other "autogenic" changes. External or allogenic changes to the natural environment continue, and the individual which initially occupied the site becomes unable to reproduce as efficiently as the individual displacing it. Consequently a gradual change in species composition occurs as species better adapted to the habitat gain dominance and perpetuate themselves at that site (Clements 1916; Westman 1985).

It was the so-called "limited applicability" of classical Clementsian succession with its holistic viewpoint that led to the development of the reductionist approach of Gleason (1926). He regarded the vegetation unit as a temporary or fluctuating phenomenon dependent on the selective action of the environment. The vegetation unit was seen as a fortuitous collection of plant species with similar requirements, each responding individually to the complex of environmental factors present. He considered succession to be the process whereby the individuals of one species were replaced by individuals of another species in response to a changing environment. This occurred when the environmental changes went beyond the physiological limits of the one group and nearly reached the optimum of the replacing one. Since the environment was varying constantly, both in time and space, a completely stable state could not be reached. On this basis the climax formation of Clements was rejected (Gleason 1926).

Tansley (1935) and Whittaker (1953) also rejected Clements' comparison of the community with an organism. Whittaker (1953) stated that "there is no absolute climax for any area, and climax composition has meaning only relative to position along environmental gradients". However, Lindeman (1942) defined succession from a trophic-dynamic viewpoint as the process of development brought about by the effects of the organisms on the environment and upon each other towards a relatively stable condition of equilibrium. This functional energetic concept has been adopted by many ecosystem ecologists, the most notable being Margalef (1968) and Odum (1969) who defined succession in terms of three parameters. Firstly, the community development must be orderly and reasonably directional and therefore predictable. Secondly, the process must result from modifications of the physical environment by the community, and lastly, it must culminate in a stabilized ecosystem (Margalef 1968).

These definitions have been the target of criticisms, the most devastating being that of Drury & Nisbet (1973). They refute contemporary theories of succession on the basis of a lack of field evidence to support the hypotheses of bioenergetics (Margalef 1968), soil development (Whittaker 1975), sequence of vegetation change (Clements 1916; Egler 1954; Whittaker 1975) and diversity, stability and reproductive strategy (Whittaker 1965; Margalef 1968). In conclusion, they state that "most of the phenomena of succession should be understood as resulting from the differential growth, survival and perhaps dispersal of species adapted to grow at different points on stress gradients" (Drury & Nisbet 1973).

These criticisms and the disagreement between the reductionist and holistic viewpoints resulted in the development of a number of new theories (Connell & Slatyer 1977; Peet & Christensen 1980; Noble & Slatyer 1980). All these emphasize life history properties (colonizing ability, dispersal, growth rates and longevity) of individual species. Connell & Slatyer (1977) suggested three main pathways, namely the Facilitation, Tolerance and Inhibition pathways.

In the formulation of their models, Connell & Slatyer (1977) considered the mechanisms which determine the changes during succession and the relationship between succession and community stability and organization. However, all these mechanisms have not yet been elucidated, and others have been ignored. Connell & Slatyer state that in most recent reviews of ecological theory (Odum 1969; Drury & Nisbet 1973; Horn 1974) physical stress and competition between plants have been considered as the main mechanisms determining the course of succession. The Connell & Slatyer models therefore included interactions with herbivores, predators, etc, and were defined in the form of testable hypotheses, but recent research has shown that these models are not testable (Peet & Christensen 1980; Noy-Meir & van der Maarel 1987; Picket *et al.* 1987).

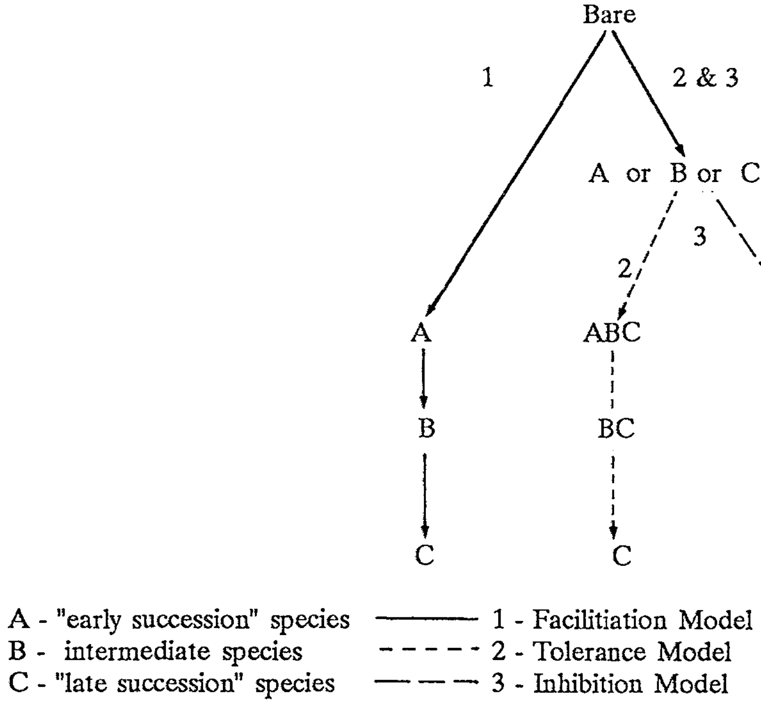


Figure 1 Simplification of Connell & Slatyer (1977) models, based on their Figure 1. Facilitiation is similar to Horn's (1976) obligatory succession, but for the other two models any species that arrives and is able to survive can become established. Although the environment is modified in the Tolerance Model (2), "late succession" species grow despite the presence of "early succession" species, but in the Inhibition Model (3) early occupants modify the environment so that it becomes less suitable for subsequent recruitment by other species (competative exclusion).

In all three Connell & Slatyer models (Fig. 1), early occupants modify the environment so that it is unsuitable for further recruitment of more "early-succession" species. The Facilitation Model, which is broadly based upon Clements' original concept of autogenic succession, assumes that only certain early successional species are able to colonize the site. These species then modify the environment so that it becomes more suitable for "later succession" species to invade and grow to maturity. This sequence continues until the resident species no longer modify the site sufficiently to facilitate the invasion and growth of a different species.

In the Tolerance Model, modifications by the earlier colonists do not affect the rates of recruitment and growth of later colonists. Species that appear later are simply those that arrived initially and then grew slowly. The sequence of species is therefore determined solely by their life-history characteristics and tolerance to environmental factors. In the Inhibition Model, once the early colonists have secured the resources, they inhibit the invasion of subsequent colonists or suppress the growth of those already present. The latter can only flourish once the dominating species are damaged or killed. The later colonists need not have different life-history characteristics from the original residents they are replacing, and may have "early succession" characteristics. If this is the case, then the successional sequence will not occur. However, if the replacement species have "late succession" characteristics, then the traditional successional sequence will occur (Fig. 1).

The fundamental difference between the Facilitation and the other two models is that in the former, only certain early successional species are able to colonize, whereas in the latter two models, any arriving species can colonize. Egler (1954) noted this distinction by calling the former process "relay floristics" and the latter, "initial floristic composition". Horn (1976) referred to this facilitation process as "obligatory succession". He also noted that many of the striking patterns of succession are direct consequences of stochastic replacements of one plant by another. Horn's statement that "Early successional species should persist in the climax as long as a few openings occur from time to time ..." lends support to Connell & Slatyer's Inhibition Model (Horn 1974). The differences between these models emphasizes the functional difference between the original concept of succession proposed by Clements (1916) and portrayed in the Facilitation model, and the other two models which entertain different concepts.

Picket *et al.* (1987) have reviewed the Connell & Slatyer models to clarify conceptual and terminological problems concerning models and mechanisms of succession, and demonstrated their limits as alternative, testable hypotheses. A general review of contemporary concepts of community organization by Shipley & Keddy (1987) concur with the conclusions of Picket *et al.* (1987) regarding testable hypotheses (see also Noy-Meir and & van der Maarel 1987). Picket *et al.* (1987) discussed succession in terms of three fundamental concepts:

1. Pathway - the temporal pattern of vegetation change.
2. Mechanism - the interactions (competition, predation, environmental resource and stress levels) that contribute to successional change.
3. Model - a conceptual construct to explain successional pathways by combining various mechanisms.

Each Connell & Slatyer model implies a particular pathway. For example, the Facilitation Model implies a linear, obligatory succession of stages. However, the number of pathways found in nature is larger than the range suggested by the models (Peet & Christensen 1980; Horn 1981). Secondly, actual successions may exhibit complex combinations of pathways, and their various mechanisms should be combined in the study of an actual sere. Lastly, the models do not account for the full range of successional causes as each allows for only one mechanism of succession. Consequently, Picket *et al.* (1987) concluded that the models will be appropriate only when applied to specific mechanisms within a pathway, and a single model cannot be applied to a complete sere. This is because different mechanisms of replacement may act in one sere at a given time, and one species can participate in several mechanisms. These mechanisms can only be discriminated by determining demographic and ecophysiological causes of turnover. Thus, Connell & Slatyer models should be restricted to describing particular replacements of species in succession.

In response to the limitations of these models, Picket *et al.* (1987) presented a comprehensive mechanistic framework, since they believed that a complete understanding of succession must ultimately consider all important influences, and not just mechanisms of turnover. This framework is a conceptual construct to help organize various aspects of successional theory, and is based on the Clementsian classification of successional causes. It provides linkages between different aspects of successional process, and is not biased towards a single or dominant mechanism or particular pathway.

The framework is hierarchically organized, and begins at a general level by asking what causes succession. The three suggested causes are (1) open sites become available, (2) species are differentially available at a site, and (3) species have different capacities for dealing with a site or each other. The second level looks at what interactions, processes or conditions contribute to the general causes of succession. These broad categories of ecological phenomena suggest the range of processes that must be considered. The third level encompasses site-specific factors that determine the nature or outcome of interactions of the plants and other organisms that affect them. This framework shows the context of specific models of various components of succession, and outlines factors that must be considered when translating from general theoretical statements to testable predictions relevant to specific areas.

Most of the literature cited above provides new insights for successional theory, but there has been little critical analysis of their interpretations, except for the recent review by Picket *et al.* (1987). Most are also critical of Clements holistic, organismic theory of succession, and the alternative models proposed usually advocate a population-based approach and emphasize life - history attributes of organisms as the essential basis of a modern theory of succession (McIntosh 1981). However, Picket *et al.* (1987) do build on Clements' (1916) classification of successional causes, and this approach towards a synthesis is echoed in McIntosh's (1981) call for a common platform from which to view ecological succession.

A PHILOSOPHICAL APPROACH TO DUNE MANAGEMENT

Odum (1989) believes that a change in environmental ethics is required to protect the planets life-support systems. He believes that an ethical relationship between humans and their environment still needs to be developed, since "the land-relationship is still strictly economic, entailing privileges but not obligations" (Leopold 1949 in Odum 1989). Approaches to coastal dune management will also be coloured by one's ethical credence towards environmental conservation. The utilitarian ethic is based on the credo that "Conservation is for Man", as it will produce the greatest amount of good for mankind. This ethic presumes a common currency with which to judge whether actions are advancing the greatest good to man, and does not allow for incommensurable values (Fuggle & Rabie 1983). However, an ecological approach to coastal zone management requires the adoption of a Judeo-Christian ethic, where man is not the owner of nature and is accountable for his actions. He should act as steward and should regard the earth and its resources as things held in trust, and must recognise that subhuman nature has a right to exist over and above its utility to man (Fuggle & Rabie 1983). Man has the responsibility to ensure that natural processes are sustained and that natural phenomena are not destroyed.

The utilitarian attitude towards nature has its roots in the development of human consciousness, which has been tainted by Faustian images of control, power and agency. Man is not dedicated to the values of Philemon, the humble tramp who gave hospitality to destitute gods as they wondered homeless in a technocratic age. These images of Faust and Philemon are metaphors of consciousness; they are images which shape the quality of consciousness as it calls the world into being, and, as such, they determine the contours, textures and values of that world (Brooke 1992). A utilitarian attitude has its roots in the Faustian consciousness that the world is there to be set upon and seized for technological exploitation (Heidegger 1954); for Philemonic consciousness it is there to be witnessed for all its beauty, multiplicity, and awesome majesty (Brooke 1992). It is for these reasons that western attitudes to the natural world have centered on the subjugation of nature for human benefits. This attitude has recently been criticised, and in the 1990s alternative ideas about the relationships between human beings and the natural world are becoming more widespread. These alternatives suggest a greater responsibility to care for the world (Mannion & Bowlby 1992) which is in line with Heidegger's (1954) "Gelasenheit" or "letting-be-ness". This illuminates the importance of recovering and respecting our care for all the things in the world, and a general shift in the 1990s towards the view that humanity must learn to live with rather than exploit nature has been noted (Bowlby & Lowe 1992).

Unfortunately, this caring stance has not filtered into the consciousness of most South Africans, and I believe that current use and perception of the coastline reflects a utilitarian ethic, with recreational use and social and economic values far outweighing the importance of ecological processes (Fig. 2a). However, it is important to realise that the maintenance of ecological processes is of greater importance than the utility functions offered by the coastline (Fig. 2b). We must treat these areas not as supply depots, but as our *oikos*, or home. We must not follow the writings of Francis Bacon (1561-1626) who believed that human beings should develop and apply science to conquer and organise nature (Bowlby & Lowe 1992). Rather, we must use this knowledge to manage natural systems within the limits dictated by the very nature of those systems, as without fully functioning, self-perpetuating and sustainable ecosystems, the utility functions to society (recreation; social; economic) will not reach their full potential. Thus, an ecological approach to dune management, with a Judeo-Christian ethic, also makes sound utilitarian sense, since it is better to work with, rather than against nature (Canis *et al.* 1985).

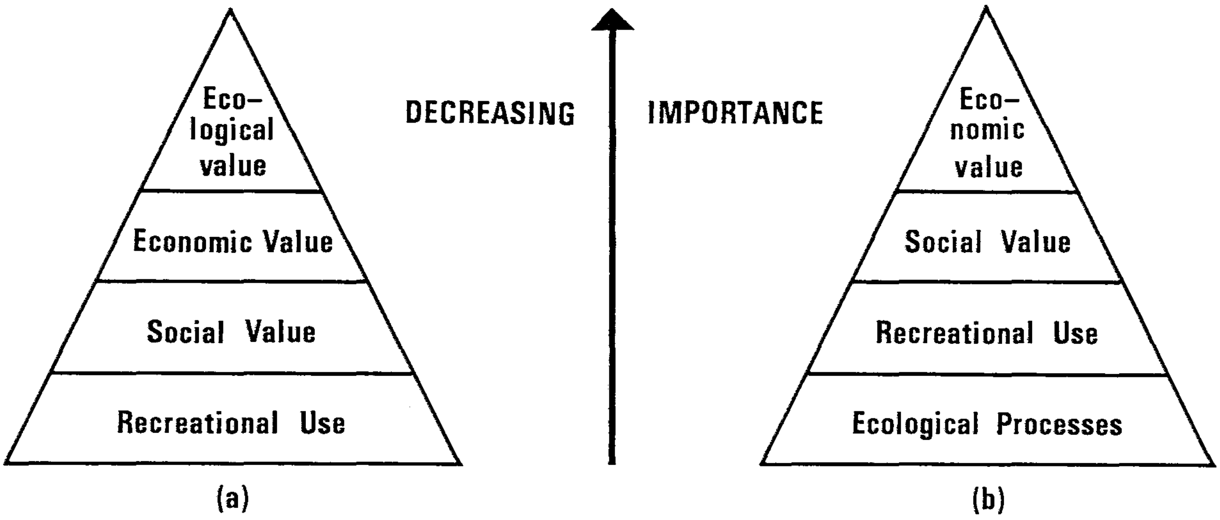


Figure 2 Human use/perception of the coastline (a) reflects a utilitarian ethic towards the value and importance of ecological processes, but maintenance of these processes is required for the correct management of the coastal zone, which will ensure sustainability (b).

To effectively manage dune and coastal systems, the coastal manager must know how to instigate and steer processes which act in the way he wishes, impede others which are disadvantageous for his purpose, and compensate for processes desirable but not present. Thus, to achieve effective management, scientific guidance is required to map, measure and model the relevant processes and their interactions, evaluate the effects of various activities and present alternatives based on knowledge of cause - effect relationships (van der Meulen & Jungerius 1989). However, the decision environment of the coastal manager is influenced by a number of extraneous factors, and the inter-relationships between these is presented in Figure 3. Priorities are dictated by outside policy makers, usually at central or regional government level. In South Africa existing guidelines for coastal zone management (Council for the Environment 1989 & 1991) influence the decision making process. However, since there is no legal basis to these guidelines, it is the functions and needs of society which exert the greatest impact on coastal dune systems. Main functions are focused on activities which centre around the recreational use of the coastline; such as holiday homes, resort and hotel developments, and primary recreational activities such as swimming, sunbathing and fishing. All of these impact at various temporal and spatial scales on the dynamic coastal environment and on coastal dune systems, where biological and geomorphological process interact in a complex manner with each other to give rise to the dune landscape (for more details see van der Meulen & Jungerius 1989). The need to manage this system to ensure sustainability is self evident, but to be effective input from basic and applied research is required (Fig. 3). It is important to know whether some processes are self-regulating, or in accord with the requirements set by the functions. If not, it will be necessary to intervene in the processes.

THE APPLICATION OF THESE CONCEPTS TO THIS THESIS

Using the basic principles described above the research in this thesis follows two lines of approach, namely ecological studies of a fundamental nature, and applied ecological studies of a management nature. Part One focuses on determining the ecological importance of dune vegetation at a regional scale, and to obtain information on an important ecological process in the dune landscape, namely plant succession (Fig. 3). The management studies in Part Two firstly examine the disruption of ecological processes, and secondly the resilience of dune vegetation to disturbances caused by recreational activities. These studies, as well,discuss the process of dune stabilization, used as a remedial measure to manipulate disturbed systems. Information generated from this thesis could therefore be fed into a dune management plan, as indicated in Figure 3. The work is presented in eight chapters which are outlined below.

The main objective of Chapter One was to describe the regional and local distribution patterns of plant species along the Eastern Cape coast, with a view to determining the most important factors controlling this distribution. The expectations were that at a regional scale distribution would be affected by climatic factors, particularly rainfall, and the phytochorological affinities of the various taxa. At a local scale, successional changes corresponding to the steep environmental gradients that exist in coastal dunefields were perceived to be most important. Relevant data were collected and analyzed, using multivariate analysis, to produce an objective classification of the plant communities occurring along the coastline. The distribution of the more common species was determined and the phytochorological affinities of all species assessed. Finally, the inter-relationships between the various communities that were defined was investigated.

Results of Chapter One revealed a successional sequence from foredune colonizers to thicket and forest communities, as noted elsewhere by many researchers (Cowles 1899; Olson 1958; Morison & Yarranton 1973; Barbour *et al.* 1981). Of note, however, was the disjunct position of dune slack communities in the ordination diagrams, which appeared to relate to moisture variability and species diversity. Earlier work on these dune slacks suggested that they were very important habitats within mobile dunefields, despite their small size (Lubke & Avis 1982a). They appeared to act as nuclei, or centres of diversity, linking the succession from foredunes to dune scrub. A temporal study of community change in a typical dune slack in the study area was undertaken in Chapter Two and a conceptual model of a number of pathways of community change was generated.

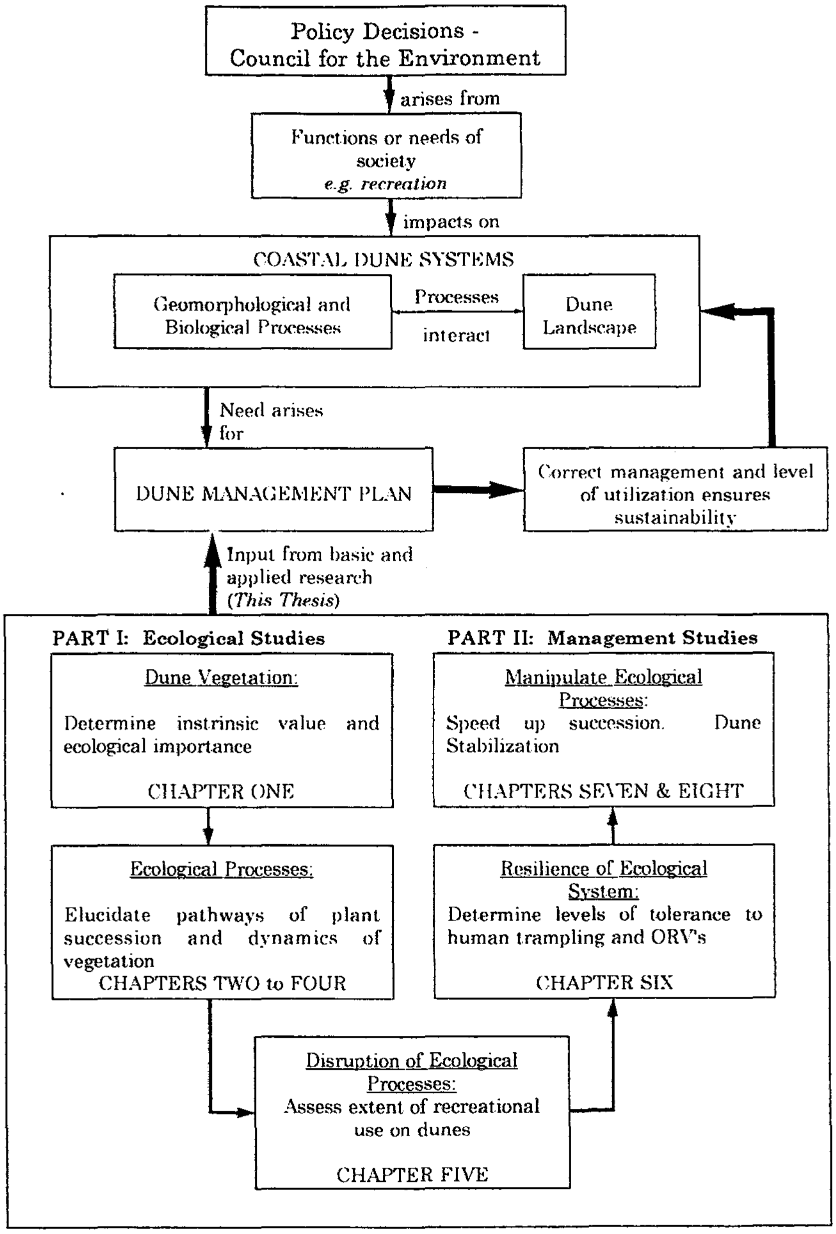


Figure 3 Flow chart to show how the studies undertaken in this thesis link together and contribute towards the formulation of a management plan which considers ecological processes (Based on Fig. 1 of van der Meulen & Jungerius 1989).

Since studies on dune systems were used to generate the first detailed hypothesis on plant succession (Cowles 1899; Clements 1916), a comparative study of an excellent example of a primary, autogenic succession (Weisser & Muller 1983) was undertaken in Chapter Three on the dunefield system at Mtunzini on the north coast of Natal. It was hypothesized that communities were linked spatially along a successional gradient that could be correlated with temporal changes in species abundance and soil properties. It was also suggested that the mechanism of change was by means of facilitation (*sensu* Connell and Slatyer 1977), and that changes in species were community based (Clements 1916), rather than individualistic (Gleason 1926).

Chapter Four reports on an identical study undertaken at Kleinemonde. This study lent support to the earlier model of succession developed from the temporal study of a dune slack (Chapter 2). Although not spatially linked and as well defined as the succession at Mtunzini, it was also hypothesized that the mode of transition was autogenic, and that changes in species composition were community based. Dune slacks and foredunes were thought to play a more important role in this succession, which appeared to have a number of pathways due to the harsher climatic and environmental factors along the Eastern Cape coast.

Chapter Five studies the peak recreational use of three urban beaches in East London, as assessed for three years using an aerial census. A questionnaire survey was also undertaken to determine if the physical and perceptual carrying capacity of these beaches had been reached. The ecological carrying capacity was assessed by exposing vegetation to measured amounts of human trampling in an experimental study, and measuring the change in height and cover of the vegetation in the sample plots. This chapter highlighted the problems associated with increasing access on the preservation of coastal resources (Vogt 1979).

Chapter Six describes the resilience of three commonly occurring dune plant communities to human trampling and off road vehicle effects. These were investigated experimentally using the same techniques developed in Chapter Five. Studies abroad, particularly those undertaken at Cape Cod, Massachusetts, showed that dune vegetation was very susceptible to off-road vehicles (Broadhead & Godfrey 1979a). These effects were expressed as a reduction in plant height, and impacts on a single day and rates of recovery were assessed. The effect of long term exposure at three levels of intensity was also investigated, and communities were found to be very susceptible to both types of disturbance.

A historical review of the process of dune stabilization was undertaken in Chapter Seven to outline how techniques and processes had changed, since stabilization was first implemented in 1845. The current policy concerning drift sands was reviewed, and problems associated with dune stabilization discussed.

Chapter Eight was undertaken to quantitatively evaluate the success of current techniques employed for stabilizing dunes with indigenous vegetation. A survey of 15 stabilization sites, from 5 to 17 years old, was undertaken to assess current floristic composition and species abundance. Multivariate techniques were employed to analyze floristic data, elucidate any compositional gradients and provide information on species suitable for dune stabilization. Suggestions were also made on ways of improving the process.

The concluding chapter draws together the main findings presented in the thesis. It is acknowledged that more detailed work is required on many aspects discussed here since most of these are at the descriptive level. However, it is hoped that this thesis highlights the need to understand and appreciate ecological processes so that the coastal system can be managed as a whole in a sustainable manner.

PART ONE : ECOLOGICAL STUDIES

> "An understanding of ecological succession
> provides a basis for resolving man's conflict
> with nature"
>
> E P Odum

The importance of studying and understanding succession was emphasized by Eugene P Odum, at his presidential address presented before the annual meeting of the Ecological Society of America in 1966. Odum stated that the "strategy" of succession was towards increased control of the physical environment, but felt that this strategy of "maximum protection" conflicted with man's goal of "maximum production" (Odum 1969). Man has taken for granted the protective functions, such as gas exchange and nutrient-cycling, of self-maintaining and self-perpetuating ecosystems. This is particularly evident in fragile but highly valued coastal areas, where dune vegetation is continually destroyed or successional processes disrupted due to man's over zealous quest for achieving "maximum production". There is an urgent need to manage the dune landscape as a whole; and, as discussed in the introduction, an understanding of ecological succession is pivotal, so that manipulative skills (such as dune stabilization) do not run too far ahead of our understanding of the impacts of these changes.

The first part of this thesis therefore explores the intrinsic value and ecological importance of dune vegetation, and focuses on the process of plant succession within mobile dunefields. Since the efficacy of any study is enhanced if it contributes towards a better understanding of the dynamic interactions between and within the communities under study, an attempt has been made to generate testable hypotheses concerning the causative factors of plant distribution and succession. These will improve our ability to predict the tolerances of these systems to various perturbations, either anthropogenic in origin or otherwise, and it is this basic philosophy which underpins the fundamental ecological studies undertaken in this thesis.

CHAPTER ONE

DUNE VEGETATION FROM CAPE ST FRANCIS TO KEI MOUTH : DISTRIBUTION, PHYTOCHOROLOGICAL AFFINITIES AND SUCCESSION

INTRODUCTION

Perhaps because of its apparent simplicity, but also because of the fact that it is not a distinct entity or region, few studies of coastal dune communities have been undertaken in South Africa. Descriptions of dune systems and plant succession were made in Natal by Moll (1968; 1969), Ward, (1980), Weisser & Marques (1979) and Weisser *et al.* (1982), by Jeffrey & Moll (1987) in the southwestern Cape and by Dyer (1937), Olivier (1986), McLachlan *et al.* (1987) and Young (1987) in the Eastern Cape. Tinley (1985) has summarized the dune systems of South Africa most adequately and the CSIR has undertaken a broad survey of coastal vegetation in the Cape Province (CSIR 1989). Collection of more detailed quantitative data in selected areas of the Eastern Cape has been undertaken by Burns (1986) and Lubke & Strong (1988) in the East London region, Young (1987) for the Alexandria dunefields, and Lubke (1983) and Lubke & Avis (1982a) at Kleinemonde. However, none of these studies have taken a broad quantitative overview of the types of plant communities, the distribution of the species, their phytochorological affinities and their succession both within a region and along a large section of the coastline as has been undertaken by Moreno-Casasola & Espejel (1986) and Johnson (1977) along the US Gulf coast and Pacific and Gulf coasts of Mexico respectively. A detailed study was therefore initiated to explain:

1. Distribution of the coastal plant species along climatic gradients.
2. The phytochorological affinities of these plant species and communities.
3. Succession between the different plant communities in their habitats.

STUDY AREA

The region of coastline sampled is that commonly recognized as the Eastern Cape (Bruton & Gess 1988), stretching from Kei Mouth in the north-east to Cape St Francis in the south-west, being some 450km in length (Fig.1.1). It is not a geographically distinct region which can be distinctly demarcated by natural boundaries into separate entities. It should rather be regarded as a continuous coastal belt connecting the southern Cape to Transkei.

GEOLOGY & GEOMORPHOLOGY

On the basis of geology and geomorphology, the region can be divided into 3 sections (Marker 1988). Firstly, from Cape St Francis to Woody Cape the coast is embayed and aligned approximately east to west. Quartzite ranges terminate seawards as headlands on the western edges of half-heart bays, which extend up the southern coast as far as Woody Cape. Erosion occurs on the headlands and, as a result of easterly long-shore drift, sand accumulates on the eastern and northern shores of the bays (Tinley 1985). This is most notable in Algoa Bay where the largest coastal dunefield on the eastern coast of South Africa - the Alexandria dunefield - occurs east of Sundays River (see Fig.8.1, pg 251).

North-east of Cape Padrone the second section of the coastline is straighter in gross outline as a result of faulting (Marker 1988) and has a narrower continental shelf. Up to Begha Mouth (Sample 56, Fig. 1.1) this region consists of upper Cape Supergroup Bokkeveld shales and Witteberg quartzites and lower Karoo Dwyka and Ecca rocks. In the third section north of Begha Mouth, only upper Karoo rocks are present, but Beaufort Group sand stones and shales are intruded by harder dolerite sheets and dykes (Plate 1.3). As one approaches Kei Mouth spectacular dolerite headlands dominate the scenery.

Calcareous sands have hardened by lime cementation to form aeolinite or dune rock mainly in the south-western part of this region. These form conspicuous aeolinite headlands and promontories at Nahoon Point, Three Sisters, Cove Rock, Kenton, Kwaaihoek and Woody Cape (Fig. 1.1).

COASTAL SAND DUNES

Much of the vegetation is found on coastal dunes and thus an understanding of their morphology is important. Tinley (1985) has described the dune systems for South Africa and only the relevant types found in the Eastern Cape are discussed in detail by Lubke (1988) and briefly described here. Tinley's classification is chosen above that of Olson & van der Maarel (1989) as it relates specifically to the South African coastline and is therefore more relevant to this study. The main types of dunes are crescentic or transverse, with the concave or steep curve of the slipface facing downwind. Transverse dunes have straight or curved ridges and axes orientated at right angles to the wind. Barchanoid dunes are crescent-shaped, with linked axes at right angles to the wind (Plate 1.1). Because the predominant wind direction is either from the west or east at different seasons of the year, these dunes are continually changing and move east and west. Because of the greater intensity of westerly winds, the dunes show a net movement to the east of between 2 to 3 my^{-1} (La Cock *et al.* 1992). The invading vegetation modifies the slope and shape of the dunes, thus forming characteristic foredune hummocks and beach ridges, especially on accreting shorelines (Hesp 1984). Parabolic or hair-pin parabolic dunes, with an advancing concave tongue and leeward slipface and sides partially stabilized by vegetation advance into the coastal thicket (Plate 1.2). Headland bypass dunes develop as strips of migrating dunes across the headlands and feed the shoreline of the embayment on the opposite side with sand (Tinley 1985).

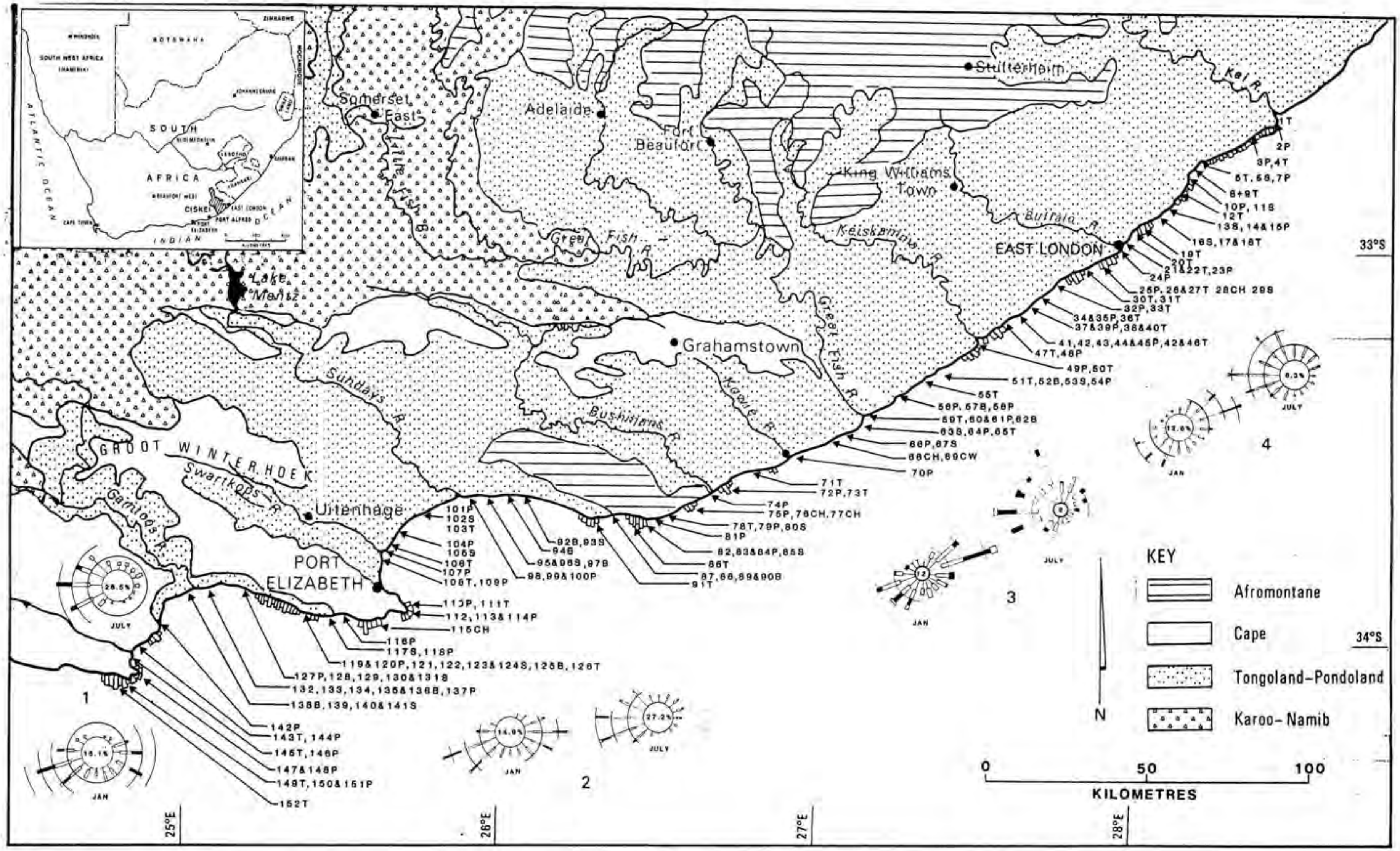


Figure 1.1 Map of the Eastern Cape, from Cape St. Francis in the west, to Kei River Mouth in the east, showing the extent of the four phytochoria as given in the key. Actual sample sites are arrowed, and the relevé numbers at each site and corresponding community is given. The communities are abbreviated as follows: P-Dune Pioneer; S-Dune Slack; B-Bushpockets; T-Dune Thicket; CH-Rocky Cliff Herbaceous; CW-Rocky Cliff Woody. Wind roses give average wind speed, direction and percentage calms in the circles, for four localities. The base map has been modified from Lubke *et al.* (1988a).

More complex dune types are found in the study area, particularly in the Alexandria dunefield, which stretches from Sundays River Mouth 50 km east to Woody Cape (Plate 1.1). Illenberger (1988) gives a detailed account of this area, which is a sand source area with active translocation of sand landwards from the back beach. The rest of the study area consists of a narrower dune cordon with the various dune types discussed present. A more detailed account of the physiography is given in Tinley (1985).

More than 40 estuaries occur along this stretch of coastline, over half of which are closed except during the rainy season. The estuaries may cut through the dunefields and because of the net movement of sand from west to east are often diverted to the east at their mouths.

CLIMATE

The climate is unpredictable and very variable (Fig.1.2). On the basis of the Köppen system it can be classified as subtropical, with all months having temperatures usually in the range of 10 to 20°C and at least 60mm of rainfall (Kopke 1988). The temperatures are mild in both winter and summer with on-shore winds reducing the heat and humidity in summer.

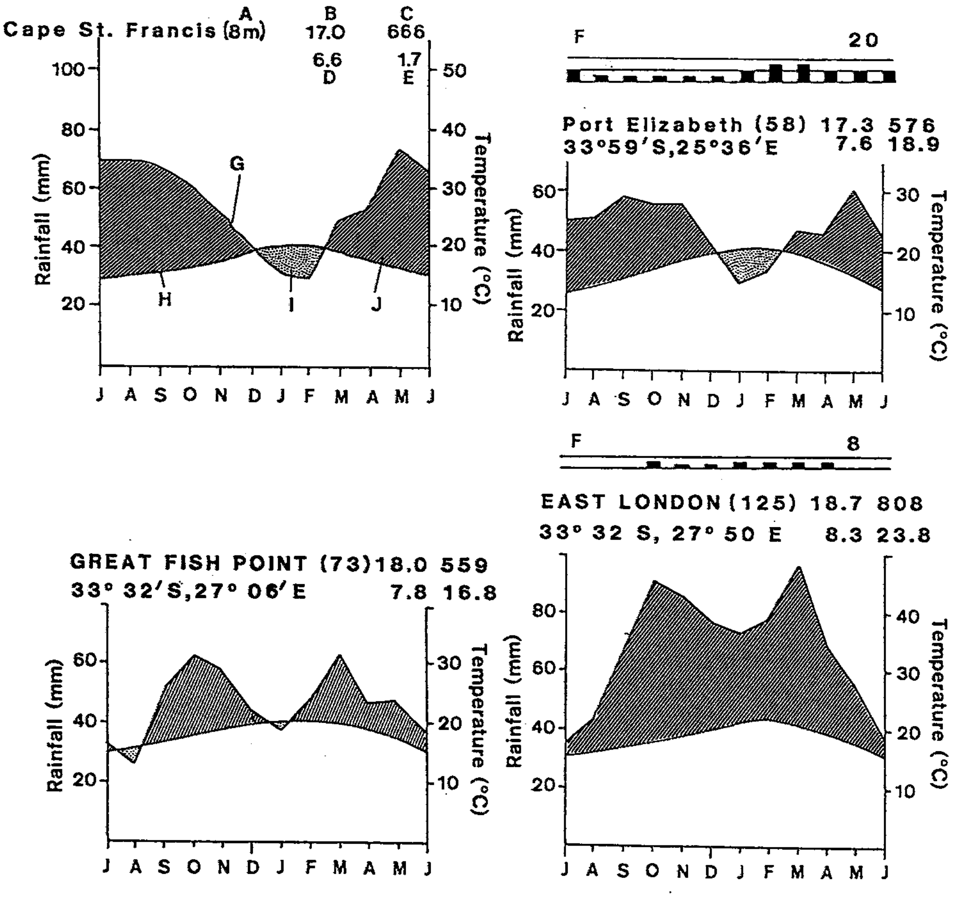


Figure 1.2 Walter-Leith climate diagrams for : A-Cape St Francis; B-Port Elizabeth; C-Great Fish Point and D-East London. (A-elevation in metres; B-mean annual temperature (°C); C-total annual precipitation (mm); D-mean diurnal range in temperature (°C); E-mean annual temperature range; F-number of days with fog; G-rainfall curve; H-temperature curve; I-dry season; J-moist season).

From the south-west to as far as Bushmans River the rainfall occurs mainly in the winter months, although west of the Gamtoos River spring maximum rains are more common. This is evident in the Walter & Leith (1967) climate diagram for Cape St Francis, the rest of the region showing a bimodal distribution of rainfall with peaks in both spring and autumn (Fig.1.2). As one moves eastward to Kei Mouth the pattern changes to more abundant summer rains and a greater chance of a summer maximum peak. On the basis of rainfall this coastal region is a transition zone with the Port Elizabeth area receiving the tail end of the fronts that bring winter rain to the Western Cape. The south-easterly winds can bring spring and autumn rains to the coastal areas in flood proportions.

Mean annual temperature increases slightly, from 17°C at Cape St Francis to 18.7°C at East London. Mean monthly lowest and highest temperatures also increase slightly from west to east, as does the difference between these two values (10.4°C for St Francis; 15.5°C for East London, Fig. 1.2).

The Eastern Cape coast is one of the windiest parts of southern Africa, calms often being a rarity. The winds are predominantly westerlies or south-westerlies in the winter and easterlies in the summer, but in the East London region, north-easterlies are more common in the summer (Fig.1.1). Wind is one of the most important environmental factors in this coastal region since it influences dune formation. Strong winds, mainly parallel to the coast, and often during dry conditions, cause considerable sand movement and changes in dune formations (see Plate 2.2,pg 75). Pioneer plants have the ability to survive in the mobile sand, with rapidly elongating stems, rhizomes, roots or runners, but occasionally wind-blown sand is so great that entire communities may be buried. This instability of the substratum coupled with the high incidence of wind is given as the main reason why many dunefields are completely devoid of vegetation (Lubke 1983).

Wind is also important on exposed rocky cliffs or promontories and seaward facing slopes, as it carries salt spray inland, which inhibits or stunts plant growth in exposed coastal habitats (Lubke & Avis 1982a & b). Salt spray and wave splash may result in extremely saline conditions on rocky cliffs and promontories due to salt accumulation. In sand dunes the salt spray is more easily leached from the more permeable sand by frequent rainfalls (Lubke & Avis 1982a; Avis & Lubke 1985).

COASTAL VEGETATION AND FLORA

The climate (particularly rainfall and temperature) generally influences the type of vegetation in a region. Climax vegetation within the coastal belt varies from fynbos to coastal thicket, to forest and coastal grassland (Lubke 1988). There is a gradual change along the coast from dune fynbos in the west through thicket to coastal forest as the rainfall increases and changes from winter to summer and the temperatures become more moderate (CSIR 1989; Plates 1.1 to 1.3).

Plate 1.1 View of the Alexandria dunefield at Woody Cape, looking north. The vegetation in the foreground above the aeolianite cliffs is Dune Fynbos, and behind the dunefield (right background) Dune Scrub. Bushpockets are visible as patches of vegetation within the mobile dunefield. Note the Barchanoid dunes (arrowed).

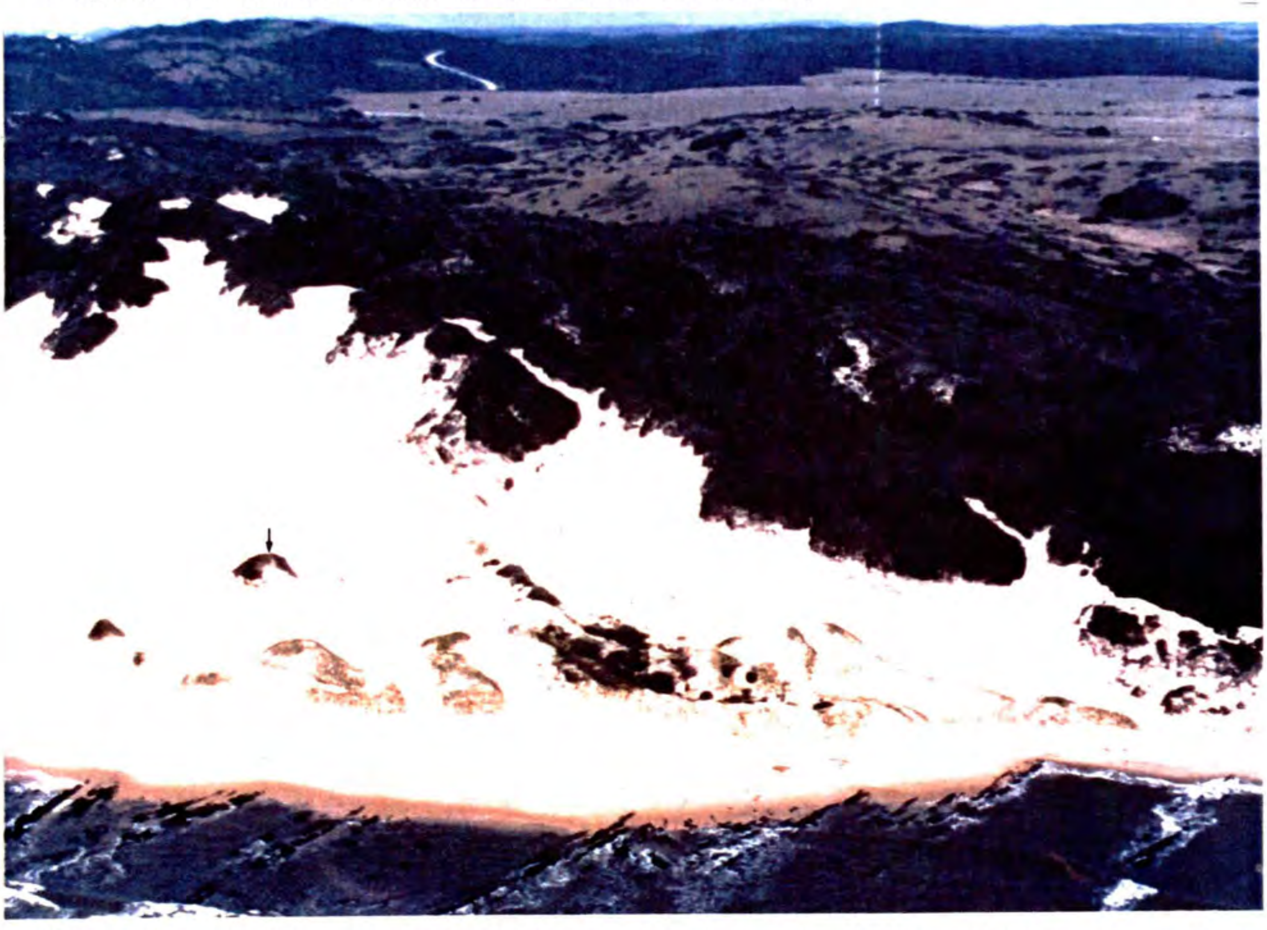


Plate 1.2 View of the Kleinemonde dunefield, looking north. In the foreground are foredunes, and the more dense patch of vegetation in the mid foreground is a duneslack which has been the subject of detailed studies (Chapters 2 & 4). Bushclumps are visible to the left (arrowed), and the Dune Thicket Margin is irregular due to the large number of parabolic blowouts (Compare with Fig. 4.1, pg 129). The vegetation along the edge of the thicket shows signs of dying.

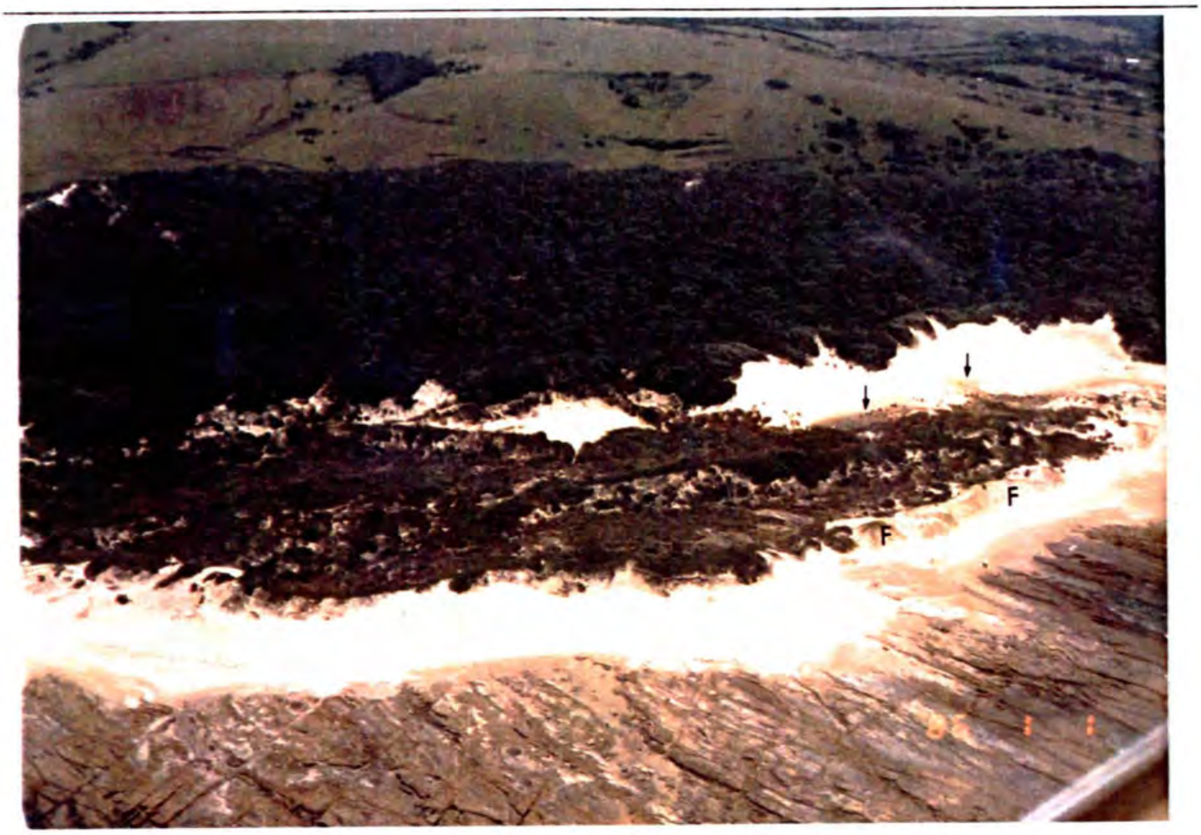


Plate 1.3 Dune Scrub in the centre seaward behind the wavecut platform in the foreground, and Dune Thicket in the centre landward, in front of the grasslands (background), near Cintsa, 31 km east of East London. Note the unistratal, dense canopy of the Thicket, and rather patchy cover of the Dune Scrub. Foredunes (F) are visible in the mid foreground behind the wavecut platform, and dune slacks in the mid foreground (arrowed).

Plate 1.4 Woody vegetation on the leeward side of the Second Sister rocky promontory at Kleinemonde. Note the effect of windpruning, which reduces the height of the vegetation to less than 2 metres. The species in the left foreground is *Mimusops caffra*.

The coastal fynbos (South Coast Dune Fynbos of Cowling 1984) is an order of the more extensive Cape Fynbos Shrubland of the southwestern Cape (Moll & Bossi 1984), which occurs on calcareous coastal deposits. Fynbos is generally characterised by heath plants and restios and is found on nutrient-poor soils of the Cape Supergroup rocks often in the winter rainfall region (Taylor 1978). Coastal fynbos is devoid of Proteaceous species and has few restios, mainly being composed of a variety of woody shrubs often with ericaceous leaves (Cowling 1984).

The coastal thicket (Kaffrarian Thicket of Cowling 1984 and Everard 1987) is composed of a dense array of woody shrubs and trees forming an impenetrable community. In the southwest it is rare and when present forms a mosaic with dune fynbos (Cowling 1983 & 1984; CSIR 1989). Dune thicket is most abundant in the central part of this region (Lubke & van Wijk 1988; Tinley 1985; Plate 1.2).

In areas of high rainfall such as Alexandria, East London and eastwards to Kei Mouth patches of coastal forest are common, although in other regions scattered patches of thicket may also reach forest proportions in sheltered parts of dunes, usually on the leeward side (Burns 1986; Plate 1.3). The woody species in both forest and thicket are often the same, but environmental factors determine the physiognomy of the community. In some regions along this coastline grassland is found, particularly on shallow soils above rocky shores or on exposed windcropped promontories. A more comprehensive account of the Eastern Cape coastal vegetation will be presented here, and a summary of the communities is given in Table 1.1.

The affinity of plant species in the Eastern Cape to the different phytochorological regions has been well documented by Cowling (1983) and Lubke *et al.* (1988b). Lubke & van Wijk (1988) further relate these affinities with respect to the coastal species of these regions. There are four major phytochoria (Moll & White 1978; White 1983) which converge in this region (Fig.1.1). Predominantly Cape species are common in the fynbos and coastal fynbos regions which occur on infertile sandy soils derived from Cape Supergroup rocks (Cowling 1983). Woody elements of the Tongaland-Pondoland or subtropical region extend west along the coast and up the river valleys, and are the most common species of thicket communities. Some of the coastal forest species have Afromontane affinities, extending down the mountain chains of Africa. Further west the coastal forests are composed almost entirely of Afromontane species. The Karoo-Namib flora is only represented by the occasional succulent species in the coastal region.

METHODS

VEGETATION SAMPLING

Between 1981 and 1984, 62 sites along the coastline (Fig.1.1) were visited and the abundance of vegetation in various communities assessed using the Braun-Blanquet technique (Mueller-Dombois & Ellenberg 1974). Therefore, in some cases it was neccesary to take more than one sample. This technique was proved to be inffective in a similar survey along the Gulf Coast of Mexico (van der Maarel 1982). The site was described and the locality mapped for future reference. Unknown species were collected and identified, and are deposited in the Rhodes University (RUH) and the Albany Museum (GRA) herbaria. Nomenclature follows Gibbs-Russel *et al.* (1987). Ten metre by 10 metre (100m^2) relevés were sampled in the following communities, which were identified in the field on the basis of species composition, structure and locality: dune pioneer (P); dune slack (S); rocky promontory - herbaceous (CH); rocky promontory - woody (CW); bushclump (B) and dune thicket (coastal thicket) (T), (Fig.1.1). However, the size and shape of the relevés varied according to the abundance or structure of the plants in each community. For example, pioneer species of the foredunes were often widely dispersed and a larger relevé was sampled to include all foredune species. Due to time constraints the coastal thicket was not always sampled as it was quicker to sample thicket margins. In these cases thicket relevés were 2m wide and 50m long, along the thicket margin. At most localities homogenous vegetation units were selected at relevé sites as it was not possible to sample the whole region more extensively.

DATA ANALYSIS

A total of 197 species were identified in the 152 relevés sampled (Fig.1.1). Each species was given a numbered code and the Braun-Blanquet symbols converted to numerical values as follows (Hill 1979a):

r & +	1	2m	2a	2b	3	4	5
1	3	8	18	30	40	60	90

These data were then subjected to Two Way Indicator Species Analysis (TWINSPAN) to create a hierarchical classification, and ordinated using Detrended Correspondence Analysis (DECORANA; Hill 1979b). This method alleviates some of the limitations of other ordination methods such as reciprocal averaging, resolves the non-linear structure of the data and avoids the arch effect by demanding not merely that there shall be no correlation, but rather that there shall be no systematic relation of any kind between the higher axes and the first. Consequently, Hill (1979b) states that DCA is a more reliable method than reciprocal averaging and principal components analysis, but Hill & Gauch (1980) warn that DCA does have limitations, and that it is better to remove extreme outliers and discontinuities prior to analysis. However, van der Maarel (1980) has shown that in European ordination studies this arch does not exist. DCA also avoids the lack of uniformity in scaling of intersample ecological distances, by equalizing local, mean, standard deviations of each species.

This technique has been criticized recently by Wartenberg *et al.* (1987), who believe that the archlike curvature is an important and inherent property of successive replacement data. They also state that the methods of rescaling are arbitrary and based on assumptions about relative species importance. They believe that scaling should be reported in terms of the units recorded by the investigator and measured along the path of the arch, thus providing a common frame of reference (Wartenberg *et al.* 1987). This critique has been opposed by Peet *et al.* (1988) who state that "DCA is one of the most powerful multivariate tools available for representing pattern in communities composed of attributes (species) that vary unimodally along underlying compositional gradients". They counter most of the arguments put forward by Wartenberg *et al.* (1987), but admit that DECORANA achieves detrending in a rather *ad hoc* way. However, with multidimensional species data, detrending and rescaling facilitates data interpretation, and the method should not be rejected without testing it. Consequently it was felt that the technique was well suited to analyze the data set. TWINSPAN constructs a classification of the samples, and then uses this classification to obtain a classification of the species according to their ecological preferences. The two classifications are then used in association to obtain an ordered two-way table that expresses the species synecological relations as succinctly as possible (Hill 1979a). This table is derived from the repeated dichotomization of samples and species into groups based on the division of ordinations. The form of the ordered two-way table approximates the tabular matrix arrangement of the Zurich-Montpellier School. Gauch & Whittaker (1981) compared five hierarchical clustering techniques, and showed that two-way indicator species analysis gave the most satisfactory results in most cases. Since these techniques have been used successfully in a number of similar studies (Williams *et al.* 1969; Onyekwelu 1972; Kachi & Hirose 1979; Kirkpatrick & Hassal 1981; Henriques *et al.* 1984; Moreno-Casasola & Espejel 1986; Sacheti & Scott 1986; Young 1987; Lubke & Strong 1988), they were considered most suitable for analyzing the data of Chapters One, Three, Four and Eight. Furthermore, according to van der Maarel (1982), coastal dunes provide a pattern of vegetation which can be effectively described with the help of numerical classification techniques, and the zonation from beach to inland dunes involves a gradient which can be described with numerical ordination.

Four major communities were initially identified by TWINSPAN and this large data set was subdivided into three subsets and re-analyzed to identify species subgroups. Initially the results were unsatisfactory ("noisy") due to the presence of outlier species which only occurred once in each relevé, and these were subsequently deleted. A more meaningful classification was achieved and these data sets were then subjected to DECORANA to elucidate the relationships between sub-groups. The initial classification revealed distributional patterns at a regional scale, and the latter at a local scale.

For each relevé Simpson's dominance and diversity and Shannon's diversity indices were calculated (Brower & Zar 1984). Within each community the percentage of herbaceous, graminoid and woody species were calculated.

The phytochorological affinities of the 197 species recorded in this study (Appendix 1.1) were assessed on the basis of published distributional records (Ross 1972; Taylor 1978; White 1978; Moll & White 1978; Coates Palgrave 1984; Bond & Goldblatt 1984; Lubke & van Wijk 1988; Lubke & Strong 1988). Any species found in more than one phytochorion was considered to be widespread and no attempt was made to classify ecological and chorological transgressor species (White 1978).

RESULTS

COMMUNITY TYPES

The results of the TWINSPAN classification revealed eight major groups, with the first division separating relevés with a large woody component (37%) from those with a low woody component (14%, Fig. 1.3). The second division separated Dune Slack and Cliff Pioneer communities from Dune Pioneers, and Thicket community from the Bushclump/Thicket groups. The third division defined these communities more clearly (Fig. 1.3). Thus, it appears that the grouping of relevés by TWINSPAN into distinct groups is based on the location, habitat and successional stages of the communities rather than a geographical gradient along the coast. Obviously the distribution of particular species will influence the grouping, but this is not of over-riding importance. However, the separation of the Dune Pioneer community into two groups may be related to the geographical distribution of pioneer species. One group has relevés from 2 (Kei Mouth) to 109 (Port Elizabeth), and the other from 34 (west of East London) to 150 (Cape St Francis; see Fig. 1.1). It also appears that the Thicket community is only found east of the Great Fish River, and Bushclumps west of this location. This is most likely due to the higher rainfall in the east, and larger dunefields in the west. The various communities separated by TWINSPAN (Fig. 1.3) will be described in more detail below, and are summarized in Table 1.1 together with an overview of synonyms from other published data. Species richness, various measures of diversity and the life form composition of the communities are given in Table 1.2. A total of 148 genera and 197 species representing 61 families were identified, and a checklist of all species indicating which communities they occur in is given as Appendix 1.1.

Dune Pioneer Community

This community is closest to the sea and consists of pioneer plants able to colonize mobile sands, thus stabilizing them and building up embryonic dunes. Despite species richness being relatively high, the lowest species diversity was recorded due to the low number of species per relevé. This is not surprising in a young community dominated by herbaceous species (Table 1.2). Graminoids and shrubs are common, but the latter are mainly hardy species such as *Passerina rigida* and *Scaevola plumieri*. Vines and geophytes are not very common, and no trees were recorded. Dune pioneer communities are dominated by the herb *Arctotheca populifolia*, the shrub *Scaevola plumieri*, the grasses *Sporobolus virginicus* and *Agropyron distichum*, and the creeper *Ipomoea pes-caprae* (see Plate 2.1,pg 71). Although succulents are not very common, most of the herbaceous species have succulent leaves and are generally low

Table 1.1 Description of the plant communities recognized in this study, and comparisons with other definitions of communities in the Eastern Cape from various authors.

PLANT COMMUNITY	DESCRIPTION	SYNONYMS AND AUTHORITY
Dune Pioneer Communities	Dominated by small, creeping herbs often with succulent leaves; or grasses (*Sporobolus virginicus*) or the woody shrub, *Scaevola plumieri*. Often dominated by a single species. Diversity usually low and cover sparse. Found mainly on foredunes or in exposed positions. Three community types were distinguished: Embryonic, Hummock and Incipient Foredune Communities.	Dune Pioneer Zone (Burns & Lubke 1986); Primary Dune Colonizers (Lubke & de Villiers 1991); Strand Plant Community (Tinley 1985); Pioneer Community (Lubke 1983, Lubke & van Wijk 1988); Dune Slack and Strand Vegetation (CSIR 1989); Littoral Strand Vegetation-in part (Lubke *et al.* 1987); Forebeach Community and Hummock Dunes (Young 1987; McLachlan *et al.* 1987).
Dune Slack Communities	Herbs dominate, but sedges and rushes are abundant (*Scirpus nodosus* and *Juncus krausii*). Diversity and cover are relatively high. Shrubs may be fairly common in older slacks, which may have two strata. Usually found in interdune hollows behind foredunes as isolated patches of vegetation. Four slack community types were distinguised: dry, River mouth, mature and wet slacks.	Dune Slack and Strand Vegetation (CSIR 1989); Dune Slacks (Lubke & Avis 1982a; Lubke 1983; McLachlan *et al.* 1987; Avis & Lubke 1985; Young 1987; Lubke & van Wijk 1988); Littoral Strand Vegetation-in part (Lubke *et al.* 1987)
Rocky Cliff Community	Severely wind pruned community restricted to rocky headlands. Two distinct community types occur. The herbaceous community is dominated by pioneer species, and grasses, succulents and halophytes are common. Diversity and cover similar to Dune Pioneer Community. Thicket community dominated by herbs and shrubs, but most life forms are represented. Diversity and cover are high, but community seldom taller than 1m.	Communities of Rocky Cliffs (Lubke & van Wijk 1988); Halophytic Fringe Community (CSIR 1989); Rocky Promontory Community (Lubke 1983; Lubke & Strong 1988; Lubke & de Villiers 1991).
Bushpocket Community	Creepers and shrubs dominate, but the grass *Ehrharta villosa* is also common. The shrub, *Myrica cordifolia* and a predominance of woody species characterise this community. Diversity is similar to Dune Scrub, to which it is closely related. This community occurs as isolated patches in wide dunefields.	Thicket and Shrubland pockets (Talbot & Bate 1991); Bushpockets (McLachlan *et al.* 1982; Young 1987; Lubke 1988); Erosion and Deposition Mounds (Hesp 1986).

PLANT COMMUNITY	DESCRIPTION	SYNONYMS AND AUTHORITY
Dune Scrub Community	All life forms are represented, but shrubs and herbs dominate. Community is fairly diverse, with a species composition similar to the Bushpocket community. Most species are not restricted to this community, and trees are not common. Shrubs form a fairly open canopy of 2-3 m high. Occurs on slipfaces and on margin of Dune Thicket. More frequent in the central portion of the coastline.	Zone II Shrub Community (Tinley 1985); Dune Thicket (CSIR 1989); Dune Scrub or Thicket (Lubke & van Wijk 1988); Dune Margin Scrub (Lubke & Strong 1988); Scrub/Thicket Mosaic (Daines 1991); Dune Scrub (Parker-Nance *et al.* 1991); Open Scrub Community (Burns & Lubke 1986); Coastal Thicket (Lubke & de Villiers 1991).
Fynbos Community	Species rich community dominated by species with a Cape floristic affinity. Two distinct types occur. The Scrub Fynbos is dominated by broad-leafed shrubs, and is physiognomically similar to Dune Scrub, but differs floristically. Shrubs such as *Pterocelastrus tricuspidatus* are most conspicuous, whereas herbs and restios such as *Restio eliocharis* dominate the Dune Fynbos. Usually found further west in similar habitat to Dune Scrub.	Zone III Scrub-Thicket and Dune Heath (Tinley 1985); Fynbos/Thicket Mosaic (CSIR 1989); Dune Fynbos (Lubke & van Wijk 1988); Cape Fynbos Shrublands (Lubke *et al.* 1986); Sub-stable Coastal Fynbos (Taylor 1978) & *Restio-Agathosma* Fynbos (Cowling 1984) = Dune Fynbos. Coastal Scrub (Taylor 1978) & *Restio-Maytenus* Fynbos (Cowling 1984) = Scrub Fynbos. *Olea exasperata* Fynbos (Young 1987); Dune Fynbos (Lubke & de Villiers 1991).
Dune Thicket	Diverse and species rich, dominated by herbs, shrubs and trees. Latter form a compact canopy at about 5m, but may be pruned by wind and salt spray. Shrubs are more common than trees, and form a dense undergrowth. Distinct from Dune Scrub due to presence of trees, typically *Mimusops caffra* and vines. More common further east on rear dunes, and grades into forest as rainfall increases and climate becomes more favourable. In Dune Forest, larger trees are more common and the undergrowth is less dense.	Zone III Shrub-Thicket community (Tinley 1985); Dune Scrub or Thicket (Lubke & van Wijk 1988); Dune Forest and Thicket and Stunted Dune Thicket (CSIR 1989); Xeric Kaffrarian Thicket (Everard 1987); Coastal Scrub (Lubke & Strong 1988); Scrub/Thicket Mosaic (Daines 1991); Dune Thicket (Parker-Nance *et al.* 1991). Scrub/Thicket community (Burns & Lubke 1986); Seaward Dune Forest Community (Burns 1986); Coastal Forest (Lubke & de Villiers 1991).

creeping plants with rhizomatous, stoloniferous and sympodial growth forms. Cover is usually sparse (50-70% aerial) and the average height of plants is less than 0.5 metres.

Dune Slack Community

Dune slacks or swales, defined by Tansley (1949) as "low lying ground between dunes where the ground water is near the surface" are fairly common along this stretch of the coastline. They occur as interdune hollows and may be open to the beach as is the case in the Alexandria dunefield (McLachlan *et al.* 1987). More commonly, they occur behind the foredunes which trap most of the mobile sand, allowing sufficient quiescent time for more mesic species to colonize (Plate 1.3). Slacks are found along the entire coastline, and have a greater species diversity than foredunes, being similar to the woody communities (Table 1.2). Species richness is less than the Dune Pioneer community, but on average more species were recorded per relevé. Herbs still dominate this community, but shrubs and graminoids are more common. The presence of sedges and rushes indicates favourable moisture conditions, and *Scirpus nodosus* and *Juncus krausii* dominate (see Plate 2.4,pg 84). Following periods of high rainfall, and depending on their location in the dunefield, standing water may be present. Herbs such as *Arctotheca populifolia* and *Vellereophyton vellereum* are common, as is the grass *Sporobolus virginicus*. Similar shrub species to those found on foredunes occur, but they are more abundant and larger. Cover is usually greater than 70%, and in more mature slacks a field layer of less than 1 m and shrub layer of about 2 m may be differentiated.

Rocky Cliff Communities

Rocky promontories are restricted to specific localities along this stretch of the coastline. These include Cove Rock west of East London, Fish River mouth and the Three Sisters slightly west of the latter locality, Bushman's River and Cape Receife near Port Elizabeth (Fig. 1.1). There are two distinct communities, one dominated by herbs and the other woody species (Plate 1.4; Table 1.1). The former has species richness and diversity values similar to but slightly higher than the Dune Pioneer community. Graminoids and succulents are common and no creepers, vines, geophytes or trees are present (Table 1.2). Common species include *Felicia capensis* and *Sporobolus virginicus* and the succulent halophyte *Chenolea diffusa*. The Cliff Thicket vegetation is surprisingly the most diverse community sampled, although species richness is not greatest (Table 1.2). These rocky headlands seem able to support fairly complex communities, with all life forms except sedges and rushes present, despite the shallow soils and a high incidence of salt spray which results in a wind pruned dwarf community. This is mainly due to the long period of establishment of plants, as indicated by the large number of trees and shrubs such as *Maytenus procumbens* and *Eugenia capensis,* which dominate.

Bushpocket / Scrub Community

Relevés dominated by woody species were separated into four main groups, but the two groups in the bushpocket/scrub community were combined as they are similar (Fig. 1.3). The Cliff Thicket community has already been discussed. The bushpocket/scrub group occurs at various localities along this stretch of the coastline, but is more common west of the Keiskamma River (Fig. 1.1; Plates 1.5 & 1.6).

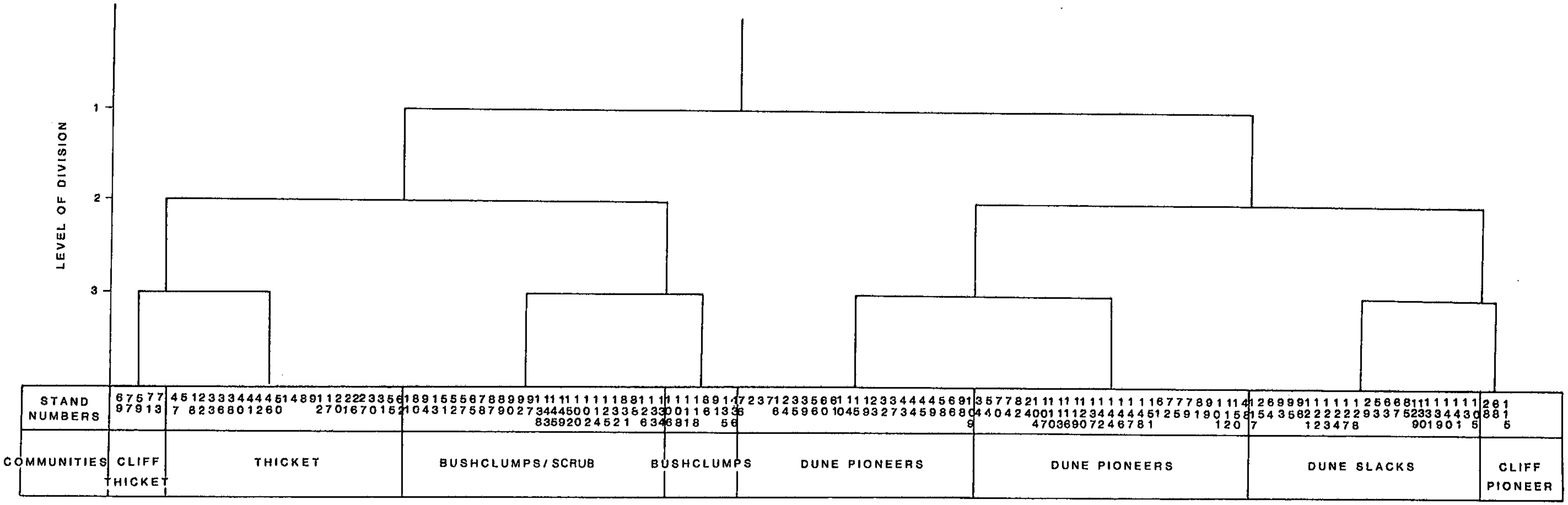


Figure 1.3 Dendrogram generated by the TWINSPAN classification of 152 relevés surveyed from Kei Mouth to Cape St Francis, showing major communities.

Table 1.2 Measures of diversity and life form composition of the seven major plant communities identified by twinspan (Figure 1.3).

PARAMETERS	Species richness	Mean no species per relevé	No of relevés	Simpson's		Shannon Diversity	Lifeform Composition of Communities (%)								
COMMUNITIES				Dominance	Diversity		Grasses	Sedges/ Rushes	Succu-lents	Herbs	Creepers	Vines/ Climbers	Geo-phytes	Shrubs	Trees
DUNE PIONEER	68	10.36 +/- 0.96	56	0.356 +/- 0.025	0.644 +/-0.025	0.600 +/-0.029	18	2	7.5	38	11	3.5	2	18	0
DUNE SLACK	53	12.42 +/- 1.42	24	0.333 +/- 0.038	0.682 +/-0.032	0.642 +/-0.040	14.5	10.5	6	42	6	2	0	19	0
CLIFF HERBACEOUS	27	14.25 +/- 0.75	4	0.263 +/- 0.035	0.737 +/-0.035	0.700 +/-0.037	23	9	23	41	0	0	0	4	0
CLIFF WOODY	65	32.4 +/- 3.21	5	0.187 +/- 0.0129	0.833 +/-0.085	1.011 +/-0.045	9	0	5	26.5	5	5	3.5	30	16
BUSHPOCKET /SCRUB	78	19.7 +/- 2.48	37	0.316 +/- 0.022	0.683 +/-0.021	0.710 +/-0.064	14	4.5	5	35	7.5	5	1.5	33	10.5
DUNE THICKET	92	23.8 +/- 1.63	26	0.300 +/- 0.002	0.686 +/-0.089	0.850 +/-0.044	7.5	1.5	6	30	14	6	3	20	12

Most relevés falling within this group were either sampled in dune scrub adjacent to thicket or from isolated pockets of vegetation within the mobile dunes (Table 1.1), commonly referred to as bushpockets (Young 1987; Lubke 1988; Talbot & Bate 1991). Species richness and the mean number of species recorded per relevé is lower than for Dune Thicket, but Simpson and Shannon diversity values are similar (Table 1.2). All life forms are present, and although herbs and shrubs are most common it is shrubby species that dominate and characterise this community. These included fine-leaved shrubs such as *Passerina rigida* and *Stoebe plumosa*, composite shrubs such as *Chrysanthemoides monilifera* and *Metalasia muricata* and shrubs with a sympodial growth form, namely *Rhus crenata* and *Myrica cordifolia*. *Ehrharta villosa*, a tall grass which thrives in mobile sand is fairly common, as is the creeper *Cynanchum natalitium*. It is important to note that although trees such as *Maytenus procumbens* are present, they are not conspicuous. The shrubs form a fairly open canopy of 2 to 3 m high with a ground layer of herbs and graminoids.

Dune Thicket Community

This community was not sampled further west than the Great Fish River, but does commonly occur west up to Bushman's River (Lubke 1988). Further west is the Alexandria coastal forest with Afromontane species, but closer to Port Elizabeth in the Sunday's River basin Xeric Kaffrarian Thicket and Dune Fynbos are found (Everard 1987; CSIR 1989; Plate 1.7). The thicket/forest communities (Tinley 1985) of rear and ancient dunes are not discussed as only the first well vegetated barrier dune was sampled. The vegetation covering these barrier dunes is diverse, with a high species richness and large number of species per relevé (Table 1.2; Plate 1.8). All life forms are present, with herbs and shrubs being most common. The high number of herbs is the result of samples being taken along the margin of the community, as more commonly the groundlayer is sparse in this Zone III Scrub-Thicket community (*vide* Tinley 1985). Vines and creepers are also common, as are trees which together with shrubs form a dense community with a compact canopy of up to 5 metres (Table 1.1). Height is dependent on dune relief, and the canopy may be pruned due to salt spray (Burns 1986). The most conspicuous species along this section of the coast is *Mimusops caffra*, which dominated all relevés. *Maytenus procumbens*, *Scutia myrtina* and *Brachylaena discolor* are other common trees. The vine *Rhoicissus digitata* and the succulent *Carpobrotus edulis* are also very common (see Appendix 1.1).

Plate 1.5 Bushpocket community in the Alexandria dunefield. The grass in the foreground is *Ehrharta villosa*, and the woody shrub behind it *Brachylaena discolor*. The large patch of vegetation on the right at the bottom of the slipface is *Myrica cordifolia*, a characteristic species of this community.

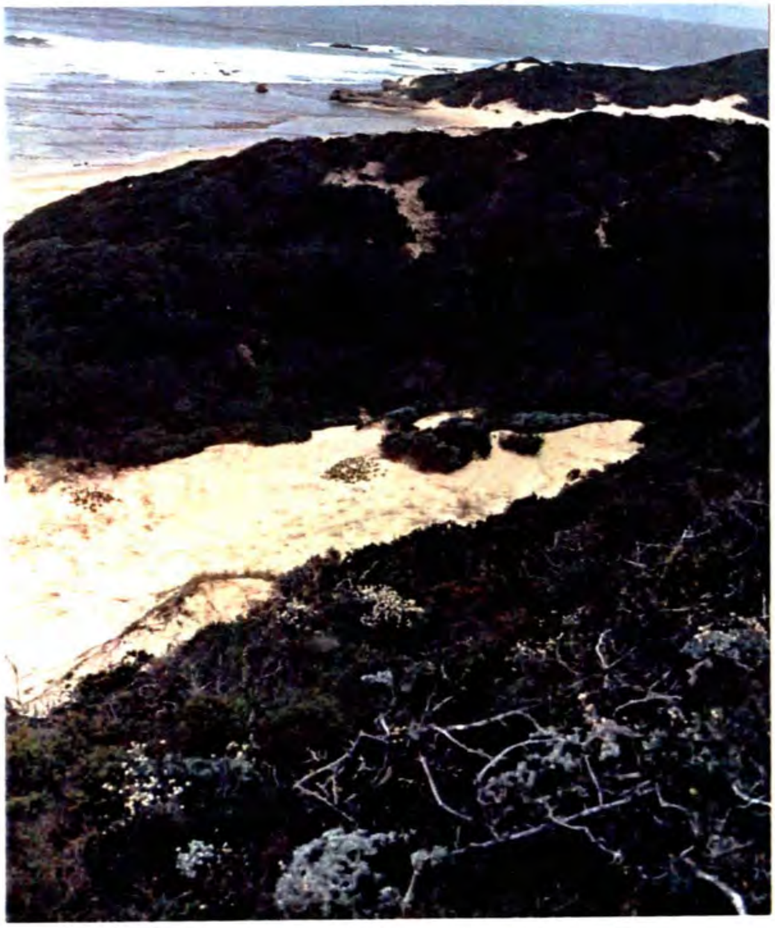


Plate 1.6 Dune Scrub community in the Joan Muirhead Nature Reserve at Kenton-on-Sea. The vegetation is less than 2 m tall and dominated by shrubs such as *Metalasia muricata*, with its characteristic cream flowers.

Plate 1.7 Dune Fynbos community behind the Alexandria dunefield near Woody Cape. The low (less than 1 m), small-leaved woody shrubs form a dense community.

Plate 1.8 Dune Thicket/Forest Community backing the Eastern Beach in East London. This community is dominated by trees such as *Mimusops caffra*, which form a mature, closed forest canopy at a height of about 4 to 6 metres. Note the damage due to recreational pressure in the foreground, and the influence of salt spray on *M. caffra*.

SPECIES DISTRIBUTION

In describing the various communities, their distribution along the coastline was discussed. However, it is also important to look at the distributional ranges of species which typify these communities. Figure 1.4 illustrates the ranges of 50 species, which may either be widespread, or occur mainly towards the west (Cape) or east (Tongaland/Pondoland phytochoria). The dominant dune forming species, *Sporobolus virginicus, Arctotheca populifolia* and *Scaevola plumieri* range the entire length of the study area and beyond. However, *S. plumieri* becomes infrequent further west of the study area as it is a pantropical species. *Mariscus congestus* and *Tetragonia decumbens* also occur throughout the study area, but never dominate the pioneer communities. Towards the west, dunes are built by the introduced rhizomatous grass, *Agropyron distichum*, and although *Ipomoea pes-caprae* does occur west of the study area, it is more abundant along the eastern portion, where it commonly occurs with the subtropical creeper, *Launaea sarmentosa* (Fig. 1.4).

The Asclepiad creeper, *Cynanchum natalitium* is widespread and common in both Dune Slack and Bushpocket/Scrub communities. *Juncus kraussii* and *Vellereophyton vellereum* are widespread but restricted to the dune slack habitat. *Ficinia lateralis* is abundant in dry slacks, small pebble plains and sand slips, and together with *V. vellereum*, which is endemic to the Eastern Cape, reaches its eastern range limit near East London. *Chironia decumbens* and the sedge *Scirpus nodosus* are typically restricted to dune slacks, but have a widespread range. The latter frequently dominates moist slacks, but becomes less abundant further east. *Helichrysum cymosum, H. praecinctum* and *Senecio elegans* are widespread and common on dunes and dry slacks and along the margin of dune scrub, with the latter being more abundant. *Psoralea repens* is a creeper common in dune slacks but reaches its eastern range near Port Alfred (27^0 east, Fig. 1.4).

Shrubs which typify the Bushpocket/Dune Scrub communities and are widespread throughout the study area include *Passerina rigida* and *Chrysanthemoides monilifera*. Both *Metalasia muricata* and *Rhus crenata* are abundant, but appear to reach their eastern range limit at the Kei River. *Stoebe plumosa* is only found west of 27^0 30' east (midway between the Buffalo and Keiskamma Rivers) where it is a characteristic species of dune scrub. The above are usually dominant species of the communities in which they occur. The tree *Brachylaena discolor* and shrub *Eugenia capensis*, both with simple mesophytic leaves, are more typicial of the Dune Scrub and Bushpocket communities east of the Alexandria dunefield (26^0 20' Fig. 1.4). *Myrica cordifolia* and *Ehrharta villosa* dominate the bushpockets which first appear west of the Keiskamma River, and only occur in stabilization sites east of this locality (Chapter 8). *Imperata cylindrica*, a pantropical rhizomatous grass is widespread but only becomes abundant on the Natal coast (Chapter 3).

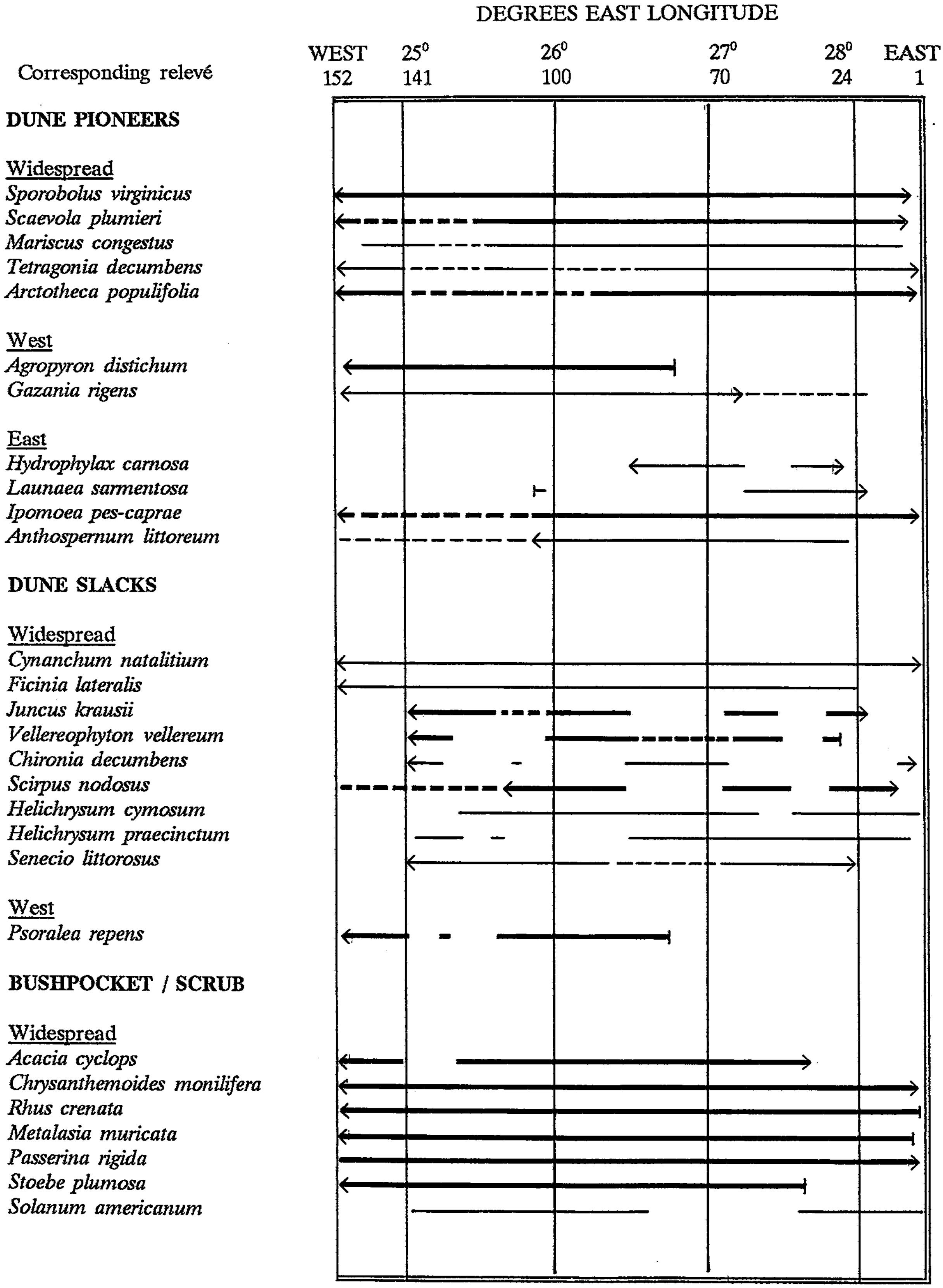


Figure 1.4 Ranges of species typical of each community along the Eastern Cape coastline. Arrows at the end of the line indicates a range extending east or west of the surveyed area; double line indicates dominant species; broken line indicates a range reported in the literature but not seen in this survey. Corresponding relevés indicate the position of samples as shown on Fig. 1.1 (pg 17).

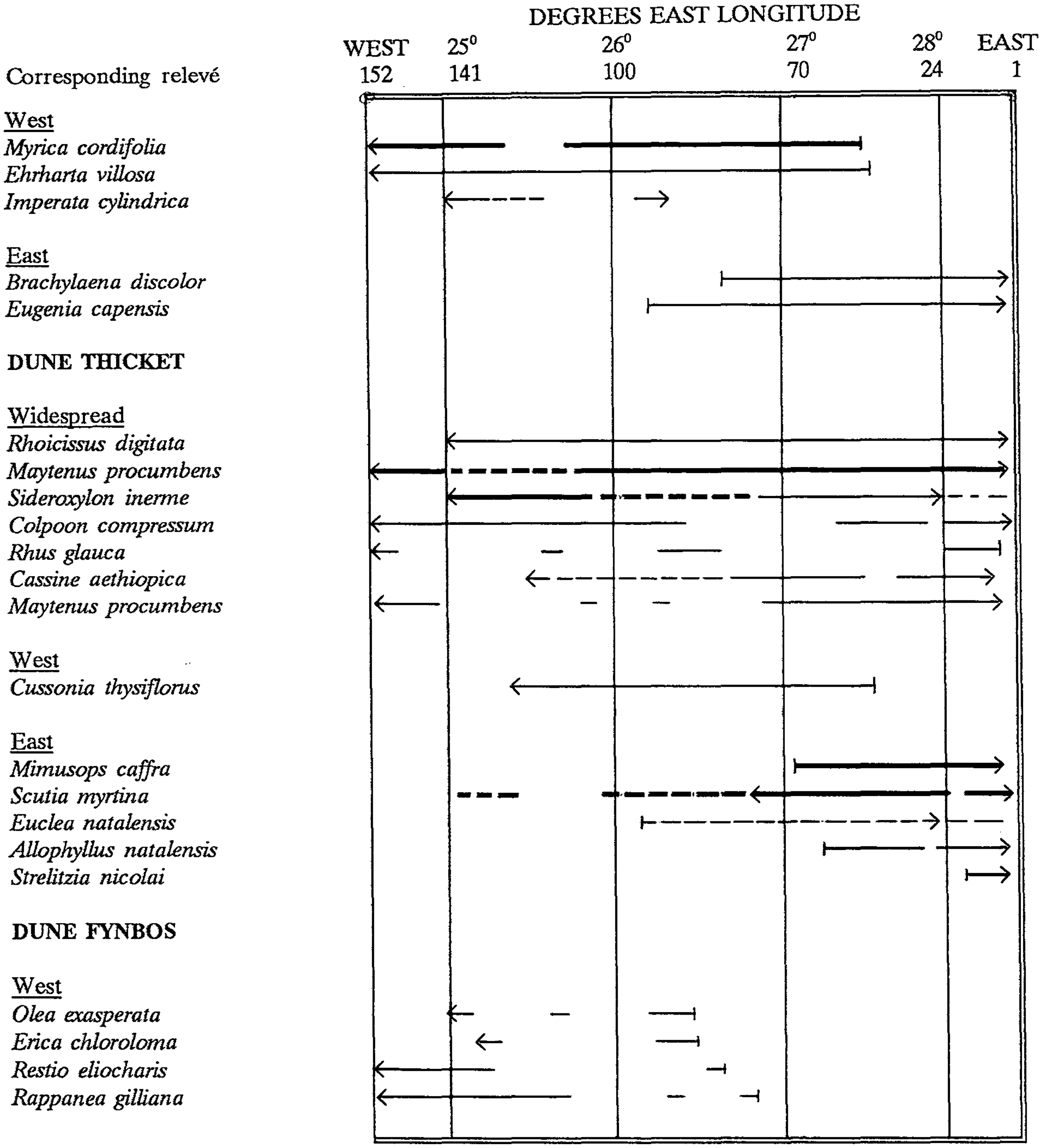


Figure 1.4 Continued.

Rhoicissus digitata, a creeper with extensive root systems, is common along thicket margins throughout the area. *Maytenus procumbens* is dominant and widespread, and *Sideroxylon inerme* characterises the more mature thickets throughout the study area, but only dominates thickets towards the west. Other common and widespread woody shrubs include *Colpoon compressum, Maytenus procumbens* and *Rhus glauca,* but the latter does not occur east of the Kei River. *Cassine aethiopica* has been recorded in bushpockets at Natures Valley 200 km west (Tinley 1985). *Cussonia thysiflorus* occasionally occurs along the coast, but is not found east of the Keiskamma River. A large number of species mainly found in the Dune Thicket community do not occur west of the Alexandria dunefield, and this corresponds to the distribution of this community east of this locality (Fig. 1.1). *Mimusops caffra* is characteristic of Dune Thicket, but is not found west of Port Alfred. *Scutia myrtina* is dominant east of this location, and has also been recorded west of Port Elizabeth (Olivier 1986). Unlike *Euclea racemosa, E. natalensis* is not widespread and probably does not occur west of the Alexandria dunefield. *Allophyllus natalensis* was not recorded west of the Great Fish River, but does occur as far west as the Bushman's River (Lubke & van Wijk 1988). *Strelitzia nicolai*, a banana-like tree of tropical origin is only found east of East London and becomes more common in the Transkei and Natal.

All species which fall into the Dune Fynbos community are not found east of the Bushman's River (Fig. 1.4), although fynbos elements occur as far east as the Great Fish River. These species are not common in the study area, but become more abundant further west on the south coast (Cowling 1983).

PHYTOCHOROLOGICAL AFFINITIES

The phytochorological spectrum (Fig. 1.5) shows widespread species to be most common as many of these may be transgressor species. However, a significant proportion of these species are cosmopolitan or pantropical. Despite the fact that the majority of the area falls within the Tongoland/Pondoland phytochorion (Fig. 1.1), there are a larger amount of Cape species present, due to the richness and diversity of the Cape flora (Bond & Goldblatt 1984) and the presence of patches of fynbos along this stretch of coastline. This may also explain the relatively large number of species endemic to the study area. There are only a few succulent representatives of the Karoo/Namib phytochorion which occur in the drier habitats, and Afromontane species are not common as they usually occur in forests (Fig. 1.5).

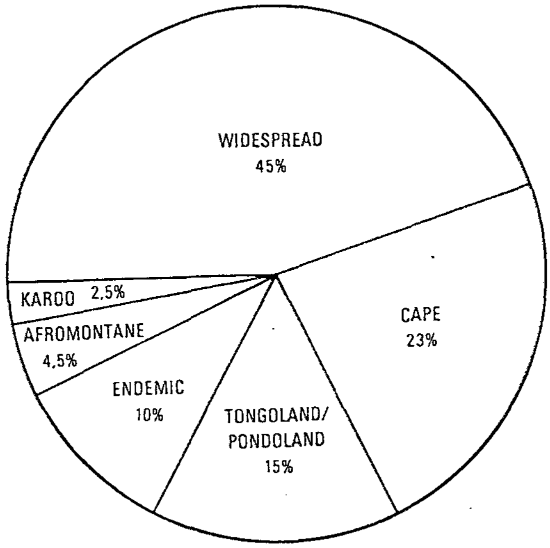


Figure 1.5 Phytochorological spectrum showing percentage of species found in each of the four phytochoria; number endemic to the Eastern Cape; and widespread species (found in more than one phytochorion).

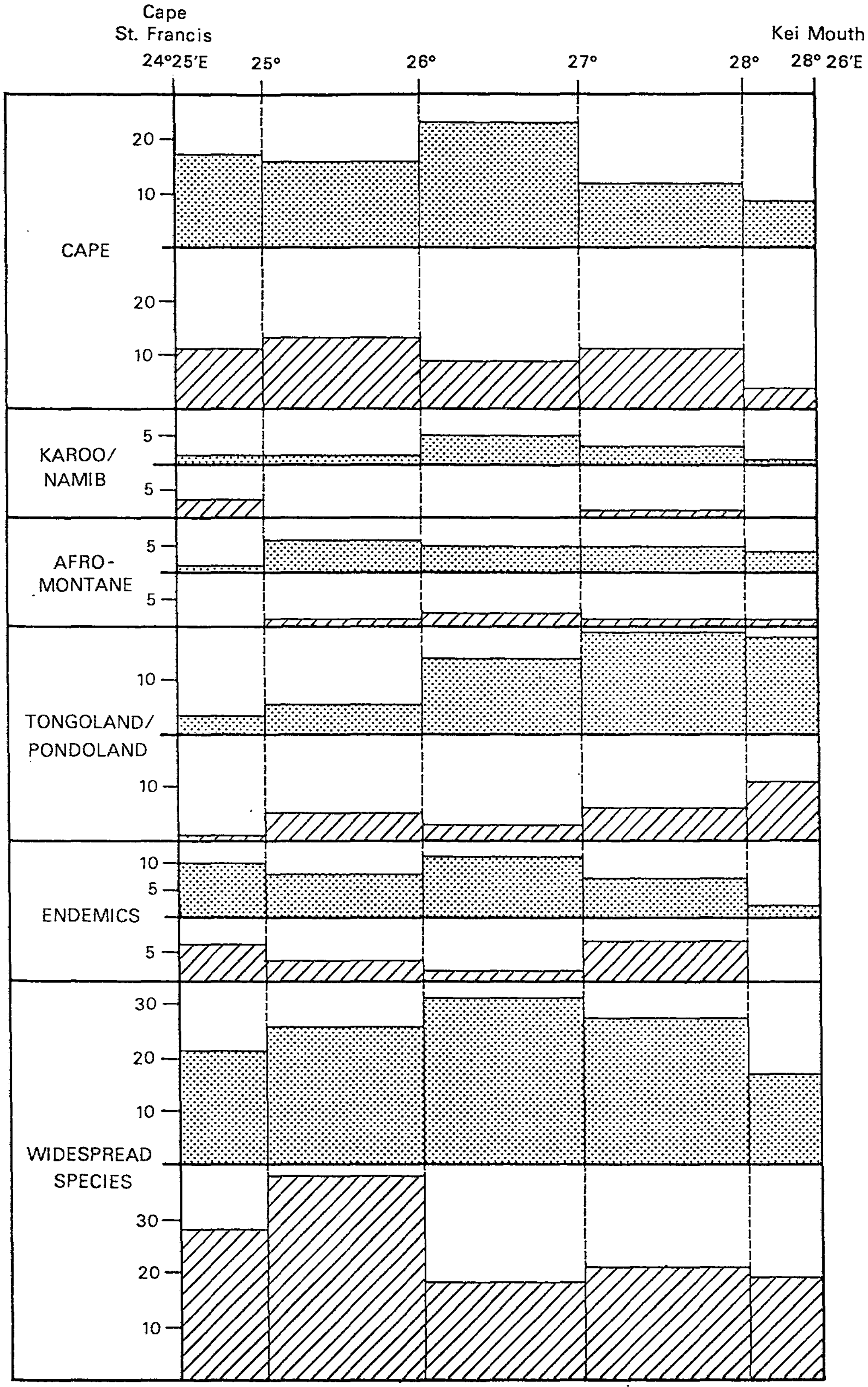


Figure 1.6 Number of species from the four phytochoria (y axis) found along major sectors of the coast (x axis), as defined by degrees east latitude. Number of endemics and number of widespread species are also given. Species are separated into two groups: those occurring predominantly in woody communities of the backdune areas (stippled), and those found on foredunes and dune slacks (hatching). Major sectors of the coast are: Cape St Francis to Gamtoos (25°E); Gamtoos to Alexandria dunefield (26°E); Alexandria to Kowie River (27°E); Kowie to East London (28°E); and East London to Kei River.

A more detailed investigation of the distribution of species from each phtyochorion shows that Cape species are common throughout the area, but decline towards the east (Fig. 1.6). The increase between the Alexandria dunefield (26°E) and Kowie River (27°E) is due to the large patches of coastal dune fynbos found at Woody Cape (Young 1987). This area of shallow soils and low rainfall also has slightly more Karoo/Namib flora in the woody communities (Fig. 1.6), but there is a definite decline in Cape species towards the east. Afromontane species, always present but never abundant in woody communities, decrease towards the west. Very few Karoo/Namib and Afromontane species occur on the foredunes and dune slacks. A steady increase in Tongoland/Pondoland species from west to east occurs. This was more pronounced in the woody communities due to the increased presence of subtropical tree and shrub species in the Dune Thicket communities, which become abundant towards the east (Figs. 1.1 & 1.4).

Generally, more endemics occur towards the west, and there are more endemic species in the woody communities of the backdune areas. This is because the species found in foredunes and slacks are usually more cosmopolitan, and it is also these species which contribute to the high number of widespread species noted in woody communities (Fig. 1.6). The number of widespread species is fairly high throughout the area, and the increase in widespread species of slacks and foredunes between the Gamtoos River (25°E) and Alexandria dunefields (26°E) is due to the greater number of weedy and hydrophilic species recorded in dune slacks along this stretch of the coastline.

COMMUNITY DYNAMICS

The complete data set was analyzed by DECORANA, and scatter plots showing stand and species positions relative to axes 1 and 2 are given in Figures 1.7 & 1.8 respectively. The position of dune slacks on the right of the diagram, followed by the Pioneer, Bushpocket/Scrub and Thicket Communities on the left (Fig. 1.7) does not follow the expected trend in succession from pioneers via dune slacks to bushpockets and thickets as reported in Chapter 2. The over-riding factor appears to be a decrease in the soil moisture variability within each habitat. Soil moisture is highly variable in dune slacks. During wet periods and after high rainfall events standing water is present in slacks, but during periods of low rainfall they may be as dry as foredunes (Compare Plates 4.2 & 4.4, pgs 129 & 133). However, despite the relative dryness of foredunes, a predictable amount of moisture is present throughout the year, and seasonal fluctuations are not as marked. Wind blowing off the sea is moisture laden and condensation on the foredunes occurs. Coupled with changes in soil properties there is an increase in community complexity on the ordination plot from right to left (Fig. 1.7). It is also suggested that during unfavourable climatic and environmental conditions retrogression of Dune Slack to Dune Pioneer communities may occur. However, during favourable conditions, slacks may be invaded by woody species, resulting in Bushpocket and Scrub communities (Fig. 1.7; Plates 1.5 & 1.6).

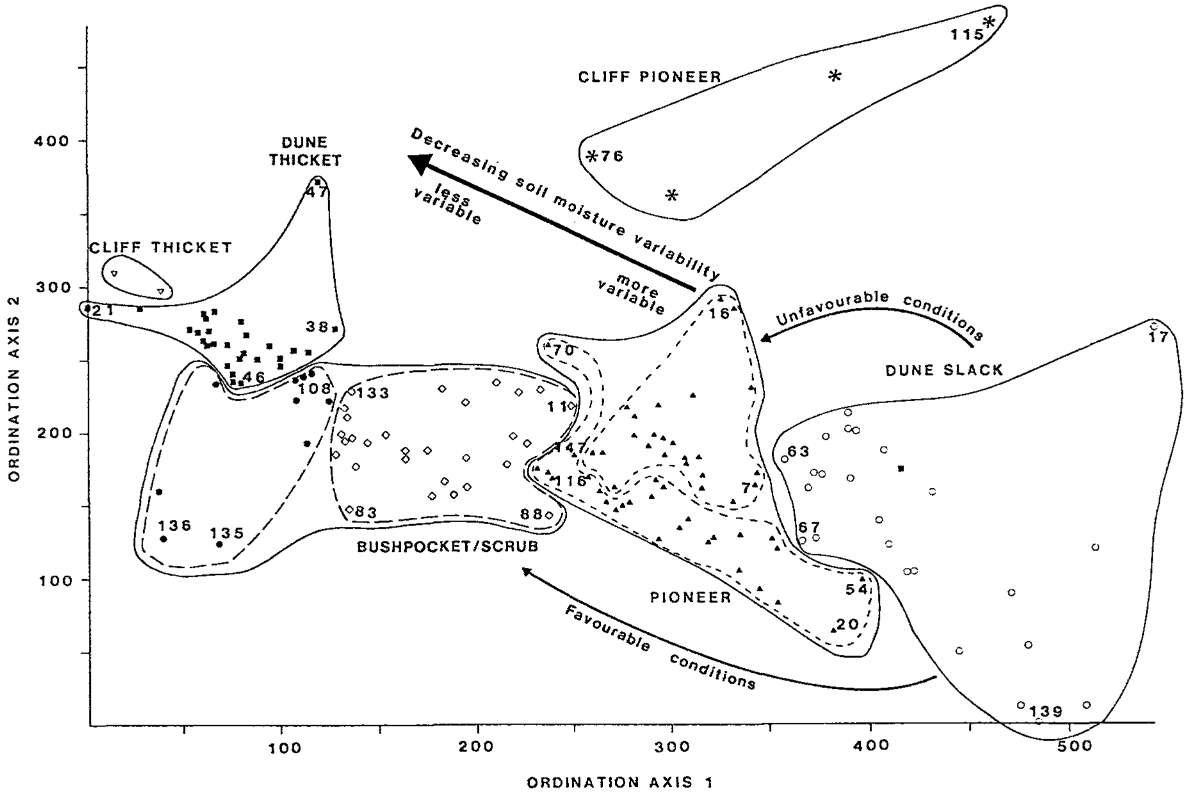


Figure 1.7 Ordination of the 152 relevés using DECORANA, showing groups as classified by TWINSPAN (Fig. 1.3).

The ordination of the species groups defined by TWINSPAN revealed a similar distribution along axis 1 and 2, with dune slacks on the right and woody communities on the left (Fig. 1.8). Again there appeared to be an increase in habitat variability from left to right. However, there is a corresponding decrease in species specialization within specific habitats from dune slacks on the right to thickets on the left. Similarly, axis 2 suggests that species along the median are more widespread, (for example, *Ipomoea pes-caprae* and *Chrysanthemoides monilifera* were recorded in the Dune Slack, Bushclump, Dune Scrub and Pioneer communities) whereas those at the extremes are confined to specific habitats (*Vellereophyton vellereum* to Dune Slacks and *Maytenus procumbens* to Dune Thicket). The group of widespread shrubs and herbs link the forb dominated Dune Slack and Pioneer communities with the Bushpocket and Thicket communities dominated by woody species (Fig. 1.8). Thus, it appears that a decrease in soil moisture variability and attendant improvement in other soil properties results in a successional change from right to left. Communities on the right are dominated by herbaceous species highly specialised for survival only in particular habitats, such as *Scaevola plumieri*, whereas communities on the left are dominated by more generalistic woody species which are able to survive in habitats other than sand dunes (for example *Chrysanthemoides monilifera*) (Figs. 1.7 & 1.8).

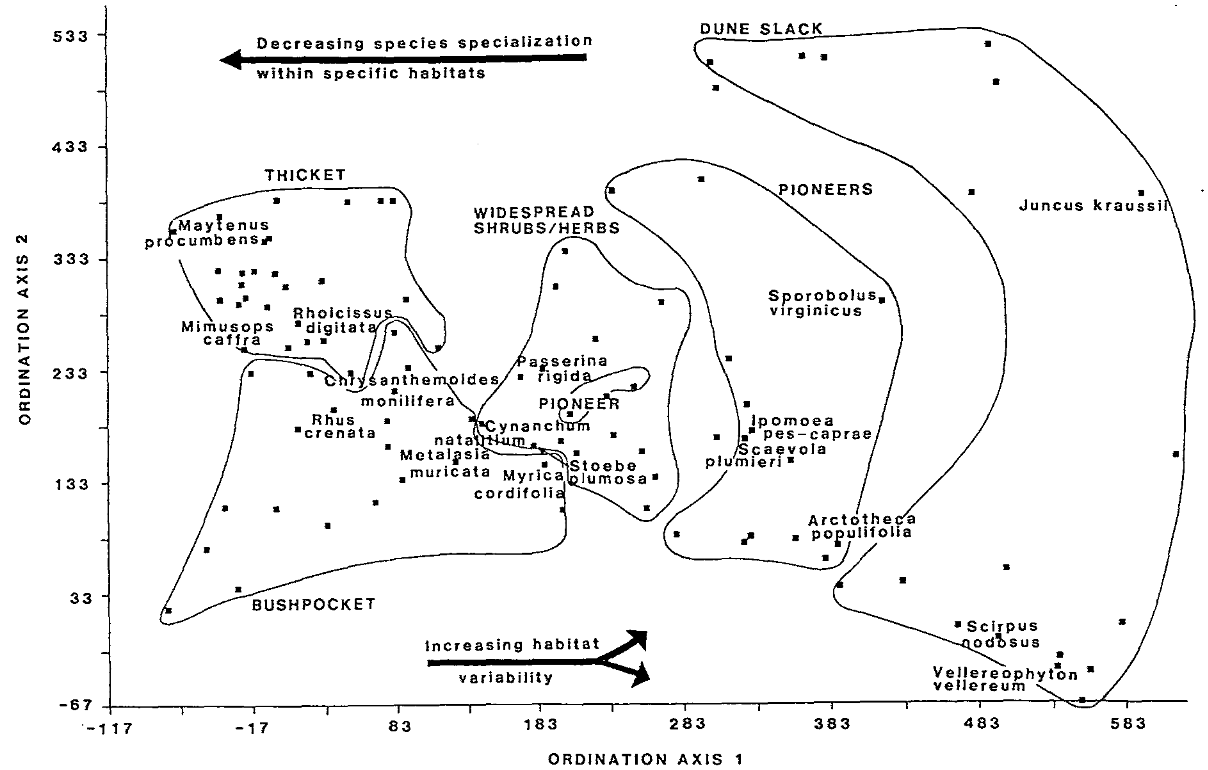


Figure 1.8 Ordination of species using DECORANA, showing species groups as classified by TWINSPAN.

SUBCOMMUNITY TYPES AND DYNAMICS

To determine whether distinct stands of vegetation existed within the Dune Pioneer and Dune Slack communities and the two groups (Bushpocket/Scrub & Dune Thicket) dominated by woody species, these three sub-sets of data were subject to re-analysis by TWINSPAN and DECORANA. Data are presented as scatter diagrams of ordination axes 1 and 2 with TWINSPAN groups outlined and dominant species in each relevé indicated (Figs. 1.9 - 1.11).

Pioneer Communities

Although the Dune Pioneer community was separated into four groups by TWINSPAN at level 3, as shown in Figure 1.9, only three communities are represented and described below.

Embryonic Foredune Community

This group consists of pioneer species, mainly *Ipomoea pes-caprae*, which colonize fairly level areas with very small embryonic foredunes. Other pioneer species include *Arctotheca populifolia* and *Mariscus congestus*. Relevés in this group were confined to the eastern portion of the study area (Fig. 1.1). They are usually located on sand spits next to river mouths or on flat level foreshores, and little foredune development occurs due to frequent erosion. Consequently, the only woody species recorded was the tough, small-leaved shrub *Passerina rigida*.

Hummock Foredune Community

Steep, well rounded and fairly high (3 metres) hummock dunes characteristically colonized by *Scaevola plumieri* have been defined as the Hummock Foredune Community (Fig. 1.9; see Plate 4.1, pg 129). Other dominant species are *Ipomoea pes-caprae*, and *Sporobolus virginicus*. Common species include *Passerina rigida* and *Cynanchum natalitium*, which are also common in mature dune slacks and bushclumps. Hummock Foredunes only occur from Cintsa East near East London to the Swartkops River near Port Elizabeth (Fig. 1.1). They are not found further east due to the lack of large sandy beaches, which supply sand for building the distinct foredunes that characterise this community (Table 1.3).

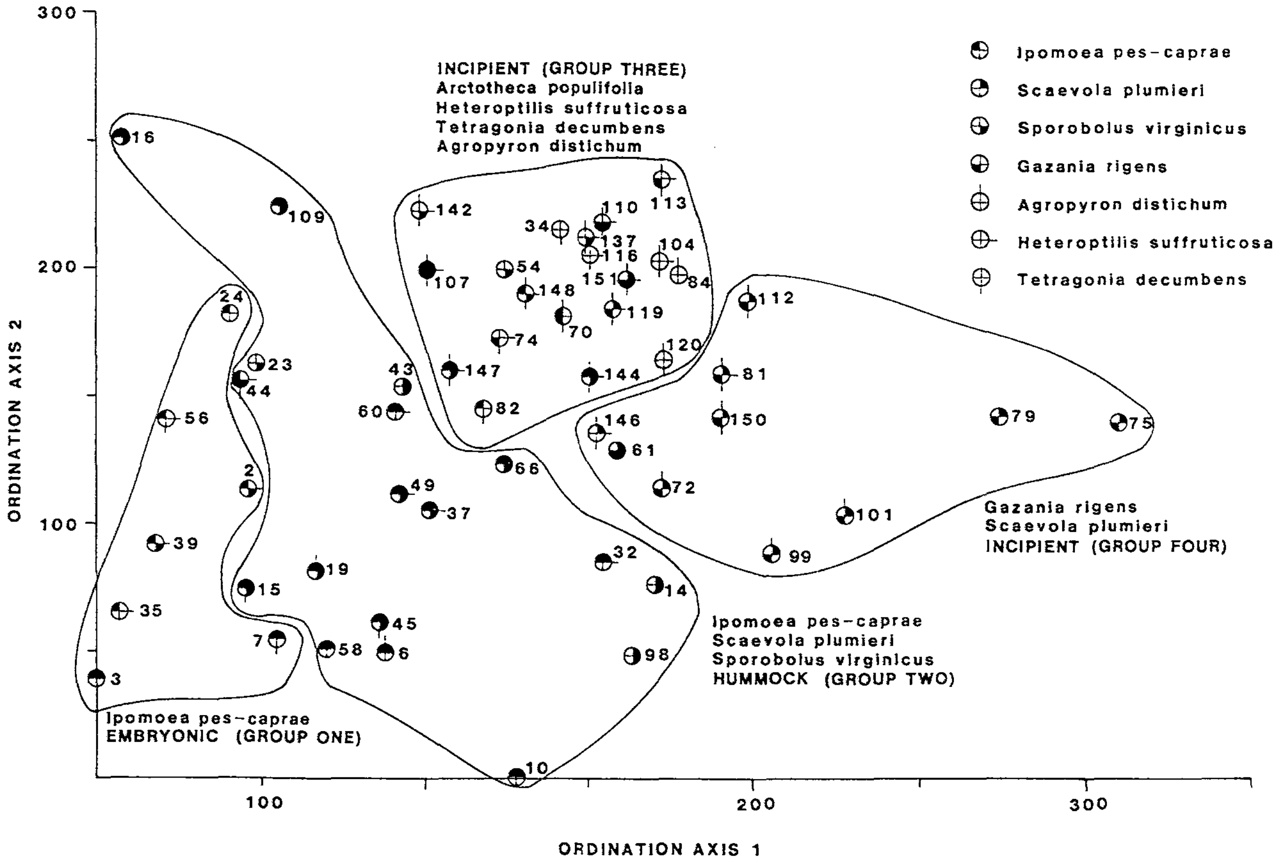


Figure 1.9 Ordination of the relevés classified as the Dune Pioneer Community (Fig. 1.3). Groups are based on a TWINSPAN classification of this subset of data.

Incipient Foredunes Communities

These foredunes are larger, but less rounded and not as steep as Hummock Foredunes. Diversity is usually high, and a number of species characterize this group. The final two groups were classified together as Incipient Foredunes. The presence of *Tetragonia decumbens*, *Agropyron distichum* or *Arctotheca populifolia* characterise this group. A total of 40 species were recorded on these foredunes which are widespread, ranging from Kidds Beach, west of East London (Relevé 35 Fig. 1.1), to Cape St Francis

(Relevé 151). The smaller group (Group 4) is not as widely distributed, found only west of the Fish River (relevé 61, Fig. 1.1). The presence of *Scaevola plumieri*, together with *Hydrophylax carnosa*, and the absence of common species such as *Ipomoea pes-caprae* distinguished this group from the previous one. This difference in species composition is due to the distributional ranges of the characteristic species discussed earlier. These two sub-communities are more diverse than the previous two groups, and the presence of woody shrubs such as *Metalasia muricata* indicate they are more mature. Table 1.3 summarises the distinguishing features of these foredunes.

Table 1.3 Foredune type, diagnostic species and topography associated with four pioneer communities.

GROUP	DIAGNOSTIC SPECIES	PLANT COVER & SPECIES DIVERSITY	TOPOGRAPHY	USUAL LOCATION	FOREDUNE TYPE
I	*Ipomoea pes-caprae*	50 to 60% variable. Low diversity	Level area with low undulating ridges	Adjacent to river mouths	Embryonic
II	*Scaevola plumieri*	70 to 80% Dominant species prominant. Diversity low.	Hummock dunes, well rounded, steep. Max 3 m high.	Wide beaches with good sand supply. Close to rivers.	Hummock
III	*Arctotheca populifolia* *Tetragonia decumbens* *Agropyron distichum*	60 to 80% Diverse. Cover variable.	Fairly large hummocks, but less rounded and not steep. Usually 5 m high. Often coalesce.	Middle of wide beaches, behind driftline.	Incipient
IV	*Scaevola plumieri* *Gazania rigens*	60 to 80% Diverse. Cover variable.	As above, but usually smaller.	As above, but west of Fish River	Incipient

Foredune Dynamics

The scatter diagram suggests a slight gradient from left to right associated with changes in species composition from east to west (Fig.1.9). Group four contained no relevés with *Ipomoea pes-caprae* and Embryonic Foredunes had no relevés with *Agropyron distichum* or *Gazania rigens*. The combined gradients along axes 1 and 2 show a clear transition from less developed Embryonic Foredunes at the bottom left (Group One), to well developed Incipient Foredunes at the top right (Group Three) with a richer species composition. Group four differs from Group three, as it is not as diverse, with only 28 species as compared to 40. These groups do not appear to be linked along a successional sequence, as differences are related more to location within the dunefield and along the coastline, as well as the distributional ranges of individual species.

Dune Slack Communities

TWINSPAN separated four distinct dune slacks types and their location on the DECORANA scatter diagram is presented in Figure 1.10.

Dry Slacks

Of the 17 species recorded in the dry slacks, which are classified after Ranwell (1972) as having a water table below 1 metre, *Sporobolus virginicus, Gazania rigens* and *Arctotheca populifolia* dominate. All these species are also common on foredunes but the location of these habitats in inter-dune hollows and/or the abundance of typical slack species such as the sedge, *Scirpus nodosus* and the annual *Vellereophyton vellereum* characterise these as dune slacks. They are usually found behind Hummock or Incipient Foredunes along the coast from Cove Rock, east of the Buffalo River (relevé 25) to the Gamtoos River mouth (relevé 128, Fig. 1.1). Cover ranges from 26 to 93% and is usually over 60%. The vegetation is always less than one metre high, and usually less than 0.5 m.

River Mouth Slacks

Only two samples were classified as River Mouth Slacks, one at van Stadens and the other at the Gamtoos River mouth. They are dominated by *Vellereophyton vellereum* and *Ficinia aphylla*, but it is the presence of the shrub, *Myrica cordifolia*, that separated these relevés. The latter is common in bushclumps and forest margins, and usually only invades dune slacks which are in a relatively advanced stage of succession. This aspect is considered in more detail in Chapters 2 and 4. Its presence indicates that these dune slacks are mature, although only 14 species were present.

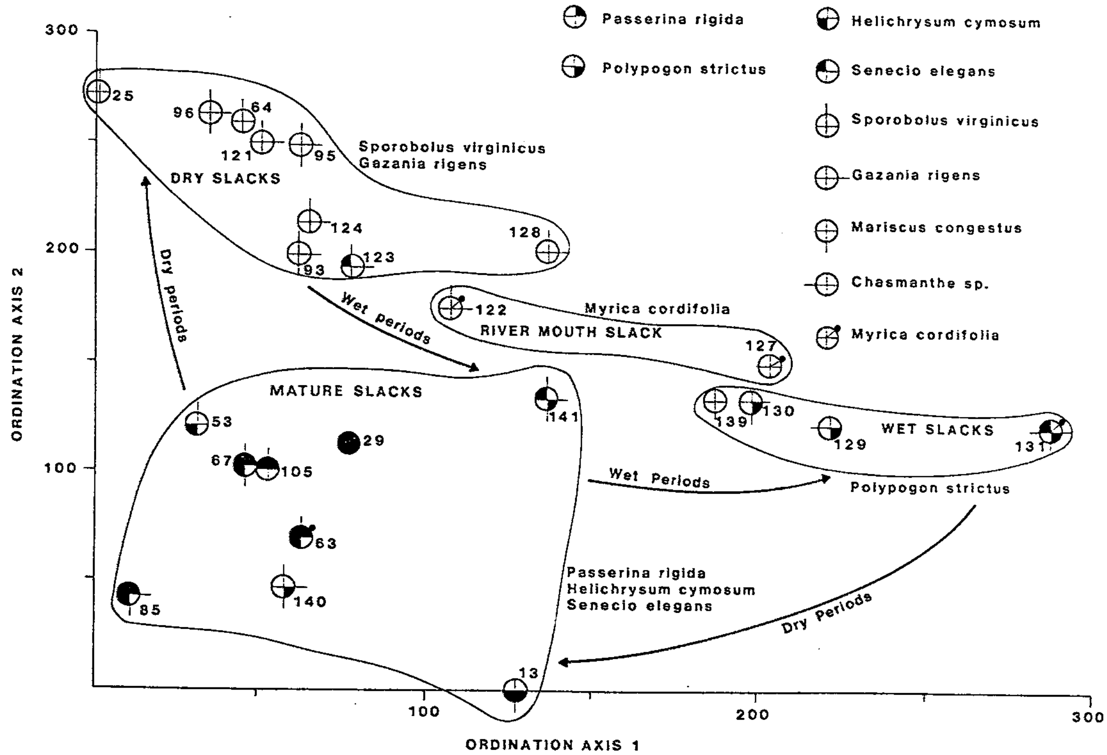


Figure 1.10 Ordination of the relevés classified as the Dune Slack Community (Fig. 1.3). Groups are based on a TWINSPAN classification of this subset of data.

Mature Slacks

The mature slacks are dominated by the sedge, *Scirpus nodosus*, the rush, *Juncus krausii* and the cosmopolitan grass *Sporobolus virginicus* (see Plate 2.3, pg 79). These slacks have a water table above 1 metre, and would therefore be classified as wet slacks after Ranwell (1972). The sedge and rush are abundant in all mature slacks, but it is the presence of the woody, fine leaved shrubs *Passerina rigida* and *Stoebe plumosa* and the composite herbs *Helichrysum cymosum* and *Senecio elegans* that characterise this community (Fig. 1.10). This is the most diverse slack community, and has a species richness of 58. Cover is usually over 90% and the vegetation has two strata, the lower of less than 1 m making up the majority of the community. The upper strata is usually not taller than 2 metres and dominated by shrubs. This community is widespread along the coastline, ranging from Glengarrif (relevé 13) to west of the Gamtoos River near Humansdorp (relevé 141; Fig. 1.1).

Wet Slacks

Four relevés were classified as wet slacks, (Ranwell 1972) and at the time of sampling all had standing water present. They are also dominated by *Scirpus nodosus* and *Vellereophyton vellereum*, but the most characteristic of the 25 species recorded are *Isolepis cernua* and *Polypogon strictus*. The former, an annual sedge, and the latter, a grass, are only common in moist areas (Lubke 1988). Cover is also high (over 90%), but the community has a single strata of less than 1.5 m, depending on species composition. These slacks were also restricted to the mouths of the Gamtoos (relevés 129-131) and the Kabeljouws Rivers (relevé 139, Fig. 1.1). Many of the species which characterise this community rely on periods of high rainfall for their survival. During these periods it is likely that more wet slacks will occur along the coastline.

Dune Slack Dynamics

Dune slacks are the subject of more detailed studies (Chapters 2 & 4), but it is germane to draw some initial conclusions here, based on the data presented in Figure 1.10. Dry and Mature slacks occur throughout the area, but the River Mouth and Wet slacks are restricted to the western part of the study area. Axis 1 suggests a gradient from dry (left) to wet (right) and axis 2 a gradient from less diverse Dry slacks to more diverse Mature slacks (Fig. 1.10). During favourable periods of high rainfall it is possible that Dry slacks will be invaded by more species and develop into Mature slacks, and that some of the latter may develop into Wet slacks. During dry periods Wet slacks may be invaded, as waterlogged conditions disappear, by more species and develop into Mature slacks, but if retrogression occurs in the latter, they will become Dry slacks. This suggests that rainfall and soil moisture are the most important climatic and environmental factors controlling the dune slack environment, and this aspect has been investigated in more detail (Chapter 2).

Woody Plant Communities

The TWINSPAN classification of relevés dominated by woody species initially produced similar groups to those generated by the analysis of the whole data set (Fig. 1.3) by separating the Dune Thicket from other communities. However, lower levels of division split the Dune Thicket and Bushpocket/Scrub communities into six smaller groups which occur along definite compositional gradients (Fig.1.11).

Bushpocket Community

This group is similar to the Bushpocket and Dune Scrub community described earlier, but contains fewer species more typical of the Dune Thicket as these have been separated out into the Dune Scrub group (Fig. 1.11). It only includes relevés from bushpockets which are common west of the Keiskamma river due to the larger mobile dunefields and less frequent occurrence of rocky shores along this stretch of the coastline (Fig. 1.1; Plate 1.5). The creeper *Cynanchum natalitium* and sedge *Ficinia lateralis* are common along the margins of bushpockets, and the shrubs *Passerina rigida*, *Metalasia muricata* and *Chrysanthemoides monilifera* are also common. However, it is the predominance of *Myrica cordifolia*, and to a lesser extent *Stoebe plumosa*, that characterise this community. In only a few cases are small trees such as *Maytenus procumbens* present, but they are never abundant. This vegetation is usually confined to inter-dune hollows within dunefields of over 200 m wide, and is best represented in the Alexandria dunefield (Talbot & Bate 1991).

Dune Scrub Community

This community differs from bushpockets both in species composition and location in the dunefield. It is usually found adjacent to the Dune Thicket community or on the margins of blowout dunes, forming fairly large stands of shrubs with an open canopy (Table 1.1; Plate 1.6). Dune Scrub was sampled west of the Kowie River, and only occurs in isolated patches further east since the Dune Thicket community becomes more common due to the higher rainfall (Fig. 1.2). It also becomes less frequent west of the Gamtoos River as fynbos becomes more common. There are less woody species and herbs such *Tetragonia decumbens* and creepers such as *Carpobrotus edulis* and *Solanum americanum* are more conspicuous than in bushpockets. Common shrubs include *Chrysanthemoides monilifera* and *Passerina rigida*, but *Myrica cordifolia* and *Stoebe plumosa*, characteristic of bushpockets were absent from this group. Few trees are present as this community is usually exposed to salt laden winds and it is probably this exposed position that prevents the establishment of a tall canopy dominated by trees.

Fynbos Communities

Two small groups of 3 relevés each differed from the other groups due to the presence of fynbos species (Fig. 1.11). These patches of fynbos were only recorded west of the Bushman's River at Woody Cape, Port Elizabeth, Cape Receife and the Gamtoos River (Fig. 1.1; Plate 1.7). Further west the coastal vegetation is of Cape origin and fynbos species become more common (Cowling 1983). The eastern extent of communities with a significant proportion of fynbos species appears to be the Great Fish River.

The Scrub Fynbos occurs as patches of scrub dominated by the broad-leafed shrub *Pterocelastris tricuspidatus*, which together with *Rappanea gilliana* and *Helichrysum teritifolium* characterise this community. *Rhus crenata, Euclea racemosa, Passerina rigida* and *Metalasia muricata* are shrubs common to both groups. The Dune Fynbos community has a lower diversity and less woody species than the Scrub Fynbos, and is characterised by the presence of *Restio eliocharis* and *Imperata cylindrica*. It is also structurally more similar to the bushpocket vegetation, and occurs in the same habitats, whereas the Scrub Fynbos is structurally and floristically similar to Dune Scrub.

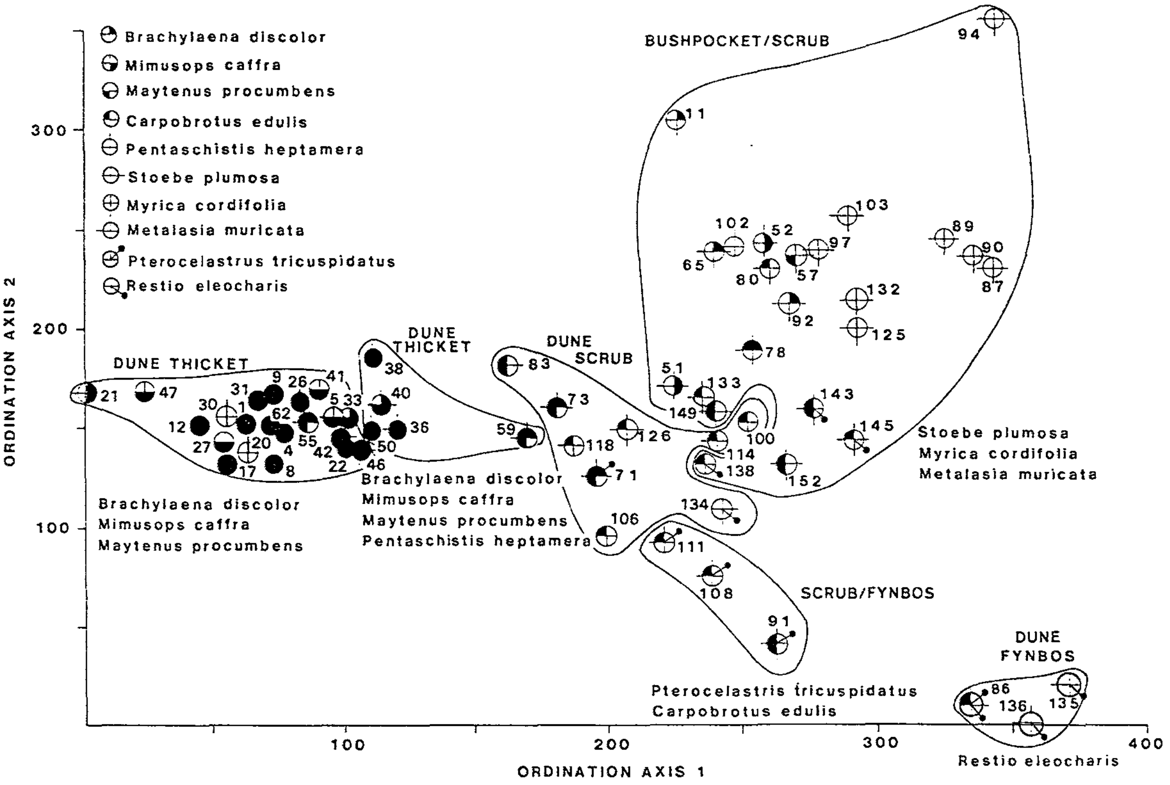


Figure 1.11 Ordination of the relevés classified as Dune Thicket and Bushpocket/Dune Scrub (Fig. 1.3). Groups are based on a TWINSPAN classification of this subset of data.

Dune Thicket Community

The TWINSPAN classification of woody species produced an almost identical group to that generated by an analysis of the entire data set. This community was described earlier, and is distinct from Dune Scrub due to the larger number of trees and vines present, which form a dense canopy (Plates 1.3 & 1.8). Shrubs common in Bushpockets such as *Myrica cordifolia* and Dune Scrub, such as *Metalasia muricata* were not recorded in this community. Although separated into two groups, dominant species do not differ. The group closest to the Dune Scrub (Fig. 1.11) is less diverse with only 41 species recorded more than once. The other group had 54 species, most of the additional ones being trees such as *Cassine tetragonia* and *Pavetta natalensis*. If more samples had been taken in the Thicket/Forest community of Zone IV (Tinley 1985) it is likely that some of these relevés would have fallen into this community.

Woody Community Dynamics

The ordination of these communities suggests a putative succession from Bushpockets on the right to Dune Thicket on the left along axis 1 (Fig. 1.11). There is a definite increase in the number of woody shrubs and trees along this axis, and although shrubs are abundant in bushpockets, there are not that many species, and trees are absent. It is also important to note that the Dune Scrub community appears to link the Bushpocket and Dune Thicket communities. The convergence of relevés along the median of axis 2 towards the left is probably due to an increase in the floristic similarity of relevés in Dune Thicket, and to a lesser extent Dune Scrub (Fig. 1.11). In other words, relevés in Dune Thicket all have similar species, whereas those in Bushpockets often contain very different species, to the extent that relevés dominated by *Restio eliocharis* have been classified into a separate Dune Fynbos group (Fig. 1.11). There is also a greater amount of habitat variability in groups on the right hand side. Relevé 94 is from a pebble plain and 11 from a Mature Dune Slack, but both are classified as Bushpockets due to the presence of *Myrica cordifolia* (Fig. 1.11). Thus, there is a definite trend, from right to left, of increasing habitat stability coupled with an increase in the number of larger species such as trees and predictability of species composition (i.e. equatability increases). However, it also appears that relevés on the left are from the eastern part of the study area, and those on the right from the west suggesting that axis 1 may also be related to species distribution and changes in rainfall (Fig. 1.2).

DISCUSSION

THE PLANT COMMUNITIES

This quantitative overview of dune vegetation along the Eastern Cape coastline has provided more detailed descriptions of the plant communities, their distribution and location within the dunefield, and phytochorological affinities. The communities determined by multivariate analysis of the data are similar to those described by Tinley (1985) and the CSIR (1989), but are more definitive (Table 1.1). Tinley's classification is fairly broad, and most other more detailed studies are confined to isolated areas (Lubke & Avis 1982a; Lubke 1983; McLachlan *et al.* 1987; Young 1987; Lubke & Strong 1988; Parker-Nance *et al.* 1991; Talbot & Bate 1991). Consequently, our understanding of the inter-relationships and dynamics of plant communities in this region is incomplete (Lubke 1988). From this study it is clear that communities and their distribution along the coastline cannot simply be related to climatic and environmental factors such as rainfall and sand movement, as is the case along the Gulf of Mexico (Moreno-Casasola 1988). The situation is far more complex due to the influence of four major phytochoria (White & Moll 1978), and the range of communities and diversity of plant species found in the Eastern Cape (Lubke *et al.* 1986). This diversity and chorological complexity has a marked influence on the coastal vegetation in this region, which has not to date been described adequately.

Pioneer communities are generally least influenced by local vegetation due to the high proportion of cosmopolitan species. They therefore have more shared species (Moreno-Casasola 1988), and these species are usually succulents or non-succulent forbs with pubescent leaves (Barbour *et al.* 1987). Pioneer communities are usually physiognomically simple and uniform, with relatively low cover (Johnson 1977). These general trends were noted in this study, but it appears as though these pioneer communities may be more complex. Despite the relatively short stretch of coastline (450 km) studied, it was possible to distinguish three main pioneer communities on the basis of species composition, topography and location (Fig. 1.9). The Embryonic Foredune Community is similar to Doing's (1985) perennial tidemark community, and the Hummock Foredune Community to his central foredune ridge. The larger group of Incipient Foredunes are found in the sheltered zone (Doing 1985), but since they are not dominated by woody species, they cannot be classified as established foredunes after Hesp (1984). All of these communities are subject to erosion due to their position immediately behind the driftline, and Hesp (1984) would classify them all as Incipient foredunes. *Scaevola plumieri*, which characterizes Hummock and Incipient Foredunes, is the most widespread foredune pioneer. This is because it is stimulated to grow in accreting sand (Pammenter 1983; 1985). Johnson (1977) reported a similar diversity of foredune types at Baja California, Mexico, but her study area was much larger (1390 km). These differences in species composition are due to the influences of the Cape and Tongoland/Pondoland phytochoria (Fig. 1.6), and the differences in foredune types are due to this as well as variable environmental factors such as sand availability, wind and microenvironmental heterogeneity (Figs. 1.1; 1.2). The latter, together with sand movement, nutrient content and organic matter are important along the Gulf and Caribbean Sea of Mexico (Moreno-Casasola *et al.* 1982; Espejel 1986).

The mobile dune systems within the study area also support more luxuriant communities in dune slacks found behind the foredunes. Detailed studies of these have been undertaken at Kleinemonde by Lubke (1983) and Lubke & Avis (1982a) and at Alexandria by McLachlan *et al.* (1987). Four types of dune slacks were distinguished on the basis of species composition and location within the dunefield, but the most important factor appeared to be prevailing moisture conditions (Fig. 1.10). Both Ranwell (1972) and van der Laan (1979) saw the moisture continuum as explaining most of the variation in vegetation found in slacks, and Lubke & Avis (1982a) concluded that soil moisture was the major factor controlling the establishment of dune slack species at Kleinemonde. In a similar study along the coastline of Mexico, near Veracruz, Moreno-Casasola *et al.* (1982) found that the ordination of their humid slack community showed a positive correlation with water table depth and period of inundation. McLachlan *et al.* (1987) studied a dune slack in the Alexandria dunefield, which would be classified as a dry slack in this study, and concluded that moisture was not a limiting factor, but that sand movement and salt spray were important determinants in limiting dune slack vegetation. These factors have also been shown to be important in South African dunefields (Lubke & Avis 1982b; Pammenter 1983; Avis & Lubke 1985), but the situation is more complex. Sykes & Wilson (1987) conclude that there is environmental control in dune slacks to the same degree as in most communities. Since dune slacks represent diverse communities in an otherwise unvegetated dunefield (Lubke 1983; McLachlan *et al.* 1987; Young 1987), and since there appears to be a successional gradient dependent on moisture conditions (Figs. 1.7, 1.8 & 1.10), a more detailed temporal study of a dune slack previously investigated (Lubke & Avis 1982a) was initiated (Chapter 2).

Vegetation of rocky promontories has only been described for communities at East London (Lubke & Strong 1988), Kleinemonde (Lubke 1983) and Kenton-on-Sea (Lubke & de Villiers 1991). This vegetation type is restricted to the rocky and calcareous headlands which typically form points subtending half heart bays. They are very exposed and may occasionally have strips of migrating dunes behind them (Tinley 1985). These are termed bypass dunes and are found at Cape St Francis, Cape Receife and Nahoon Point (Fig. 1.1). Floristically, the herbaceous vegetation is similar to that found on foredunes and dune slacks, but more halophytic species usually found in salt marshes occur. The older headlands are covered by similar woody species to those which occur in Dune Thickets, but the communities are so severely wind pruned that majestic trees such as *Sideroxylon inerme* only reach heights of 20 to 50 cm. Lubke (1983) described a zonation of vegetation from herbaceous communities on more exposed sites, to thicket communities on more sheltered sites (Plate 1.4), and similar results were noted from this study. This zonation is probably related to factors such as wave action, salt spray, wind and interspecific competition for soil nutrients and places to root in the shallow soils. These factors are also important in the zonation of coastal cliff vegetation in Japan (Takayama 1987).

Bushpockets are isolated patches of vegetation found within mobile dunes, which have an active zone of wider than 200 m (Talbot & Bate 1991). Although not separated by TWINSPAN, bushpockets associated with aeolianite outcrops were sampled in narrower dunefields such as those in the Kleinemonde area. These aeolionite communities are best described as bushclumps, as opposed to bushpockets, due to their elevated nature, and are most likely patches of remnant forest formed due to gravity slides and erosion of the steep forested parabolic dunes which characterise this section of the coast (Tinley 1985). Hesp (1986) has referred to these as erosion knobs and Talbot & Bate (1991) as thicket pockets. The vegetation is more exposed and damage due to salt spray is evident on the seafacing slopes where vegetation may be less than 0.5 m tall. Conversely, sand movement is more important than salt spray in bushpockets, and although these habitats are fairly stable, they migrate at a rate of 2.2 m yr^{-1} in the Alexandria dunefield (Young 1987). The best examples of bushpockets are those which occur in the Alexandria dunefield. Young (1987) noted gradients of species composition, manner of growth and growth form, canopy height and percentage cover in these bushpockets, in response to this migration. Talbot & Bate (1991) recorded bushpockets in four transgressive dunefields which occur in the study area, and were able to separate these into two types based on differences in floristics and geomorphology. Shrubland pockets were dominated by *Myrica cordifolia* and *Stoebe plumosa*, and these patches were more elongate, with their long axis in the direction of the dune crest. Thicket pockets were dominated by broad-leafed species such as *Rhus crenata* and were less elongated and aligned more or less normal to the dune crest. These knolls of vegetation are equivalent to bushclumps described here, and unlike shrubland pockets may be found on narrower dunefields. Bushpocket communities are not unique to the

South African coastline, and Wiedemann (1984) described remnant forest mounds on the Pacific Northwest coast of Washington and Oregon that have a similar structure and location within the dunefields to the bushpockets described in this study. However, they are not common elsewhere and do not seem to occur anywhere along the Gulf Coast of Mexico (Johnson 1977; 1982; Moreno-Casasola & Espejel 1986; Barbour *et al.* 1987) or California (Barbour *et al.* 1981).

The presence of the Dune Fynbos community as far east as Bushman's River (Fig. 1.1) lends support to the observation made by Talbot & Bate (1991) that the eastern limit of dune asteraceous fynbos at Port Elizabeth (Cowling *et al.* 1988) needs to be extended to Bushman's River. Communities with a strong Cape affinity and a predominance of fynbos species (*Erica's, Restio's*) have been noted as far east as the Great Fish River (Avierinos 1991), and it is plausible that this large river acts as the eastern boundary of dune fynbos. Although only a few relevés were sampled, it appears that the Dune Fynbos community (Fig. 1.11) is similar to the sub-stable coastal fynbos community described by Taylor (1978) as forming dense clumps dominated by *Restio eliocharis* and *Erica* spp. Cowling (1984) classified this as a *Restio-Agathosma* community on well drained deep sands with a lack of thicket development. Taylor (1978) noted that if the sub-stable fynbos community was protected from fire, it would develop into coastal scrub dominated by *Sideroxylon inerme* and *Pterocelastris tricuspidatus*, due to the coalescing of clumps of the latter species.

The Scrub Fynbos community described in this study (Fig. 1.11) is equivalent to Taylor's (1978) Coastal Scrub and Cowling's (1984) *Restio - Maytenus* community found on well drained soils (Plate 1.7). Similar evergreen sclerophyllous communities are found in coastal areas with a Mediterranean climate, including California, Spain and Italy (Westman 1981). The origin of Cape Fynbos and its phytogeographic relationships with these communities are complex (Taylor 1978) and will not be discussed further as Cowling (1983) has described in detail the vegetation history of South-Eastern Cape Fynbos.

The Dune Scrub community separated by TWINSPAN is probably transitional to Dune Thicket (Fig. 1.11). In the east it is less common and mainly occurs along the margins of Dune Thicket or blow-outs (Lubke & Strong 1988). West of the Kowie River, most of the relevés with woody species were either classified as Bushpockets or Dune Scrub (Plate 1.6) due to the gradation from dune scrub and dune thicket to dune forest from Cape St Francis to Kei Mouth, as noted by Tinley (1985), Lubke (1988) and the CSIR (1989). Daines (1991) mapped the vegetation of barrier dunes from the Tsitsikamma river (west of Cape St Francis) to East London using vegetation units very similar to those described here. She noted that a dune scrub/thicket mosaic was most common from Tsitsikamma to Cape Padrone (near Woody Cape, Fig. 1.1; Plate 1.1), and that the area from here to the Keiskamma River was dominated by dune thicket (Plate 1.2). From the Keiskamma River to East London, most barrier dunes were covered with dune forest. East of this locality, dune forests are even more common, but their distribution cannot be linked to any environmental gradients such as changes in rainfall and latitude, since these are not significance enough over this short distance (Burns 1986). The Dune Scrub community described here is the same as that encountered on dunes of 4 500 yrs before present (BP) at Alexandria (Parker-Nance *et al.* 1991). Dune Thicket vegetation was found to occur seaward of the 120 000 BP fossil dune ridge, which usually fell outside the area sampled in this study, and Dune Forest occurred landward of this ridge and was therefore never sampled. It is most likely that the Dune Thicket community sampled east of East London is of similar age. However, this older community immediately joins the beach along most of the eastern part of the coastline due to the removal of the Pioneer and Dune Scrub communities by wind and tidal erosion (Plate 1.8). Dune Scrub and Pioneer communities are only found together at a few sites (Plate 1.3), and it is only at these sites that a clear succession towards Dune Forest similar to that at Mtunzini, Natal (Chapter 3) has been observed (Burns & Lubke 1986; Plate 1.3).

Dune Thicket has been termed the Zone III Scrub-Thicket community by Tinley (1985), who describes it as "a unistratal community of multiple-stemmed dwarf trees and shrubs with a compact canopy". The Dune Forest community, or the Zone IV Thicket/Forest community (*vide* Tinley 1985) was not sampled in this study. Both these communities comprise part of the Xeric Kaffrarian Thicket described by Everard (1987). Burns (1986) studied the Dune Forests between Kidds Beach and the Great Kei River, and was able to separate them into three groups based on species dominance and the presence of lower order species. The dune valley forest group possessed the most characteristic features with unique dominant species. Landward and seaward groups showed certain compositional similarities but separated on the basis of the lower order taxa. Burns concluded that the seaward group, the one sampled in this study, was the earliest stage in the developmental sequence towards dune valley forest.

DISTRIBUTION AND PHYTOCHOROLOGICAL AFFINITIES

The distribution of diagnostic species in the various communities (Fig. 1.4) shows that in general species are either widespread or distributed towards the east or west. Their distribution can be related to a number of environmental factors, but the most important is probably rainfall which changes from a winter maximum in the west to a spring and autumn maximum in the east (Fig. 1.2). The length of the dry summer period decreases from west to east, due to a shift from winter to summer rainfall. In the intermediate stations rainfall peaks in spring and autumn. Rainfall and drought periods have been shown to be important factors in other coastal areas (for example Johnson 1977; 1982). The complex geology and geomorphology of the study area (Marker 1988) also affects species distribution. Gross changes in coast configuration and availability of sediments govern the width of the active dunefield, which increases from east to west. East of East London the coast is characterised by a single dune cordon with narrow beaches (Tinley 1985). As sand grain size is uniform along this sector of the coast (Marker 1988), it will have no influence on species distribution, unlike the situation on the gulf coasts of Mexico (Johnson 1977). On a broader scale, factors such as moisture and temperature, as well as wind and wave regimes influence the array of growth forms found along coastlines, although the resultant adaptations may not always be according to preconceived notions (Barbour 1992).

Salt laden winds are also important and as a geomorphic agent wind affects plant distribution as it alters dune topography and influences substrate stability. However, winds are generally of similar velocity and direction, and mainly blow parallel to the coast. It is therefore unlikely that wind and sand movement will have a significant affect on regional species distribution along this coastline, despite its importance in other coastal areas (Moreno-Casasola 1986; Moreno-Casasola & Espejel 1986). However, wind and sand does have a significant local affect on zonation and succession, when there is sufficient sand to be transported across the dunes (Avis & Lubke 1985; McLachlan *et al.* 1987).

Foredunes have more species restricted to this habitat than do the other communities, and these pioneer species are therefore more widespread (Fig. 1.6). They are generally confined to seashore habitats and often have a pantropical or cosmopolitan range. Their adaptations to the environmental conditions of coastal dunes means they are not restricted by climatic differences along the coast. Moreno-Casasola (1988) suggests that their presence or absence depends on the arrival of propagules, and micro-environmental gradients play a major role in selecting the propagules, thus determining local floristic composition of the foredunes. This also appears to be the situation along the Eastern Cape coastline, but phytochorological affinities affect plant distribution more significantly, particularly woody species found on the backdunes, but plants of the foredunes and dune slacks are also affected (Fig. 1.6).

The vegetation of the Eastern Cape, as defined by Lubke *et al.* (1986), has an equal number of widespread families as Natal, but there are less widespread families in the Cape Region due to the high level of endemism in this flora (Cowling 1984). A decrease in Cape taxa from west to east has also been noted by Cowling (1983), who attributes this to a breakdown of the edaphic barrier (infertile soils derived from quartzites and sandstones), resulting in an inter-mingling of Cape taxa with elements of adjacent phytochoria. Along the coast it is Tongoland/Pondoland species which dominate the Xeric Kaffrarian Thicket (*vide* Everard 1987) and mingle with Cape species, as the former phytochorion enters the region from the east along the coast (Lubke *et al.* 1986). There is a definite decrease in Tongoland/Pondoland taxa from east to west, and this is probably related to the change in rainfall from a summer to winter one, and an increased occurrence of infertile soils which results in the concomitant increase in Cape taxa.

On a global scale Hesp (1991) showed that endemism peaks in temperate lattitudes, and this is probably related to the fact that beach plants in these regions tend to be more narrowly restricted to a single coast or small latitudinal range (Barbour 1992). As the Eastern Cape represents a tension zone where four phytochoria merge, Gibbs-Russel & Robinson (1981) predicted high levels of endemism. However, this was not recorded due to the convergence of four phytochoria, each with flora's of distinct evolutionary history. Consequently, generalist taxa are common as the area acts as a repository for genetically diverse weedy species. It is for these reasons that a relatively low number of endemics occur along the coastline (Fig. 1.6), and it is likely that this value would be lower if the area was not influenced by the Cape region, despite the fact that South Coast Dune Fynbos has the lowest level of endemism for a Cape community

(Cowling 1983). The above reasons also explain the relatively high amount of widespread taxa found along the Eastern Cape coastline.

SUCCESSION

The hypothesis presented here is that soil moisture variability is critical in determining the pattern of species development in these dunefields. Soil moisture is related to both the water-holding capacity of the sand and its mobility during dry periods. These factors are dependent on the consistency of rainfall and the frequency of strong winds during dry periods, which will alter the microtopography of the dunefield. Low lying areas (slacks) will have higher soil moisture and will be occupied by more mesic species, as noted by Barbour *et al.* (1987) on the US portion of the Gulf of Mexico. The vegetation in dune slacks at Kleinemonde has been correlated with soil moisture (Lubke & Avis 1982a), and depth of the water table is also important in South African (McLachlan *et al.* 1987), Mexican (Moreno-Casasola 1982) and New Zealand dune slacks (Sykes & Wilson 1987). As dune slacks are generally regarded as more mesic habitats (Ranwell 1972) it is difficult to explain why they are grouped on the right hand side of the ordination diagrams (Figs. 1.7 & 1.8). This could be related to an increase in habitat and moisture variability since slacks may have ponds during certain periods of the year (Daines *et al.* 1991; see Plate 4.4, pg 133) or may be buried by sand during dry periods (see Plate 2.2, pg 75). Young (1987) working in the Alexandria dunefields showed that at night groundwater was warmer and water molecules moved up the soil profile and condensed on the soil surface. Soil moisture content in bushpockets and dune scrub communities was similar to foredunes, but less variable with depth, whereas soil moisture in slacks is more variable and increases with depth (Young 1987; Lubke & Avis 1982a; Chapter 2). Within the Dune Thicket soil moisture is higher and more predictable due to the increase in organic matter, reduction in loss through evaporation, and entrapment of rainwater in compact or slightly cemented horizons (Tinley 1985). Soil of rocky promontories with woody vegetation is similar to that of the Dune Thickets, as organic matter accumulation over long periods of time results in a complex soil (Lubke 1983). In the pioneer community of rocky promontories, Lubke (1983) showed that organic content had accumulated to a lesser extent, and soil properties were more similar to those of the foredunes

Four slack types were separated by TWINSPAN on the basis of their species composition, which appeared to be related to the depth of the water table (Fig. 1.10). Wet slacks had standing water and Dry slacks had a water table at about 1m. Moreno-Casasola (1982) found that on Mexican beaches the water table was always less than 1 metre below the surface, but in dune slacks it was more variable, with depths of more than 1 metre recorded in the dry season. The lack of evidence in the literature to support this hypothesis of the importance of increased moisture variability as a determinant of species composition in dune slacks prompted further studies on these habitats (Chapters 2 & 4).

The ordination diagrams (Figs. 1.7 & 1.8) revealed a definite increase in community complexity, species diversity, size of plants (trees) and physiognomy from right to left, but it is difficult to predict how these groups link together along a successional sequence. Unfortunately, when two gradients have similar lengths, DECORANA gives poor results for both the first and second axes, and TWINSPAN does not perform well after the first division (van Groenewoud 1992). These problems make the interpretation of these data more difficult, but it does suggest that the Bushpocket/Scrub group represents an intermediate stage linking this putative succession towards Dune Thicket. However, it is possible that the Dune Slack community is more important in initialising the process. During unfavourable climatic conditions (low rainfall and resultant increase in sand movement) retrogression of slacks may result in a Pioneer community (Fig. 1.7). However, during favourable conditions Dune Slacks may be colonized by woody species and develop into Bushpocket and Dune Scrub communities. If this were the case then Bushpockets should represent mature dune slacks, and it is possible that the shrubland pockets in the Alexandria dunefield described by Talbot & Bate (1991) are mature dune slacks. The Dune Thicket is the most floristically and physiognomically complex community sampled. Coupled with these floristic changes is an increase in the complexity of the soil. Burns (1986) showed an increase in organic matter and carbon, and corresponding decrease in pH from pioneer communities to forest near East London, and these aspects are considered in more detail in Chapter Four.

This increase in community complexity along a seral sequence starting with the colonization of the foredunes by pioneer species occurs along most of the South African coastline (Tinley 1985). These changes, which occur in response to environmental factors, have been well described elsewhere, with the general trends being very similar (Sauer 1965; Johnson 1977; Scholten *et al.* 1981; Barbour *et al.* 1981; 1987; Moreno-Casasola *et al.* 1982; Moreno-Casasola & Espejel 1986). All show a decrease in the physical severity of habitat conditions (reduced salt spray and sand movement; improvements to soil conditions; protection from wind) and increases in species diversity and life form, aerial cover and abundance of woody perennials. Similar results are presented here, but the successional changes appear to be multidirectional as they occur in response to sand movement, seasonal fluctuations and secondary disturbances. It is only in the more subtropical areas of Natal, where the coastline is prograding, that a clearer successional sequence can be observed (Weisser *et al.* 1982). More detailed studies were therefore undertaken at Kleinemonde (Chapters 2 & 4) and at Mtunzini in Natal (Chapter 3) to provide further information on the successional sequences noted in this study.

CONCLUSIONS

The Pioneer communities along this stretch of coastline are more complex than reported elsewhere (Johnson 1977), due to the greater influences exerted by the Cape and Tongoland/Pondoland phytochoria, with the variable environmental factors being less important. The Dune Slacks are more diverse and luxuriant communities due to more favourable soil moisture conditions, and a decrease in salt spray and sand movement. The separation of these dune slacks into four groups appeared to be related to the depth of the water table and soil moisture variability. Bushpocket communities are floristically similar to the Dune Scrub community, but occur as isolated patches of vegetation in wide dunefields. Bushclumps differ in that they are associated with aeolionite outcrops and dominated by broad-leafed species, and are not restricted to wide dunefields. Dune Scrub is only found west of the Kowie River as rainfall decreases, usually adjacent to Dune Thicket or along the margins of blowouts. It forms a mosaic with Dune Fynbos in the vicinity of the Sunday's River, but further west of the Gamtoos River it is replaced by the Scrub Fynbos community. Dune Thicket is found towards the east in the higher rainfall area, where Dune Forests occur further inland.

The largest number of species were widespread, but many were also distributed to the west or the east, in response to the change in rainfall. Of secondary importance were geological changes and gross changes to the configuration of the coastline. Species distribution was strongly influenced by the phytochorological affinities of the taxa, with a decrease in Cape taxa from west to east, and a decrease in Tongoland/Pondoland species from east to west. Due to the influence of these major phytochoria diluting the genetic pool, endemism is low.

The ordination of the data revealed a distributional trend of an increasing woody component from west to east, which is related to increasing rainfall and an increase in the number of Tongoland/Pondoland species. However, the data also revealed an increase in community complexity, species diversity and physiognomy from Dune Slack to Dune Thicket, with the former community playing an important role in this suggested successional sequence. These successional changes appear to be multidirectional due to the highly variable climatic and environmental factors experienced along this coast, and more detailed studies on the successional sequence noted here was therefore undertaken (Chapters 2 to 4).

APPENDIX 1.1: Annotated checklist of species recorded along the coast from Kei Mouth to Cape St Francis. Key: C - Rocky cliffs; T - Thickets; B/S - Bushpockets/Scrub; Bp - Bushpockets; S - Slacks; P - Pioneers. * Indicates alien species.

	C	T	B/S	Bp	S	P
ALGAE						
Characeae						
Chara sp.					S	
PTERIDOPHYTA						
EQUISETACEAE						
50 *Equisetum* sp.						P
ANGIOSPERMAE						
MONOCOTYLEDONS						
TYPHACEAE						
49 *Typha capensis* (Rohrb.) WE Br.					S	
RUPPIACEAE						
59 *Ruppia maritima* L.					S	
JUNCAGINACEAE						
66 *Triglochin striata* Ruiz & Pav					S	
T. balbosa L.					S	
POACEAE						
K37 *Imperata cylindrica* (L.) Raeuschel				Bp		
K38 *Miscanthus capensis* (Nees) Anderss. var. capensis					S	
K108 *Stenotaphrum secundatum* (Walt.) Kuntze	C	T	B/S	Bp	S	P
K116 *Panicum deustum* Thunb.		T				
K160 *Ehrharta villosa* Schult. f.			B/S	Bp		P
K205 *Pentaschistis heptamera* (Nees) Stapf		T	B/S	Bp		P
K214 *Phragmites australis* (Cav.) Steud.					S	
K244 *Polypogon strictus* Nees					S	
K256 *Ammophila arenaria** (L.) Link						P
K261 *Stipagrostis zeyheri* (Nees) de Wint. subsp. *zehyeri*				Bp		P
K283 *Sporobolus virginicus* (L.) Kunth	C	T		Bp	S	P
K300 *Cynodon dactylon* (L.) Pers.		T			S	
K301 *Chloris virgata* Swartz.					S	
K332 *Dactyloctenium australe* Steud.		T				P
K434 *Agropyron distichum** (Thunb.) Beauv.						
CYPERACEAE						
452 *Lipocarpha* sp.					S	
459 *Mariscus capensis* (Steud.) Schrad					S	P
M. congestus (Vahl) C.B.Cl.	C	T		Bp	S	P
M. dregeanus Kunth.		T				P
459b *Juncellus laevigatus* (L) C.B.	C				S	
465 *Ficinia lateralis* (Vahl) Kunth	C	T	B/S	Bp	S	P
F. ramosissima Kunth					S	
467 *Fuirena hirsuta* (Berg.) P.L. Forbes					S	
468 *Scirpus nodosus* Rottb.		T	B/S		S	P
468b *Isolepis cernua* (Vahl) Roem. & Schutt					S	
477 *Schoenus nigricans* L.	C					
494 *Tetraria cuspidata* (Rottb.) C:B.Cl.				Bp		

RESTIONACEAE						
804 *Restio* sp			B/S			
Restio eleocharis Nees ex Mast.			B/S	Bp		
805 *Chondropetalum microcarpum* (Kunth)	C					
JUNCACEAE						
936 *Juncus* sp.					S	
J. acutus L.					S	
J. dregeanus Kunth					S	
J. kraussii Hochst.	C				S	
LILIACEAE						
2533 *Trachyandra ciliata* (L.f.) Kunth			B/S			
963 *Gloriosa virescens* Lindl.		T				P
2532 *Velthemia bracteata* Harv. ex Bak.		T	B/S			
1113 *Myrsiphyllum asparagoides* (L.) Willd						P
Protasparagus densiflorus (Kunth) Oberm.	C	T		Bp		
Protasparagus racemosus (Willd.) Oberm.		T				
AMARYLLIDACEAE						
1167 *Haemanthus albiflos* Jacq.	T					
IRIDACEAE						
1306 *Chasmanthe aethiopica* (L.) N.E.Br.		T	B/S	Bp		P
1311 *Gladiolus gueinzii* Kunze	C	T	B/S	Bp		P
STRELITZIACEAE						
1319 *Strelitzia nicolai* Regel & Koern.		T				
MYRICACEAE						
1874 *Myrica cordifolia* L.			B/S	Bp	S	P
VISCACEAE						
2093 *Viscum capense* L.f		T				
V. obscurum Thunb.				Bp		
SANTALACEAE						
2104 *Rhoiacarpos capensis* (Harv.) DC		T	B/S	Bp		
2104a *Colpoon compressum* Berg.		T	B/S	Bp		
2117 *Thesidium microcarpum* DC.			B/S			
2118 *Thesium flexuosum* A.DC.			B/S	Bp		
POLYGONACEAE						
2195 *Rumex crispus* L.					S	
CHENOPODIACEAE						
2226 *Exomis microphylla* (Thunb.) Aell. var. *axyroides* (Fenzl) Aell.		T				
2238 *Chenolea diffusa* Thunb.	C					
2255 *Sarcocornia* sp.	C					P
S. pillansii Moss A.J. Scott	C				S	
2269 *Salsola aphylla* L.F.						P
AIZOACEAE						
2389 *Pharnaceum thunbergii* Adamson		T				
2399 *Galenia secunda* (L.f.) Sond.		T				
2401 *Aizoon rigidum* L.f.	C					
2403 *Tetragonia decumbens* Mill.	C	T	B/S	Bp		P

MESEMBRYANTHEMACEAE						
2405 *Carpobrotus edulis* (L.) L.Bol.	C	T	B/S	Bp		
2405 *Delosperma ecklonis* (Salm-Dyck) Swant.	C					
D. littorale (Kensit) L. Bol.	C					
2405 *Disphyma crassifolium* (L.) L. Bol.	C					
2405 *Drosanthemum ambiguum* L.Bol.	C					
2405 *Mesembryanthemum* sp.	C					
2405 *M. aitonis* Jacq.					P	
CARYOPHYLLACEAE						
2450 *Spergularia media* (L.) Presl						
2490 *Silene primuliflora* Eckl. & Zeyh.	C	T		Bp	S	P
RANUNCULACEAE						
2541 *Knowltonia capensis* (L.) Huth.						
2542 *Clematis brachiata* Thunb.		T				
BRASSICACEAE						
2875 *Heliophila subulata* Burch. ex.DC.			B/S	Bp		
2883 *Lepidium africanum* (Burm.F.) DC.						
2946 *Diplotaxis* Sp.						P
CAPPARACEAE						
3101 *Capparis sepiaria* L. var. *citrifolia* (Lam.) Toelk.		T				
3112 *Maerua cafra* (DC.) Pax		T				
CRASSULACEAE						
3164 *Cotyledon* Sp		T				
3166 *Kalanchoe rotundifolia* (Haw.) Haw.		T				
3168 *Crassula expansa* Dryand. subsp. *filicaulis* (Haw.) Toelk.		T				
C. nudicaulis L.	C	T	B/S	Bp		
FABACEAE						
3446 *Acacia cyclops** A.cunn. ex.G.Don	C	T	B/S	Bp	S	P
3673 *Argyrolobium* sp. Eckl & Zeyh.		T				
3702 *Indigofera incana* Thunb.	C	T				
3703 *Psoralea repens* L.			B/S	Bp	S	P
3754 *Sutherlandia frutescens* R.Br.						P
3897 *Rhynchosia carabaea* (Jacq.) DC.		T				P
GERANIACEAE						
3924 *Geranium* sp.					S	
313271 *Pelargonium capitatum* (L.) L'Herit		T	B/S			
OXALIDACEAE						
3936 *Oxalis* sp.						P
ZYGOPHYLLACEAE						
3991 *Zygophyllum morgsana* L.		T				
RUTACEAE						
4037 *Agathosma apiculata* G.F.W. Mey.			B/S	Bp		
POLYGALACEAE						
4278 *Muraltia squarrosa* (L.f.) DC.			B/S	Bp		
4279 *Nylandtia spinosa* (L.) Dumort						P

EUPHORBIACEAE						
4370 *Adenocline acuta* (Thunb.) Baill.		T				
4498 *Euphorbia serpens* (H.B.K.)	C					
ANACARDIACEAE						
4594 *Rhus crenata* Thunb.		T	B/S	Bp	S	P
R. glauca Thunb.			B/S	Bp		
R. gueinzii Sond.			B/S	Bp		
R. laevigata L.				Bp		
CELASTRACEAE						
4626 *Maytenus heterophylla* (Eckl.& Zeyh.)N.K.B.Robson						P
M. procumbens (L.f.) Loes	C	T	B/S	Bp		
4628 *Putterlickia pyracantha* (L.) Szyszy.		T				
4630 *Pterocelastrus tricuspidatus* (Lam.) Sond.			B/S	Bp		
4641 *Cassine aethiopica* Thunb.		T		Bp		
4641 *C. maritimum* L. Bol.		T				
C. tetragona (L.f.) Loes.		T				
SAPINDACEAE						
4734 *Allophylus natalensis* (Sond) De Winter		T				
RHAMNACEAE						
7874 *Scutia myrtina* (Burm.f.) Kurz		T		Bp		
4886 *Phylica litoralis* D. Dietr.			B/S	Bp		
VITACEAE						
4917 *Rhoicissus digitata* (L.F.) Gilg & Brandt	C	T	B/S	Bp		P
FLACOURTIACEAE						
5328 *Dovyalis rotundifolia* (Thunb.)		T				
CACTACEAE						
5417 *Opuntia ficus-indica** (L.) Hill.		T				
THYMELAEACEAE						
5461 *Passerina rigida* Wikstr.	C	T	B/S	Bp	S	P
MYRTACEAE						
5578 *Eugenia capensis* (Eckl & Zeyh) Horv. ex Sond.	C	T	B/	Bp		P
ONAGRACEAE						
5804 *Oenothera parodiana* Munz.						P
ARALIACEAE						
5872 *Cussonia thyrsiflora* Thunb.		T		Bp		
APIACEAE						
6004 *Apium graveolens* L.					S	
6069 *Heteroptilis suffruticosa* (Berg.) Leute	C	T	B/S	Bp		P
MYRSINACEAE						
6314 *Rapanea gilliana* (Sond.) Mez.			B/S	Bp		
ERICACEAE						
6237 *Erica chloroloma* Lindl.				Bp		
E. glumiflora Klotzsch ex. Benth			B/S	Bp		

PRIMULACEAE						
6328 *Samolus porosus* (L.f.) Thunb.	C					
S. valerandi L.	C					
PLUMBAGINACEAE						
6351 *Limonium scabrum* (Thunb.) Kuntze var. *scabrum*	C		B/S	Bp		
SAPOTACEAE						
6368 *Sideroxylon inerme* L.	C	T	B/S	Bp		
6386 *Mimusops caffra* E.Mey ex. A.DC.		T	B/S			
EBENACEAE						
6404 *Euclea natalensis* A. DC		T	B/S	Bp		
E. racemosa Murray		T	B/S	Bp		
E. undulata Thunb.		T		Bp		
GENTIANACEAE						
6503 *Chironia baccifera* L.		T	B/S	Bp		
C. decumbens Levyns.	C				S	
APOCYNACEAE						
6558 *Acokanthera oblongifolia* (Hochst.) Codd		T				
6559 *Carissa bispinosa*		T				
ASCLEPIADACEAE						
6791 *Asclepias physocarpa* (E. Mey) Schltr.		T		Bp	S	
1793 *Astephanus marginatus* Decne		T				
6834 *Cynanchum natalitium* Schltr.	C	T	B/S	Bp	S	P
C. obtusifolium L.f.		T	B/S	Bp		P
6860 *Secamone alpinii* Schultes		T		Bp		
CONVOLVULACEAE						
6968 *Cuscuta* sp.	C					
6972 *Falkia repens* L.f.	C					
7003 *Ipomoea ficifolia* Lindl.		T				
I. pes-caprae (L.) R.Br.		T			S	P
LAMIACEAE						
7290 *Salvia africana-lutea* L.				Bp		
SOLANACEAE						
7379 *Lycium* Sp.	C					
7402 *Solanum americanum* Mill.			B/S	Bp		
SCROPHULARIACEAE						
3393 *Sutera microphylla* (L.f.) Hiern			B/S			
7522 *Polycarena cuneifolia* (Benth.) Levyns		T	B/S		S	P
7523 *Zalusianskya maritima* (L.f.) Walp.	C	T	B/S	Bp	S	P
7629 *Hyobanche* sp. (L.)			B/S			P
SELAGINACEAE						
7566 *Hebenstretia cordata* L.						P
PLANTAGINACEAE						
8116 *Plantago carnosa* Lam.	C	T	B/S			

RUBIACEAE						
8383 *Pavetta natalensis* Eckl.		T	B/S			
8438 *Anthospermum littoreum* L. Bol.	C	T	B/S		S	P
8467 *Hydrophylax carnosa* Sond.						P
8489 *Rubia petiolaris* DC.		T	B/S	Bp		
CUCURBITACEAE						
8568 *Kedrostis nana* (Lam.) Cogn. var. *nana*		T		Bp		
LOBELIACEAE						
8694 *Lobelia anceps* L.f.					S	
GOODENIACEAE						
8716 *Scaevola plumieri* (L.) Vahl		T		Bp		P
ASTERACEAE						
8919 *Felicia aethiopica* (Burm.f) H.Bol & Woolley-Dod ex Adamson & Salter			B/S	Bp		
F. echinata (Thunb.) Nees		T	B/S	Bp		P
F. erigeroides DC.						P
8926 *Conzya* sp.				Bp	S	
C. scabrida DC.						P
C. pinnatifida (Thunb.) Less					S	
8936 *Brachylaena discolor* DC.		T		Bp	S	P
8937 *Tarchonanthus camphoratus* L.		T		Bp		
8992 *Vellereophyton vellereum* (R.A.Dyer) Hilliard					S	
9006 *Helichrysum* sp.			B/S			
H. anomalum Less.		T		Bp		P
H. argenteum Thunb.		T	B/S	Bp		P
H. asperum (Thunb.) Hilliard & Burtt.			B/S			P
H. cymosum (L.) D.Don		T	B/S	Bp	S	P
H. praecinctum Klatt.	C	T		Bp	S	P
H. sordescens DC	C					
H. teretifolium (L.) D.Don	C	T	B/S	Bp		P
9037 *Stoebe plumosa* (L.) Thunb.		T	B/S	Bp	S	P
9043 *Metalasia muricata* (L.) D.Don	C	T	B/S	Bp	S	P
9148 *Xanthium spinosum* L.						P
9351 *Cotula lineariloba* (DC.) Hilliard					S	
9356 *Schistostephium crataegifolium* (DC.) fenzl ex Harv.	C					
9411 *Senecio elegans* L.		T	B/S	Bp	S	P
S. inaequidens DC.		T	B/S	Bp		P
S. litorosus Fourc	C	T	B/S	Bp	S	P
S. lanceus Ait.			B/S		S	
9420 *Othonna carnosa* Less.		T	B/S	Bp		
9427 *Osteospermum fruticosum* (L.) T. Norl.	C					
9427 *Chrysanthemoides monilifera* (L.) T. Norl.	C	T	B/S	Bp	S	
9431 *Ursinia anthemoides* (L.) Poir.			B/S	Bp		P
9432 *Arctotheca populifolia* (Berg.) Norl.		T	B/S	Bp	S	P
9434 *Gazania rigens (L.) Gaertn. var.* uniflora (L.f.) Roessl.	C	T	B/S	Bp	S	P
9438 *Berkheya* sp					S	P
9593 *Launaea sarmentosa* (Wild.) Sch. Bip ex Kuntze		T		Bp		P
9595 *Sonchus dregeanus* DC.					S	

CHAPTER TWO

SUCCESSION ON THE COASTAL DUNES AND DUNE SLACKS AT KLEINEMONDE.

I : CONCEPTUAL MODEL

INTRODUCTION

The previous study (Chapter 1) showed that many of the extensive dune systems along the Eastern Cape coast are not colonized by vegetation apart from dune scrub species that occur well above the high-water level. At Kleinemonde there is a portion of the dunefield that is sheltered from the harsh coastal environment and the succession of plants on the dunes and dune slacks is more apparent. The vegetation of the area was described by Lubke (1983), who noted a greater variety of species in the dune slacks than on the mobile foredunes.

Following initial descriptions of the coastal communities, more detailed studies were undertaken on the dune slack vegetation to investigate how environmental factors affect the distribution of plants, particularly *Scirpus nodosus*, within the slack. It was noted that sand movement is not as marked in the slacks as in surrounding dune regions (Lubke & Avis 1982a) as the sand is removed to a level at which it is immobilized by groundwater (Willis *et al.* 1959). Only during severe storms is sand deposited in the dune slacks. Other factors investigated, such as available soil moisture, soil salinity and pH, and intensity of sea spray, were also found to play a role in confining the distribution of dune slack species to these sites. In particular, salt spray appeared to be an important growth-limiting factor for *Scirpus nodosus* seedlings (Lubke & Avis 1982b).

Initial observations made on the succession of plants in the dune slack indicated that *Scirpus nodosus* was the primary colonizer of moist slacks (Lubke & Avis 1982a). Seedlings of these plants were transplanted at various localities in the dunefield, and it was found that sand movement caused early death of the seedlings (Avis & Lubke 1985) thus showing that they are restricted to the slacks where little sand movement occurs.

The dune profile surveyed in 1980 (Lubke 1983) and the dune slack that was mapped in 1981 (Avis 1981) were permanently marked, and surveys repeated annually in order to monitor vegetational changes. The aim of this chapter is to present the results of these surveys, synthesize existing knowledge on the vegetation of the dune system, and explain what vegetational and environmental changes took place. A conceptual model of succession in the dunes and dune slacks that applies to this whole coastline is presented.

STUDY AREA

The dune system studied occurs at Kleinemonde, about 12 km east of Port Alfred (lat. 33°33'S; long. 27°08'E). The dune slack was formed within the transverse dunes, which are concave to the direction of the prevailing west and southwest winds. The slack is partially protected from winds by fairly large dunes to the east and west and a large dune on the southern or seaward side. It is a wet slack (Ranwell 1972) and has a greater diversity of species and abundance of plants than do most of the drier dune slacks along this section of the coast (Lubke 1983). The dune transect passed immediately to the west of the dune slack that was studied in detail. This transect line was selected as it was most representative of foredune, dune slack, and rear dune vegetation of the region, based on the broader survey undertaken (Chapter 1).

METHODS

CLIMATIC DATA

Climatic data are recorded at the Great Fish Point Lighthouse weather station, 2 km east of the study site and at an altitude of 73 m. Rainfall and maximum and minimum temperatures were taken from published records for the period January 1979 to December 1984 (Weather Bureau 1984). Wind speed and direction were taken from records at the lighthouse for April - July 1983 from a previous study (Avis & Lubke 1985) as the nearest published records are for East London (Schultz 1985).

SALT SPRAY

The distribution of wind-borne salt along the dune profile was measured with salt traps consisting of 20 cm^2 pieces of cheesecloth stretched onto light wooden frames by means of thumbtacks (Oosting & Billings 1942; Lubke & Avis 1982a). Three traps were set up facing the prevailing winds at sites 1, 2, 4 and 5 (Fig. 2.5) at noon on 12 September 1981 when a strong southwesterly wind was blowing (Lubke & Avis 1982a). Salt traps were set up at sites 1 and 3-8 at noon on 1 September 1983 when a strong easterly wind was blowing. In each case, after 24 hours the cheesecloth was removed and 1 cm^2 cut out and soaked in 200 ml deionized water for 10 minutes and the amount of chloride present was measured using an EIL chloride electrode and a Labotec Specific Ion Meter (Model 17) calibrated using standard reagents supplied by Labotec. The wind speed and direction was measured at each site when the traps were set up and when removed.

SOIL FACTORS

Soil samples were taken from the surface 5 cm at the center of quadrats 1 - 20 in the dune slack (Fig. 2.6); pH, conductivity, and moisture content were measured for each sample following the method of Lubke (1983). Using a soil auger, the depth from the soil surface to the water table was measured in each quadrat to a maximum of 1 m. In the moist center of the sample site (quadrats 11, 12 & 20) water samples were taken and pH and conductivity of the water were measured.

VEGETATION SAMPLING AND ANALYSIS

In July 1980 a 1 m^2 belt transect was sampled from the high-water mark to the edge of the Dune Thicket (Lubke 1983). This transect was positioned to pass through the most vegetated region of the dunefield. Plant height, percentage aerial cover (assessed visually), and number of rooted shoots of each species were recorded. An Abney level was used to measure the slope along the transect line. The transect was resampled in January 1985 along the same position, although the slack vegetation was no longer well represented in this area. The same parameters were recorded, and these data were used to construct the two profile diagrams (Figs. 2.4 & 2.5).

The dune slack vegetation was initially triangular in shape. Three reference points, A, B, and C (Fig. 2.6) were permanently marked with rock cairns in September 1981. A string grid was placed over the sample area and the vegetation plotted to scale on a map. Identical quadrat positions could be relocated each time the area was resurveyed.

Twenty 1 m^2 quadrats were located at the bottom left of each large quadrat (Fig. 2.6) where quantitative vegetational data and soil samples could be taken. Quadrat 9, 13, 16, 18 and 19 lay at the edge of the sample area and were not sampled for vegetation. The number of individuals of each species was recorded in each quadrat. Initially the *Scirpus nodosus* population consisted of many plants of different sizes; plants were therefore enumerated in three height classes: <5cm, 5-30cm, and mature plants >30cm. The initial dune slack survey was made in spring - September 1981, but successive studies were made in summer - February 1983, January 1984, and February 1985. The results were recorded as community maps showing the distribution of all the species in the community.

Using the quadrat count data, the mean density (plants m^{-2}) and percentage frequency were calculated for each species. The total density of plants in all the quadrats was obtained by summation and the relative density of each species determined by expressing total density of each species as a percentage of this total. Thus a quantitative comparison of abundance of all species in the dune slack could be illustrated in the form of pie charts for each sample date (Fig. 2.8).

A comparison of species diversity in the dune slack was made at each time of sampling by calculating a diversity index. This is a more reliable measure of diversity than species richness, as the diversity index takes into account the abundance or numbers of individuals in the sample (Brower & Zar 1984). Simpson's index of diversity (Ds) and dominance (ℓ) were used to show changes in diversity and dominance respectively (Simpson 1949). As a comparison, the Shannon index (H') to base 10 was also calculated (Shannon 1948).

RESULTS

CLIMATIC DATA

Mean monthly temperatures and total monthly rainfalls for the period July 1979 to December 1984, and for the total period of available records were plotted in the form of Walter & Leith (1967) climatic diagrams (Fig. 2.1). The dates of vegetation sampling are also recorded on this figure. Table 2.1 summarizes the mean annual temperature and the total rainfall. As with most summer rainfall areas of South Africa, there is evidence of a drier cycle in the 1980s as was predicted by the Tyson & Dyer (1975) model. During this period there is a predominance of arid conditions. Even within the dry cycle, wetter years are evident, as seen in 1981 when warm, moist periods and wet periods are more frequent. There is a great variation in rainfall, with almost any month being either excessively drier or wetter than the mean. Temperatures are not extreme, fluctuating around a mean of 18°C, but local temperature conditions, dependent on aspect and exposure, are more critical in the dune environment. Rapid changes have also been recorded due to berg wind conditions (Lubke 1983). These climatic factors appear to be particularly important in the initial stages of dune slack succession, as pioneer species invade when conditions are most favourable for germination and growth of seedlings.

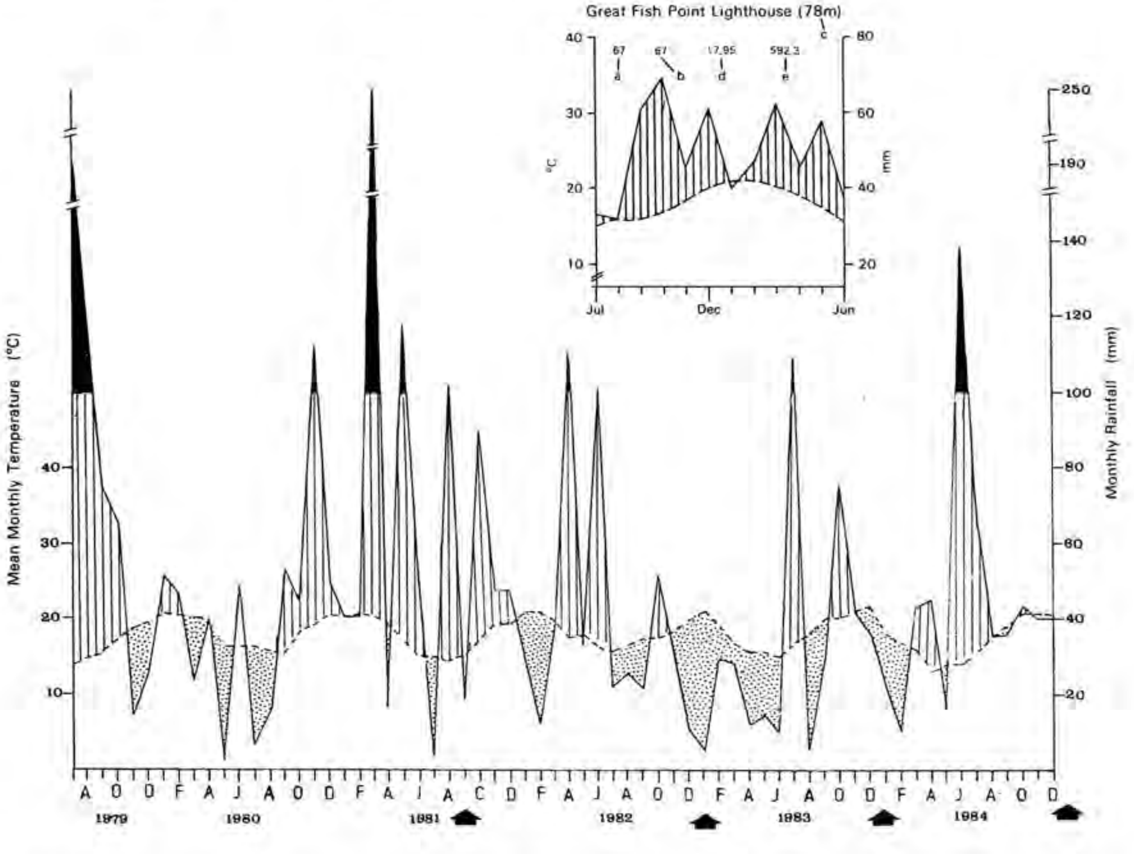


Figure 2.1 Climate diagram for the Great Fish Point Lighthouse weather station for the period 1979-1984. The inset summarizes the mean values for the total period of records. a-number of years of temperature records; b-number of years of precipitation records; c-altitude; d-mean annual temperature; e-mean annual precipitation; - rainfall; — temperature. Vertical lines indicate humid periods, stippling indicates arid periods, and shaded areas indicate a precipitation greater than 100mm. Arrows show the date of vegetation sampling.

Table 2.1 Mean annual temperature and total annual rainfall for the years 1979-1984 and for the total 67 year period of records at Great Fish Point Lighthouse

	1979	1980	1981	1982	1983	1984	67-Year Period
Mean annual temperature (^{0}C)	17.8	18.2	17.9	18.0	18.4	18.2	17.95
Total annual rainfall (mm)	748.8	495.5	903.6	493.6	399.6	523.2	592.3

Wind direction along this section of the coast is predominantly from the southwest and west during the winter months and from the northeast and southwest in the summer months (Fig. 2.2b). Severe winds may be recorded during storm periods from either the westerly or easterly direction as was evident during the period when *Scirpus nodosus* seedlings were transplanted on the dunes (Fig. 2.2a; Avis & Lubke 1985). The movement of sand from west to east during a few days of storm conditions in July 1983 was considerable, as seen in the photographs of the line transect (Plate 2.2). The net result of the extremely windy conditions on this section of the coast is the movement of sand mainly towards the east in the winter months and a reversal of direction in the summer months, when easterly winds are more frequent. The advance of a western dune into the slack at a rate of approximately 3 m yr^{-1} over a three-year period was recorded. McLachlan *et al.* (1987) also noted an easterly or northeasterly movement of dunes into dune slacks at a rate of 7 myr^{-1} in the Alexandria dunefields.

SALT SPRAY

The amount of salt spray recorded at each site was calculated as Cl$^-$ concentration (Lubke & Avis 1982a; Avis & Lubke 1985) but is shown here as the percentage of the total Cl$^-$ intercepted at each site (Table 2.2). Depending on the wind speed, different amounts of salt will be trapped; thus the distribution of salt spray along the line transect is a more useful comparative measure. On both occasions the greatest percentage of wind-borne salt is intercepted on the foredunes (sites 1 & 2, Fig. 2.5). Sites 3 - 7, which are in the slack or protected by the dunes, intercept less salt spray. The vegetation also intercepts some of the wind-borne salt, as McAtee & Drawe (1981) observed on the dunes along the Gulf coast of Texas. However, with an easterly wind, the slack at site 4 is not well protected and a higher percentage of the total salt spray was intercepted here when the second readings were made in September 1983. Wind speed is usually a good indicator of the proportion of salt that will be intercepted; but in September 1983, when the readings were taken, the wind had dropped considerably from about 13 m sec^{-1} on 1 September to about 4 m sec^{-1} on 2 September, and it had also changed direction to the south (Avis & Lubke 1985). Consequently, a high reading at site 4 indicated that during most of the period that the traps were in situ the wind was gusting from the east. At site 8, more than 200 m from the sea, a large amount of salt was intercepted, as wind is deflected upwards by the foredunes and salt is thus deposited at the next obstacle, the rear dune, as was also observed by Oosting & Billings (1942). Any winds exceeding 7 m sec^{-1} have a sufficient velocity to carry salt spray inland (Boyce 1954); thus significant quantities of salt spray can be carried inland on this section of the coast, since wind speeds often exceed this velocity (Fig. 2.2).

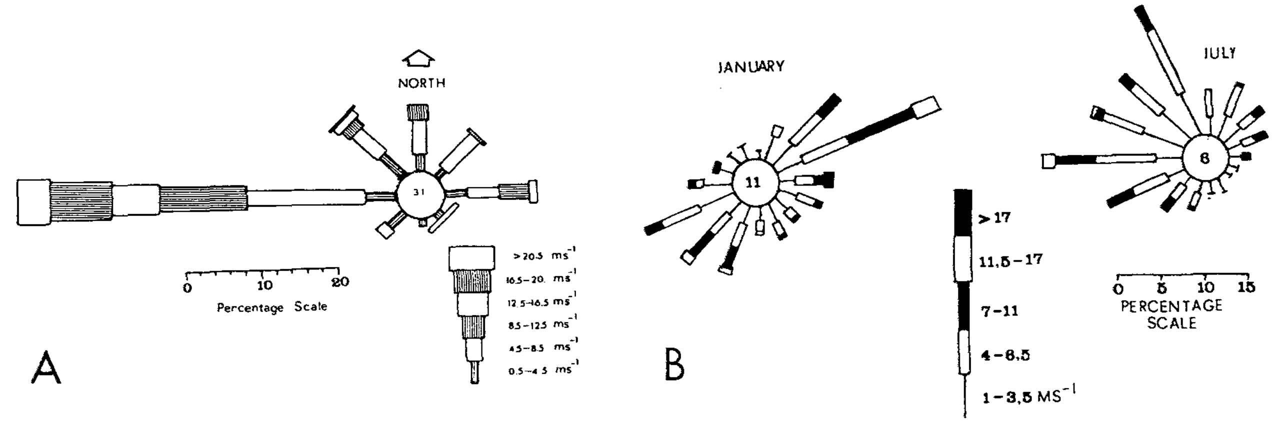


Figure 2.2 A. Wind roses for Great Fish Point Lighthouse for the period April to July 1983. Data from actual records. B. Wind roses for East London. Data from Schultz (1980).

Wind-borne salt, when deposited on the leaves is detrimental to the growth of *Scirpus nodosus* (Lubke & Avis 1982b). Salt may also accumulate in the sand, thus retarding root growth or affecting the general metabolism of the plant when absorbed. Preliminary studies by Allam (1984) were made on the effect of salt spray on other species in this area. Donnelly & Pammenter (1983) reported that salt spray was not an important factor controlling vegetation distribution in the Natal dunes. It is likely that many of the dune slack species are confined to this region because of salt spray, and this would explain the greater diversity and abundance of plants in the slack as compared with the dunes.

Table 2.2 Wind speed and amount of chloride intercepted at various sites along the transect. The location of the sites is shown in Fig. 2.5.

		1981		1983	
Locality	Site Number	% of Total Cl^- Intercepted	Wind Speed at 12 M. on Sept 13, 1981 (m $sec.^{-1}$)	% of Total Cl^- Intercepted	Wind Speed at 3:00 PM on Sept. 2, 1983 (m $sec.^{-1}$)
Foredune	1	71.60	2.87	43.40	3.6
	2	24.30	2.23		
Dune Slacks	3	3.90	1.60	3.95	0.4
	4	0.17	0.92	23.50	0.4
	5			1.37	0.0
	6			3.67	0.0
	7			0.08	0.4
Rear dune	8			24.0	0.6

SOIL FACTORS

In an earlier study on *Scirpus nodosus* (Lubke & Avis 1982a), the distribution of the plants was related to soil factors. Data were collected at grid points and along the margins of the study area, and isolines of pH, percentage moisture, and conductivity were plotted on a map (Fig. 2.3).

There was a significant negative correlation between pH and conductivity (r = -0.739, P < 0.001) and pH and moisture (r = -0.865, P < 0.001) and a positive association between moisture and conductivity (r = 0.607, P < 0.01). The isolines all followed the same trend, with different regions of the slack demarcated by these lines. A moist central region with a low pH and high conductivity was detected. Moving outwards through inner to outer and marginal regions of the slack, there was a decrease in moisture content and conductivity and an increase in pH (Table 2.3).

Figure 2.3 Map of the dune slack showing the distribution of *Scirpus nodosus* plants relative to the following isolines: -A. Soil pH. -B. Percentage soil moisture. -C. Soil conductivity.

The most significant soil factor in the dune slack is soil water content. Germination of *Scirpus nodosus* seeds is probably triggered by the amount of moisture available in the soil and subsequent growth and development is dependent on the available water supply. The lower lying regions within the dune slack will accumulate greater amounts of rainwater, and during the period prior to the first sample date of September 1981, adequate rainfall resulted in a soil moisture buildup. At this time the water table was also found to be much closer to the surface (Lubke & Avis 1982a).

Table 2.3 Soil and water factors (mean ± standard error) measured in the dune slack over a four-year period.

		Region of the Slack and Corresponding Quadrat Numbers			
	Year	Central 7, 11, 15 & 20	Inner 6, 8, 12 & 13	Outer 2, 3, 10, 14, 16 & 18	Marginal 1, 4, 5, 9, 17 & 19
Soil Factors					
Percentage moisture	1981	20.69 ± 0.79	17.05 ± 1.49	5.06 ± 2.05	3.59 ± 1.87
	1983	3.90 ± 1.56	2.55 ± 0.66	3.20 ± 1.38	2.36 ± 0.69
	1984	2.02 ± 0.28	1.82 ± 0.21	1.99 ± 0.20	1.31 ± 0.22
	1985	3.38 ± 2.04	0.83 ± 0.38	1.33 ± 0.21	1.33 ± 0.33
pH	1981	8.21 ± 0.01	8.50 ± 0.091	8.82 ± 0.035	8.94 ± 0.014
	1983	8.84 ± 0.18	9.11 ± 0.093	9.23 ± 0.045	9.13 ± 0.087
	1984	8.67 ± 0.02	8.65 ± 0.018	8.65 ± 0.053	8.62 ± 0.044
	1985	9.44 ± 0.17	9.28 ± 0.060	9.30 ± 0.041	9.34 ± 0.031
Conductivity (µS/cm)	1981	312.0 ± 52.5	213.2 ± 21.7	193.5 ± 19.1	165.8 ± 16.1
	1983	370.0 ± 6.6	289.0 ± 84.6	227.3 ± 29.7	276.7 ± 22.5
	1984	234.7 ± 117.4	216.2 ± 15.6	257.7 ± 45.9	246.2 ± 41.0
	1985	178.0 ± 4.42	210.5 ± 23.5	208.8 ± 26.7	170.2 ± 5.9
Water Factors					
Minimum and maximum depth of water table (cm)	1981	11 to 25	19 to 25	39 to 71	45 to 70
	1983	51 to >100	54 to >100	>100	>100
	1984	51 to 95	48 to >100	>100	>100
	1985	66 to >100	84 to >100	>100	>100
pH	1981	7.70 ± 0.13			
	1983	7.33 ± 0.28			
	1984	7.44 ± 0.29			
	1985	*			
Conductivity (µS/cm)	1981	798.3 ± 81.9			
	1983	2950.0 ± 949.9			
	1984	867.0 ± 133.0			
	1985	*			

* Water was too deep to obtain a satisfactory sample.

It was concluded (Lubke & Avis 1982a) that the higher conductivity recorded in the center of the slack was due to salts being leached from the surrounding sands and accumulating in the lower lying regions. It is unlikely that the slight increase in salinity, as reflected by the conductivity (Fig. 2.3), had any bearing on the establishment of seedlings of *Scirpus nodosus*. Likewise the pH isolines reflect a relationship between water content and pH and have no bearing on the growth of plants in the different regions of the slack.

Subsequent measurements of soil factors showed no marked relationship with the distribution of vegetation, with no significant correlation between factors. The isolines that were plotted (Avis 1983) did not show the same trends observed in 1981 (Fig. 2.3). Rather than illustrating this graphically, the sampled quadrats have been divided into four regions based on the isolines in Figure 2.3 and mean values of pH, percentage soil moisture, and conductivity calculated for successive years (Table 2.3). In the initial study, when the rainfall and soil moisture was high, a noticeable difference between the soil factors of the different regions existed. The very low soil moisture values measured in subsequent years are very similar to those measured on the dunes (Lubke 1983). The highest values were always recorded in the center of the slack, but the water table was much deeper after 1981 (Table 2.3).

The pH values are appreciably higher in years subsequent to 1981, and only in 1983 was there any apparent trend of an increasing pH from the center of the slack towards the outside. A similar result was observed with respect to conductivity. Whereas in 1981 there was a notable decrease in conductivity away from the center of the slack, this same trend was only noticeable in 1983. In the subsequent years no appreciable differences were detectable. Van Tooren *et al.* (1983) recorded extremely high conductivity values (>10 000 µS/cm) on a beach plain in the Netherlands under dry conditions, but in this case the area was occasionally flooded by seawater. A slight increase in conductivity along the seaward side of the slack (up to 500 µS/cm) was noted in the dry period of 1984, when there was a possible accumulation of salts in the sand from salt spray. During a low rainfall cycle one may anticipate a buildup of saline conditions in the dune slack, since there is insufficient rain to flush the salts from the slack system, but this was not observed. In 1983 there was an unexplainable increase in soil water conductivity to almost 3 000 µS/cm, but this appeared to be temporary. The soil water pH remained constant during this period (Table 2.3).

DISTRIBUTION OF PLANTS IN THE DUNEFIELD

The distribution of plants across the dunefield is best illustrated in the profile diagram of 1981 (Fig. 2.4). Changes that occurred on the foredunes were recorded in February 1985 (Fig. 2.5) and include an increase in the pioneer creeper *Ipomoea pes-caprae* and other indigenous pioneers, as well as the alien shrub *Acacia cyclops*. This resulted in an increase in species diversity, which is discussed later. The unvegetated foredunes often change in shape and character, but since the pioneer species play an important role in stabilizing sand (Plate 2.1), the topography in this region has changed very little over the period of the study. The role of *Ammophila arenaria* (Marram grass) in foredune stabilization in Europe and North America (Ranwell 1972; Weidemann 1984) and of other species in Australia (Hesp 1984) is performed by *Scaevola plumieri*, *Sporobolus virginicus*, and *Arctotheca populifolia* along this coastline. As noted in Chapter One, these pioneer species are not ubiquitous along the whole coastline due to the variable Eastern Cape climate. Young seedlings of these plants have been observed in unvegetated regions of the dunefield following periods of high rainfall, usually exceeding 100 mm in a month (Fig. 2.1), but unless favourable conditions continue they do not become established. Arid conditions prevail for long periods; mobile foredunes, as seen in the background of Plate 2.1, are thus more common. Vegetative spread of pioneer plants by rhizomes (*Sporobolus virginicus*), stems that can tolerate burying (*Scaevola plumieri*), or stolons (*S. virginicus* & *Ipomoea pes-caprae*) are the most important means of dispersal of these plants during drier periods, such as in the 1980s.

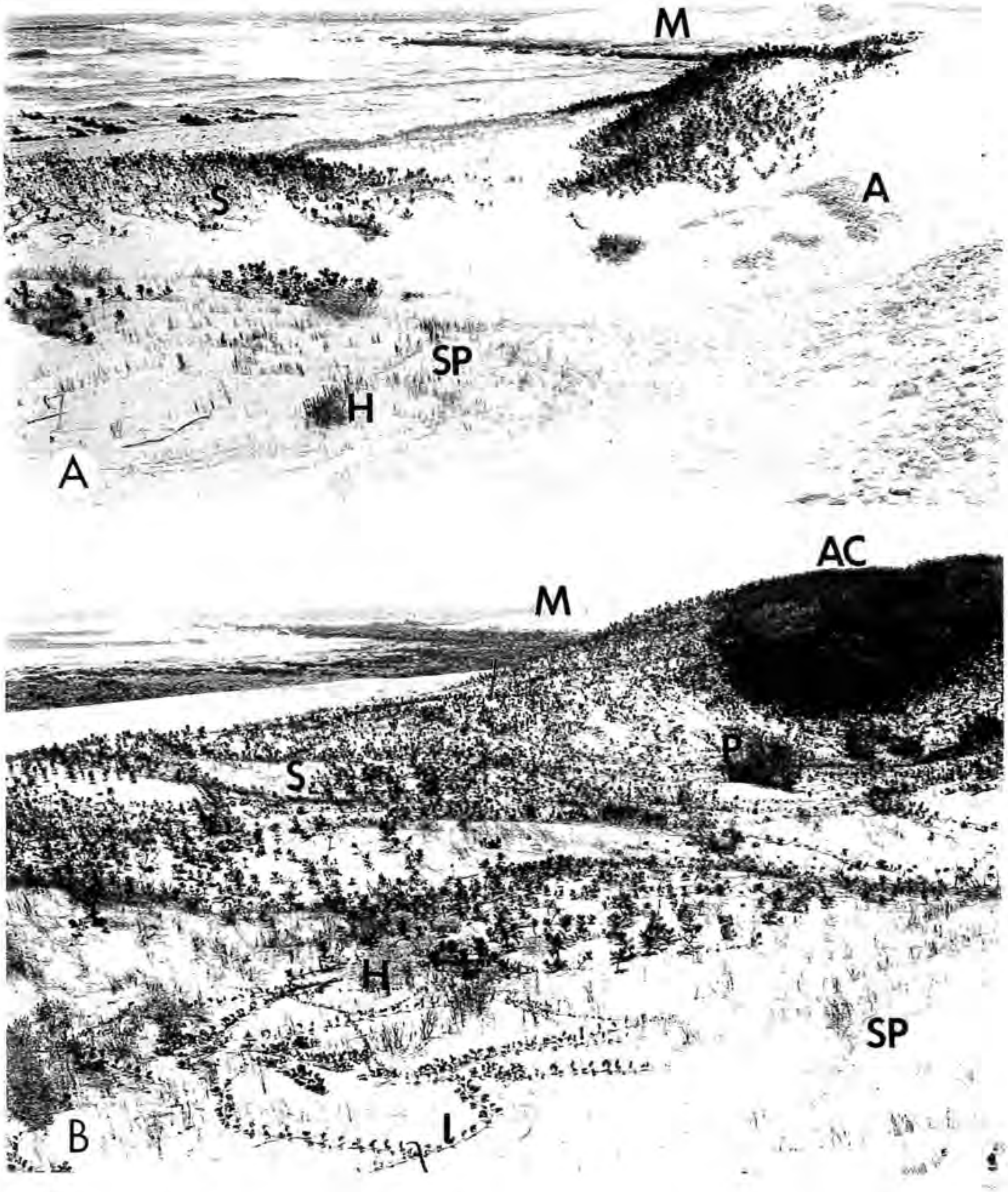


Plate 2.1 Colonization of the foredunes in 1980 (A) and 1985 (B) by *Scaevola plumieri* (S), *Arctotheca populifolia* (A), *Sporobolus virginicus* (SP), *Hebenstretia cordata* (H), *Ipomoea pes-caprae* (I), *Acacia cyclops* (AC), and *Passerina rigida* (P). Mobile dune in the background (M).

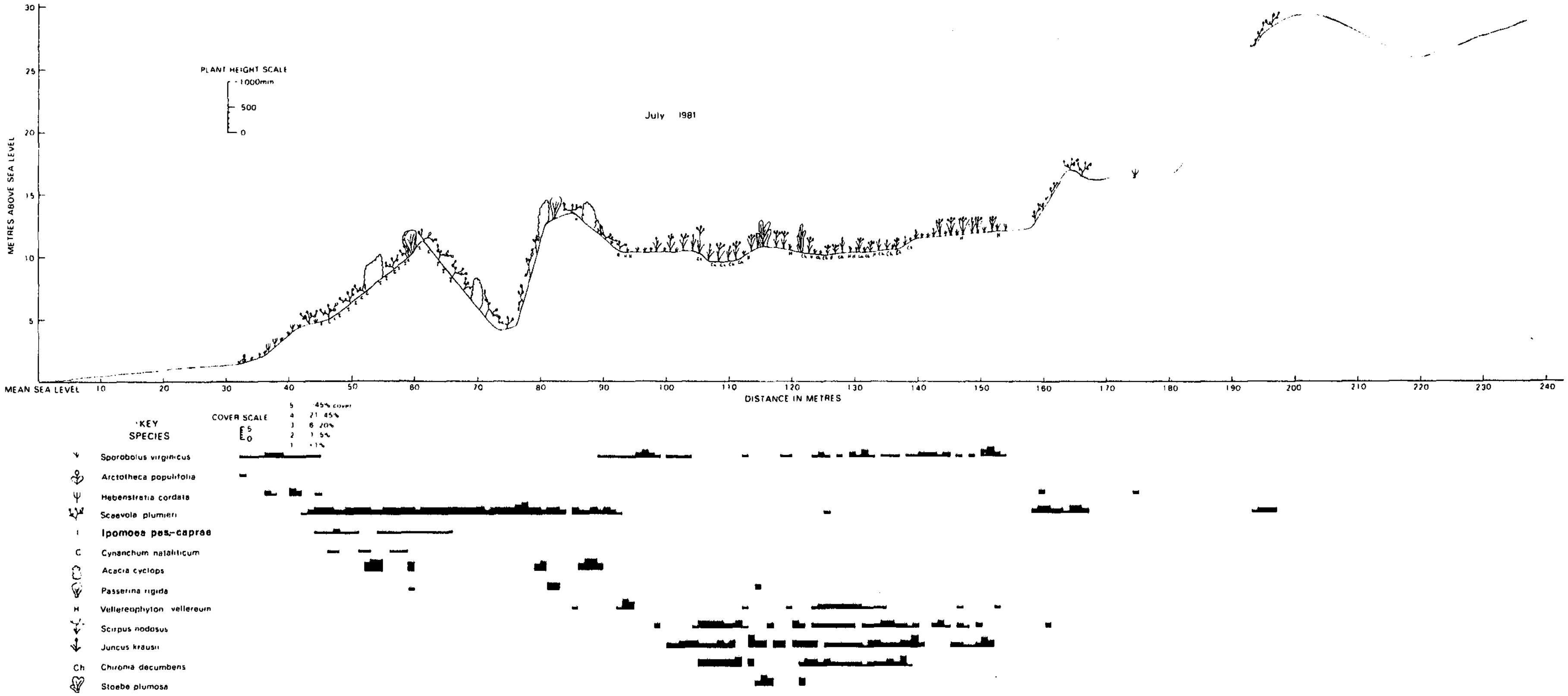


Figure 2.4 Profile diagram of the vegetation of the dunefield at Kleinemonde in July 1981. Species abundance is indicated in the lower part of the diagram as aerial cover in each 1m² quadrat along the transect.

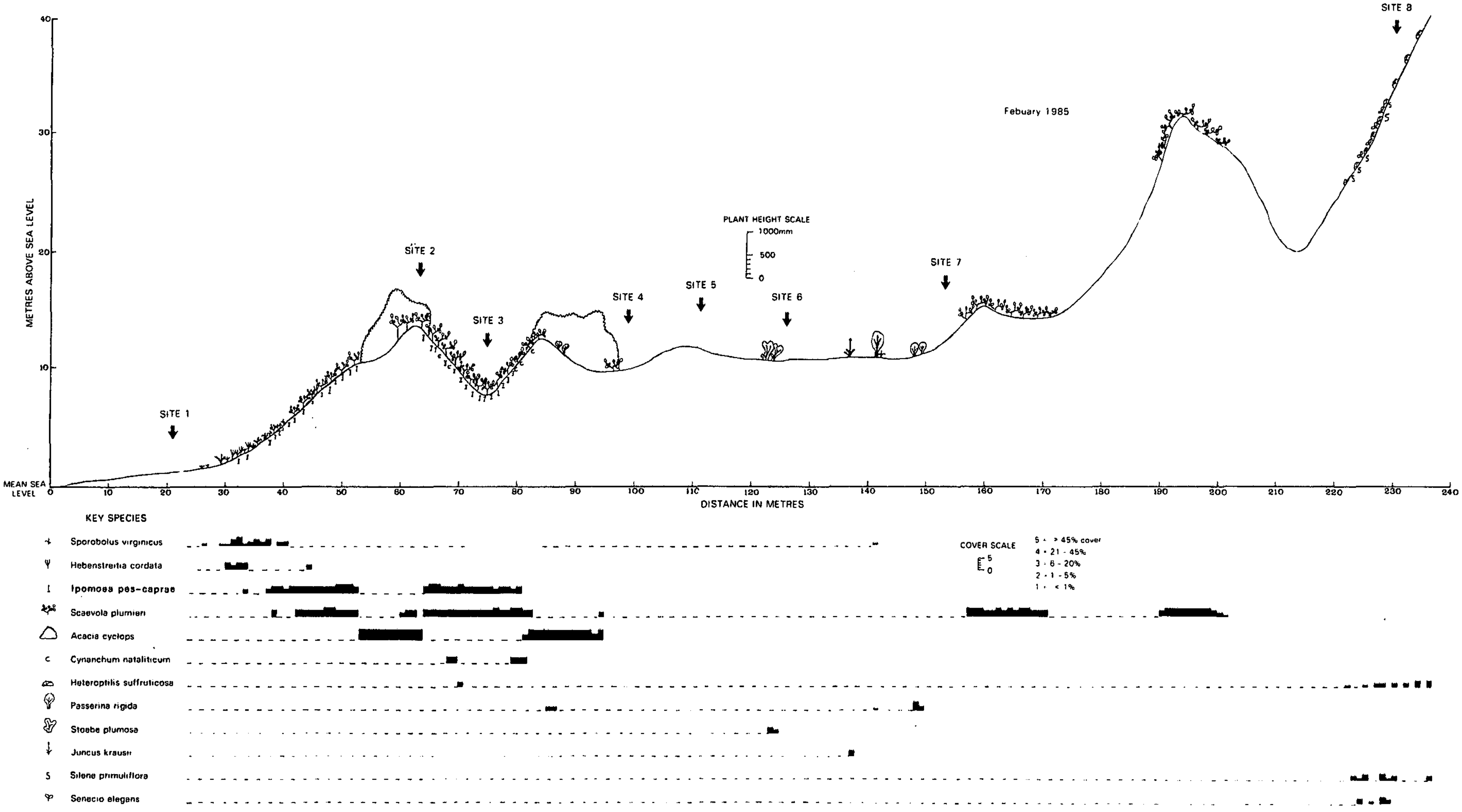


Figure 2.5 Profile diagram of the vegetation of the dunefield at Kleinemonde in February 1985. Species abundance is indicated in the lower part of the diagram as aerial cover in each 1m^2 quadrat along the transect. Sites 1-8 indicate the position of salt traps.

Following the moist periods in 1980, the dune slack community was very well developed and supported a wide diversity of species (Lubke 1983). The extensive area of vegetation at this time is apparent when comparing the photographs of the line transect (Plate 2.2a-d). The movement of wind-borne sand to the east buried much of this vegetation, resulting in the study slack becoming the center of greatest species diversity (Plate 2.2d).

Scaevola plumieri plants occasionally become established on the rear dunes (Figs. 2.4 & 2.5; Plate 2.2) if there is a continuous supply of sand. These plants, like *Ammophila arenaria* (Ranwell 1972), require mobile sands and are able to tolerate salt spray. A greater supply of salt accumulates in this area than in the dune slacks (Table 2.2).

There are more herbaceous species close to the coastal scrub in the second profile (Fig. 2.5). These species, for example, *Silene primuliflora* and *Heteroptilis suffructicosa*, are commonly found growing along the protected margins of the climax dune scrub community along this coastline (Chapter 1).

SUCCESSION WITHIN THE DUNE SLACK

The community maps (Fig. 2.6) and photographs (Plate 2.3) show the changes in abundance and distribution of species in the dune slack over a four-year period. It was fortuitous that this study, which was initiated to show the establishment of *Scirpus nodosus* in the moist slack, has proved useful in a study of succession. The percentage frequency and mean density of the dune slack species from September 1981 to February 1985 are presented in Table 2.4. The 25 species have been grouped into four categories on the basis of their role in succession. Two of these are common pioneers of dunes and dune slacks; nine are herbaceous annuals or perennials, either pioneers or secondary colonizers of dune slacks; seven are sand dune colonizers, which are rare, absent, or only present on the margins of wet slacks; and six are woody dune scrub species usually only found in dune slacks that are at an advanced stage of succession. *Acacia cyclops* is placed in this category, but it is an extremely aggressive exotic invader that is even found on stable fordunes (Plate 2.1b).

Following the moist periods in spring 1979 (Fig. 2.1), water accumulated in the triangle-shaped depression, and wind-borne seeds of *Scirpus nodosus* recruited from the neighbouring slack germinated. By September 1981 these were recorded as large plants (>30 cm) in the moist centre of the study site. Additional recruitment of seedlings occurred following the rainy period of November 1980 (plants recorded as 5-30 cm tall in 1981, Fig. 2.6). Finally, the greatest number of *S. nodosus* seedlings that were recorded in September 1981 were less than 5 cm tall, having germinated in the autumn and spring periods of 1981. The greatest germination probably occurred in April and May, as many seedlings were observed in July (Lubke & Avis 1982b). In September up to 240 plants per m^{-2} were recorded giving a mean density of over 100 plants per m^{-2} for the whole slack. Naturally, all of these plants could not survive, but because of its favourable start, this sedge remained as one of the dominant species during the years of this study.

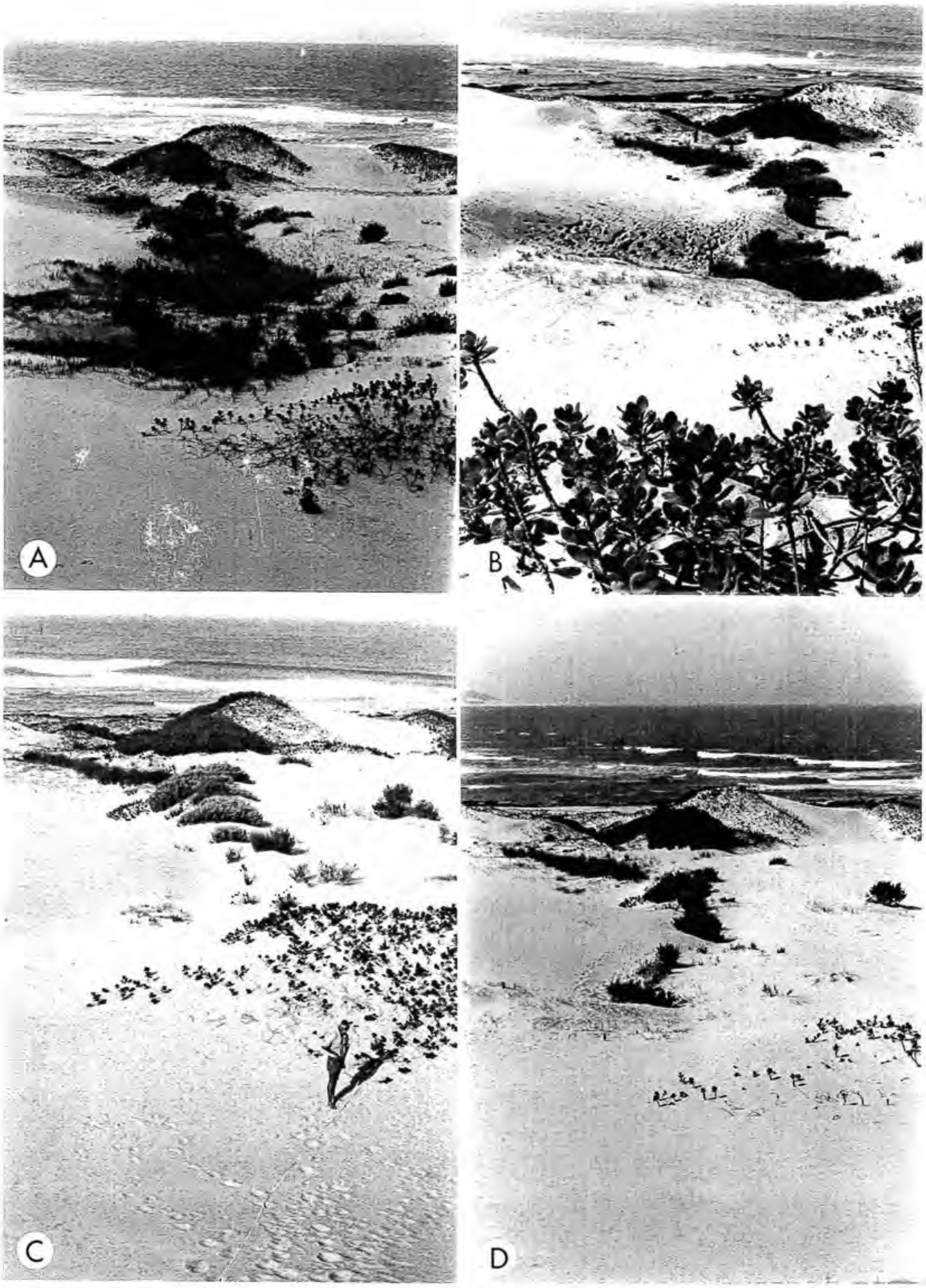


Plate 2.2 The study area and southeasterly direction of the line transect viewed from the rear dune about 200 m from the highwater mark. - A. July 1981. - B. April 1983. - C. August 1983. - D. February 1985. Note how the dune slack vegetation on the right has diminished in size. B and C illustrate the large quantity of sand that was deposited in the slack region from the July 1983 storms.

There was a very rapid invasion of the dune slack by other species once the pioneers had become established. *Chironia decumbens* and *Vellereophyton vellereum*, which are common in slacks of the Eastern Cape (Chapter 1), were recorded in the moister areas in September 1981 (Table 2.4; Fig. 2.6). The other species present at this period occurred infrequently except for *Sporobolus virginicus*, which may have invaded the wet slack prior to or at the same times as *S. nodosus*. Although common in all slacks and dunes, it favours drier open habitats, and its frequency and density decreased in the colonized slacks until January 1984, when it was very localized in extent (Fig. 2.6). By February 1985 it had increased again as fresh sand was deposited in the slack, and the spread of this grass along the northern margin of the slack where *Hebenstretia cordata* also occurred was noted and mapped. *Arctotheca populifolia* clumps increased up until 1983 but then died out as the secondary colonizers of the dune slack became more abundant. *Sporobolus virginicus* and *Arctotheca populifolia*, although commonly occurring in dune slacks, do not appear to create the right microenvironmental conditions suitable for the invasion of other slack species, as they are often the only species found in the drier slacks of this region (Lubke 1983; Chapter 1). Moreover, *A. populifolia*, being a true sand dune pioneer, will not co-exist with other species unless a continuous supply of drift sand is available.

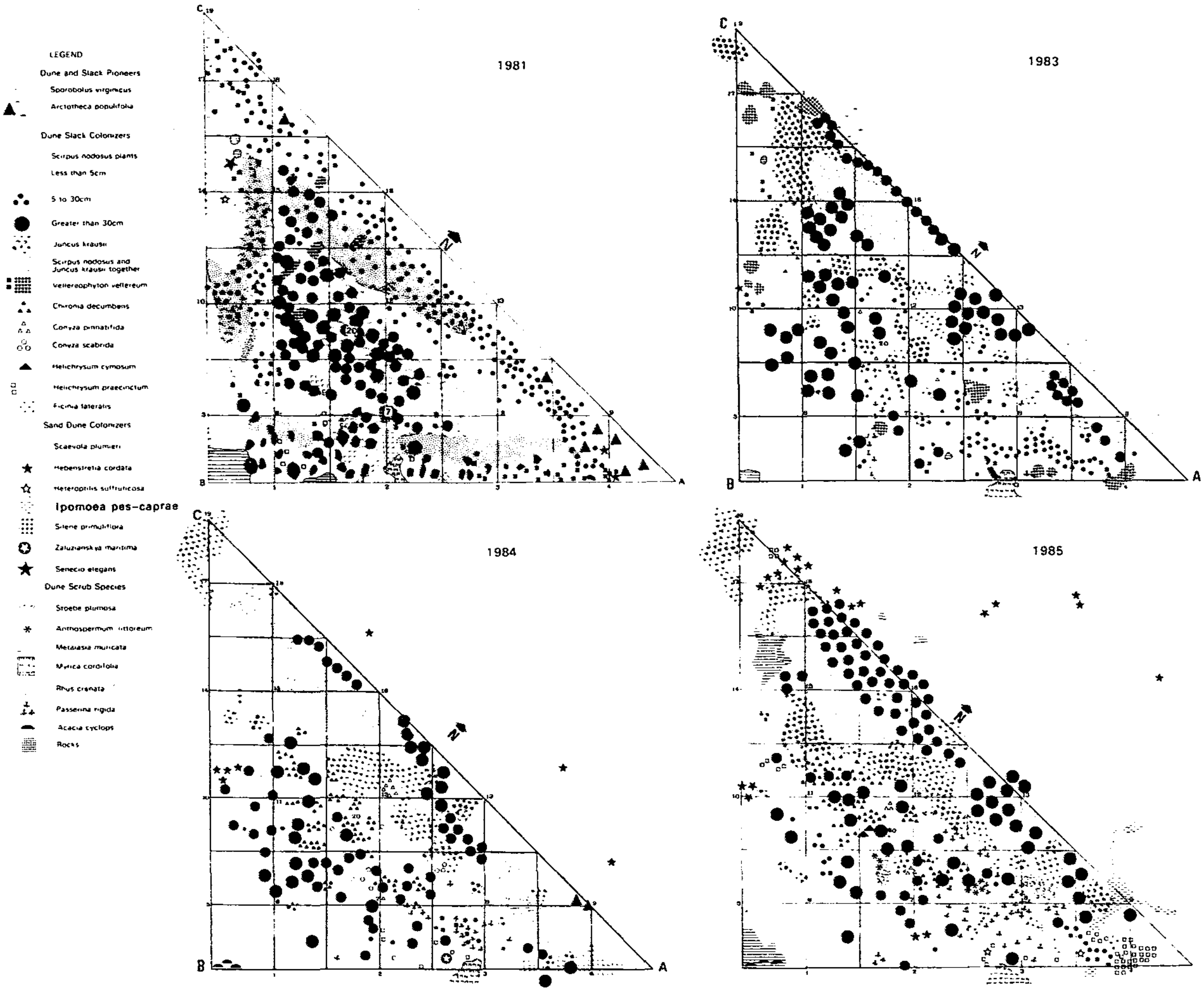


Figure 2.6 Map of the vegetation of the dune slack in September 1981, February 1983, January 1984 and February 1985

Juncus kraussii invaded rapidly from seedlings that germinated in 1982 and 1983, and large plants were recorded in February 1983. By 1984 and 1985 they had outcompeted *Scirpus nodosus* for water and light but were more common along the northern ridge of the dune slack, where dry sand was deposited by easterly winds (Plate 2.3d). *S. nodosus* and *J. kraussii* occupy similar habitats (Chapter 1), yet the latter appears to grow better in the drier slacks. Small *S. nodosus* seedlings (<5 cm) were buried by sand at the western side of the study area due to sand movement by strong westerly winds (Fig. 2.2) and were not present in 1984 (Fig. 2.6). This supports earlier observations that sand movement is important in preventing the establishment of seedlings in the dune environment (Avis & Lubke 1985).

There has been no marked recruitment of wet dune slack species by seed germination since 1981, due to the lower rainfall during the period of the study (Fig. 2.1). *Chironia decumbens* grows vegetatively from decumbent stolons and maintained its presence although the slack had become a dry slack. The Eastern Cape endemic dune slack everlasting *Vellereophyton vellereum* does not grow in dry slacks and was absent after 1983, while the dune everlasting *Helichrysum praecinctum* persisted in the dry slack. These composites are annuals, like *Conyza* spp. mentioned below, and possibly have varying germination requirements, *V. vellereum* only germinating under moist habitat conditions. Of the other dune slack colonizers, *Conyza* spp. are weeds of dry areas, *Ficinia lateralis* is common in dry slacks, pebble plains, and blow-out areas, while *Helichrysum cymosum* is a widespread mesophyte found in many coastal and inland herbaceous communities (Chapter 1).

When examining the density of the species as a whole (Table 2.4), it is notable that in 1981 *Scirpus nodosus*, even excluding the smallest seedlings, had an initial density greater than that of all other species combined (11.7 compared with 10.1 plants m^{-2}). The density of *S. nodosus* plants declined rapidly to 1.6 plants m^{-2} in 1985, while the density of the "other" species increased largely due to the increase in numbers of *Juncus kraussii*. The peak density of the "other" species was 11.5 plants m^{-2} in 1983; then as the slack dried out, some species died (for example *Vellereophyton vellereum*) or were ousted as shady stable conditions were unsuitable (for example *Arctotheca populifolia*), resulting in a decrease in density.

This dune slack is similar in species composition and abundance to the slack of the Alexandria dunefields studied by McLachlan *et al.* (1987), except for the absence of *Gazania rigens* var. *uniflora* and *Psoralea repens*, which are important slack colonizers in that region. The latter is not found at Kleinemonde and was not recorded further east than Boknes (Chapter 1). Being a Cape species (Bond & Goldblatt 1984), it is at the northeasterly limit of its range.

Table 2.4 Percentage frequency and mean density of dune slack species in successive years.

		Percentage Frequency				Density (plants m^{-2}) Mean ± Standard Error			
	Species	September 1981	February 1983	January 1984	February 1985	September 1981	February 1983	January 1984	February 1985
Foredune and slack pioneers	1. *Sporobolus virginicus*	40.0	42.8	26.7	46.7	4.9 ± 1.8	3.0 ± 1.3	1.53 ± 0.96	2.73 ± 1.06
	2. *Arctotheca populifolia*	6.7 *	14.3	0	-	0.06*	1.22 ± 0.93	0	-
	3. *Scirpus nodosus* <5cm	60	0	-	-	104.1 ± 37.7	0	-	-
	5-30cm	40	14.3	0	-	9.6 ± 6.9	0.5 ± 0.37	0	-
	>30cm	33.3	42.8	53.3	60.0	2.1 ± 1.3	1.79 ± 0.63	2.20 ± 0.81	1.6 ± 0.47
	4. *Juncus kraussii*	0	42.8	60.0	53.3	0	2.86 ± 1.32	2.47 ± 0.93	2.33 ± 0.82
	5. *Vellereophyton vellereum*	26.7	35.7	-	-	1.6 ± 1.1	2.14 ± 1.14	-	-
Dune slack colonizers	6. *Chironia decumbens*	13.3	14.3	33.3	33.3	3.06 ± 2.5	1.64 ± 1.43	2.73 ± 1.39	2.33 ± 0.60
	7. *Conyza pinnatifida*	-	0	13.3	6.7*	-	0	2.27 ± 2.13	0.87 ± 0.59
	10. *Helichrysum praecinctum*	33.3	14.3	26.7	20.0	0.8 ± 0.4	2.28 ± 1.51	0.60 ± 0.29	1.40 ± 0.01
	11. *Ficinia lateralis*	-	-	-	6.7*	-	-	-	0.13 ± 0.13
Sand dune colonizers	12. *Scaevola plumieri*	0	0	0	6.7*	0.4*	0	0	0.07 ± 0.07
	13. *Hebenstretia cordata*	6.7*	6.7*	0	13.3	0.6*	0.07*	0	0.67 ± 0.17
	14. *Heteroptilis suffruticosa*	0	0	13.3	0	0	0	0.13 ± 0.09	0
Dune scrub species	22. *Myrica cordifolia*	6.7*	0	6.7*	0	0.4*	0	0.07*	0
	24. *Passerina rigida*	-	21.4	13.3	13.3	-	0.29 ± 0.16	0.27 ± 0.21	0.27 ±0.21

* Occurred in only one quadrat; 0, present but not recorded in quadrats; -, absent from the dune slack.

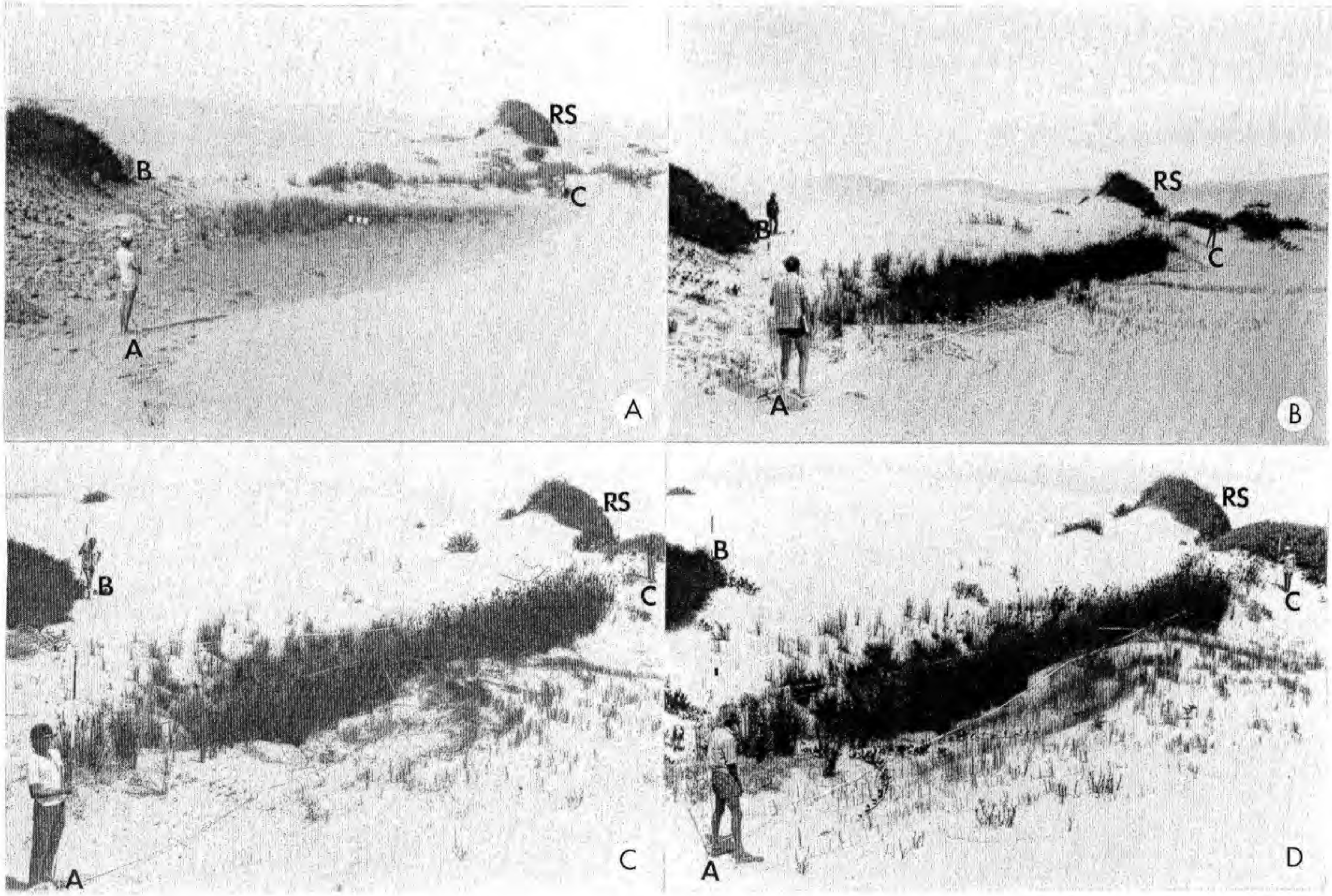


Plate 2.3 Vegetation of the dune slack. - A. September 1981. - B. February 1983. -C. January 1984. -D. February 1985. A, B and C indicate the margins of the slack. RS + Relic patch of coastal scrub.

The migration of an abundance of dune scrub woody plants into the dune slack heralded a third stage in the succession. Initially only *Myrica cordifolia* was present as it invaded vegetatively from the rocky dry southern margin of the study site. As a more diverse community of herbs became established, so more woody dune scrub species germinated from seed carried in by wind or birds. By February 1985, six species were flourishing mainly in the southern region. The exotic *Acacia cyclops* had also invaded from the dunes at point B (Fig. 2.6). Of the scrub species, *Passerina rigida, Metalasia muricata* and *Stoebe plumosa* are most important, being codominants in the scrub stage of sand dune succession. *P. rigida* is the most widespread dominant of this stage in the succession and is the only one of these three scrub species found on the Natal and Zululand coastal dunes (Moll 1968, 1969; Ward 1980; Chapter 3).

There is no easy explanation as to why and when the invasion of shrubs into the slack dominated by sedges, rushes, and small herbs should occur. Seeds are carried to remote slacks by wind in most cases except for seeds of *Rhus crenata* and *Acacia cyclops*, which are bird dispersed. *Rhus crenata* is a common shrub dominant in bushpockets and along the dune thicket margin (Chapter 1; Talbot & Bate 1991) and *Myrica cordifolia*, which is possibly dispersed by small mammals, is dominant in bushpockets within the dunefields (McLachlan *et al.* 1982) or blowout areas in the dune thicket (Chapter 1). For scrub seeds to germinate and become established in the slack, the microclimatic factors (namely light, humidity, temperature, and moisture regimes) prevailing within the dense herbaceous community must be suitable. A rapid increase in numbers and diversity of shrubs during the course of 1984 occurred, although regular counts were not made. More detailed autecological studies of these plants are required to explain the factors governing their establishment in dune slacks. The absence of high rainfall during this period indicates that the moisture conditions of the slack were not adverse to shrub seed germination and seedling establishment.

Present indications (Fig. 2.6; Plate 2.3; Table 2.4) are that under the right environmental conditions of higher rainfall and lower winds, the shrub species may replace herbaceous species in the region of the initial study site and that the pioneers will move to the north and east. Intermittant observations since 1985 have revealed that this has in fact occurred. Thus there appears to be an overall northeasterly migration of the slack vegetation as existing plants are buried by sand movement across from the west, an observation that was also made by McLachlan *et al.* (1987) in the Alexandria dune slacks.

CHANGES IN DIVERSITY AND DOMINANCE

Diversity and dominance indices were calculated for the foredunes using the cover index of each species in each linear meter along the first 90 m of the transects (Figs. 2.4 & 2.5) as the measure of abundance. There was a slight change in dominance (Table 2.5) over the five-year period, as other species apart from *Scaevola plumieri* and *Sporobolus virginicus* became more frequent on the foredunes in 1985. These foredunes are typical of the slightly older Incipient Foredunes described earlier (Chapter 1). Species such as *Gazania rigens* var. *uniflora, Tetragonia decumbens* (which were not recorded here) or *Arctotheca* *populifolia* are common locally in many areas along this coastline (see Fig. 1.4, pg 34). There was also a change in diversity from 1980 to 1985, as indicated by both diversity indices (Table 2.5). The increase in diversity is noticeable on the profile diagrams (Figs. 2.4 & 2.5). Younger adjacent foredunes are colonized more exclusively by *Scaevola plumieri*, and it would appear that this species was the original dominant pioneer of the dunes and that the other species are invading in the process of succession. *Passerina rigida*, a notable dominant of the dune scrub stage (Moll 1969; Chapters 1 & 3), is also present on the foredune (Plate 2.1b).

Table 2.5 Diversity and dominance of species in the foredunes in 1980 and 1985. (Foredunes are defined as the first 90 m of the transect).

INDEX	1980	1985
Simpson's Diversity - Ds	0.642	0.766
Shannon Diversity - H'	0.604	0.700
Simpson's Dominance - ℓ	0.358	0.234

The diversity and dominance indices for the dune slack site were calcuated using the density data of all species in the measured quadrats. These results are plotted in Figure 2.7. There was an initial rapid increase in diversity as new species invaded the slack, with little observable differences in the values obtained for the two indices. Dotted lines were extrapolated back to 1979 (Fig. 2.7), when it is assumed that *Scirpus nodosus* was the sole colonizer of the slack and, hence, diversity would have been zero. After 1983 the diversity increased more slowly as other species invaded the slack. After reaching a maximum diversity one would expect a drop in diversity in the climax dune thicket community as one or more trees become dominant (Margalef 1968). There was a corresponding decline in dominance starting from the point when *Scirpus nodosus* was the only species, but the dominance index will probably increase with time as a climax dune scrub community is attained.

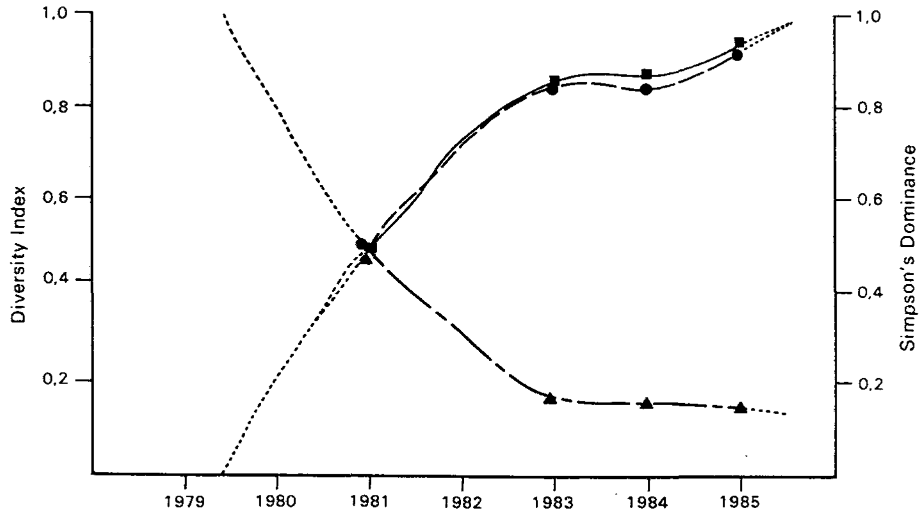


Figure 2.7 Changes in diversity and dominance of the species in the dune slack over a six-year period. ■ - ■ Shannon index (H'), ● --- ● Simpson's index (Ds), and ▲ -- - ▲ Simpson's dominance (ℓ).

DISCUSSION

Ideally, a study of succession requires long-term observations, a record of environmental variables during the period of study, and experimental evidence to substantiate the findings. Although a study period of five years is not very long, in conjunction with experimental and environmental data, it is possible to draw conclusions about the dynamics of the sand dune and slack vegetation (Fig. 2.9). Of the other studies on coastal dune vegetation in South Africa, Moll (1969) and Ward (1980) discussed successional changes along the Natal coast, but their findings were not substantiated by experimentation or long-term data records. Pammenter (1983) and Donnelly & Pammenter (1983) have made detailed ecophysiological studies of dune species, and McLachlan *et al.* (1982; 1987) studied the total dune slack ecosystem and drew some conclusions about succession.

Weisser (1978a; 1978b) and Weisser & Marques (1979) used air photo interpretation to show gross vegetation changes in the dune areas near Richards Bay between 1937 and 1974. In this more tropical region with a hot, humid climate and a mean annual rainfall of over 1 200 mm, successional changes are fairly rapid. These are described and compared in more detail later (Chapter 3). By contrast Lubke (1983) studied air photographs of the Kleinemonde area for the same period and was unable to detect marked vegetational changes. Thus climate is undoubtedly the major controlling factor in dune succession.

The dune slack region of the dunefields is the critical zone of colonization and stabilization. Even if the foredunes have been stabilized by pioneer vegetation, it is only after a mature dune slack community is produced that the climax dune thicket or dune forest vegetation may develop. The complete process of succession has not been observed in the last five years, but observations on the dune slack together with experimental evidence has led to a better understanding of succession on the whole dune system (Fig. 2.9).

Following the wet period of 1979 (Table 2.1; Fig. 2.1), the slack was colonized by *Scirpus nodosus* (species number 3) in 1979 and 1982. The changes in relative density of all species (1981 to 1985) are summarized in the form of pie charts (Fig. 2.8) that show that this pioneer sedge was most abundant in September 1981. Moving in a clockwise direction, the arrows illustrate species replacement under wet conditions. *Juncus kraussii* (4) became increasingly important. A much greater diversity of species was recorded from 1983 to 1985, and the dominance of *Scirpus nodosus* (3) decreased (Figs. 2.7 & 2.8). Since it favours wet slacks, *Vellereophyton vellereum* (5) disappeared during the dry period, when the soils dried out, the water table dropped (Table 2.3), dry sand was blown into the slack by strong winds (Plate 2.2), and rainfall decreased (Table 2.1; Fig. 2.1). The weedy *Conyza pinnatifida* (7) increased in abundance during this period.

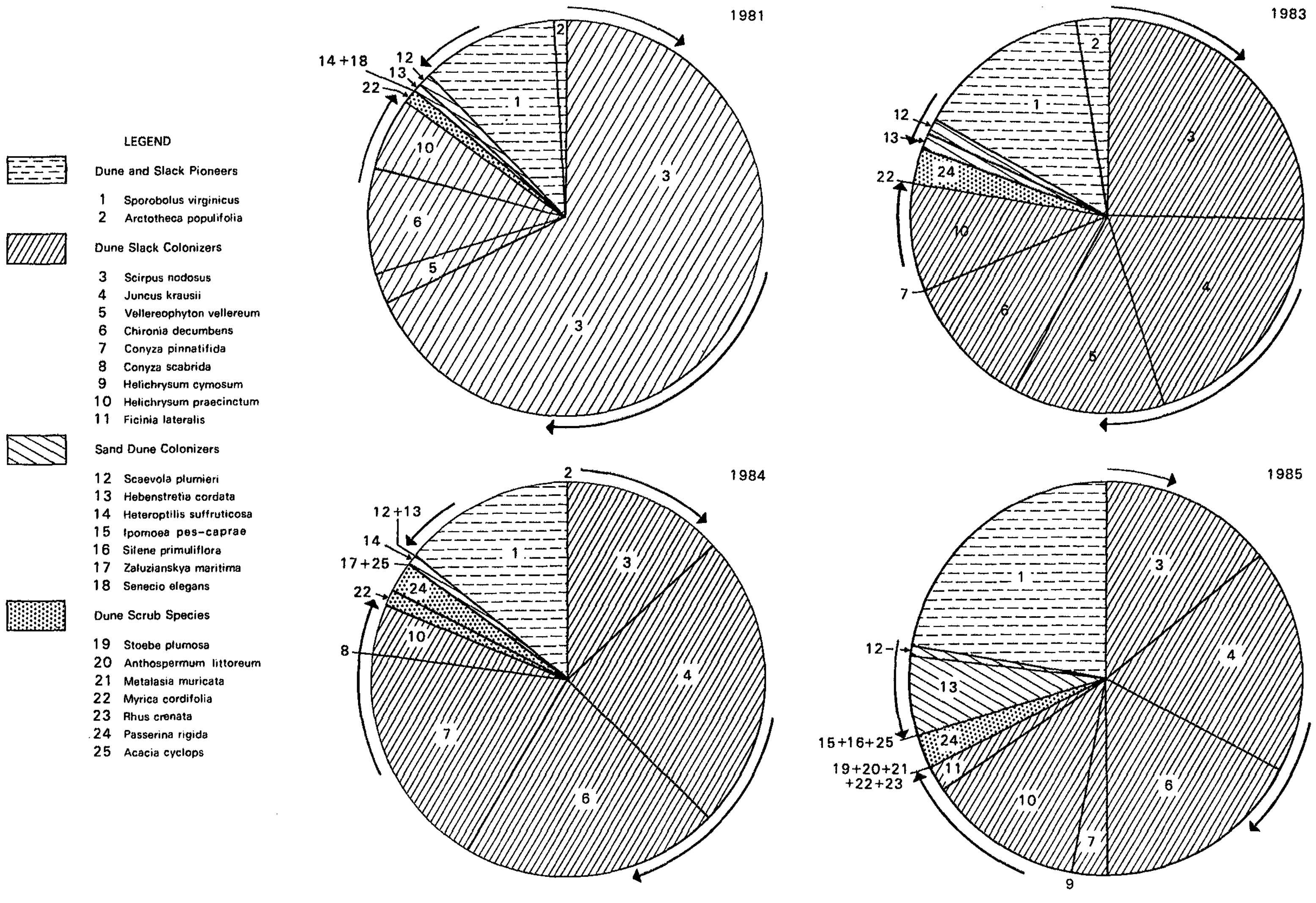


Figure 2.8 The changes in relative density of all the species of the dune slack over the period September 1981 to February 1985. Clockwise arrows represent successional replacement of species from wet slack to dune scrub and counterclockwise arrows illustrate replacement of species from dry slacks or dunes to dune scrub.

The counterclockwise arrows on the pie charts (Fig. 2.8) illustrate the successional replacement of species in dry regions of the slack moving towards the more advanced stages of succession. The widespread grass *Sporobolus virginicus* (1) was always abundant, and sand dune colonizers (12-18) increased in abundance during the course of this study as dry conditions prevailed. Succession from both dry (counterclockwise arrows) and wet (clockwise arrows) slack conditions resulted in the Dune Scrub stage. *Passerina rigida* (24) a hardy shrub capable of invading drier areas (Chapter 1), was most common, but five other species (19-23) were also recorded in 1985. These young shrubs were evident in the photograph of the slack taken in February 1985 (Plate 2.3d). Should favourable conditions continue, these species will become more abundant as was observed in the older slack community of 1980 (Fig. 2.4; Plate 2.2). More recent observations have revealed an increasing abundance of Dune Scrub species (see Plate 4.3, pg 133). There is evidence of a much more widespread and extensive Dune Thicket vegetation in these dunefields as relic patches of thicket occur within the drift sands (see background of Plate 2.3 & Chapter 1) and the Dune Thicket is probably contracting (Plate 2.4).

Plate 2.4 The study slack photographed in January 1984 with the direction of the line transect illustrated. The arrow indicates the retracting coastal scrub at the top of the rear dune.

Seed dispersal and the establishment of seedlings within the dune and slack environment are the most critical stages of succession (Moreno-Casasola 1988). Studies in the Gulf of Mexico by Altamirano & Guevara (1982) and Castillo & Carabias (1982) on phenology and seed distribution of dune species respectively have shown that seed production is prolific and a mean density of 629 seeds m^{-2} is common in dunefields. Records on coastal species of the Eastern Cape (Lubke 1988) indicate that local dune species also flower and produce seeds throughout much of the year, and the availability of seed in all habitats is unlikely to be limiting.

Models of seed germination and seedling establishment in the dune environment have been produced by van der Valk (1974) and Guevara (1982) for the North Carolina and the Mexican Gulf coasts respectively. While they note the importance of many factors, shifting sand appears to be the most vital in determining the successful establishment of young plants. The germination of species on the foredunes and in the slacks were observed during the course of this study following periods of high rainfall (Fig. 2.1), and these seedlings were used in experimental studies (Avis 1983). Whereas Buckley (1982) found soil catena were major factors in the success of transplants on sand ridges in central Australia, these studies (Avis & Lubke 1985), like those of van der Valk (1974), showed that sand movement due to high winds caused burial and subsequent death of the seedlings. Even in regions out of the normal range of *Scirpus nodosus*, where sand movement was minimal (next to the Dune Thicket, at site 8 in Fig. 2.4), survival of the transplanted seedlings was more successful.

On the foredunes, *Scaevola plumieri*, *Ipomoea pes-caprae*, and *Arctotheca populifolia* seedlings are commonly found during cooler moist periods (Fig. 2.1). There is less likelihood of erosion or burial of the seedlings when the sand is moist. Seeds of *Sporobolus virginicus* are difficult to germinate (Breen *et al.* 1977), and the vegetative spread of mature plants is the common method of dispersal of this species. Once pioneer plants have become established (Fig. 2.9), they play an important role in sand stabilization and dune building (Hesp 1983; 1984). *Scaevola plumieri* produces woody stems that ramify and branch as sand is deposited, resulting in large extensive foredunes parallel to the coast (Pammenter 1983). This species is widespread along tropical (Morton 1957) and subtropical coasts of Africa (Moll 1969; Ward 1980) and is very common along the Eastern Cape coastline (Chapter 1). *Sporobolus virginicus*, a cosmopolitan grass with shallow underground rhizomes and surface stolons, stabilizes dunes in a similar way (Henriques *et al.* 1984; Gooding 1947), but it is also found in the dune slack and is probably not dependent on a continuous supply of sand and salt spray as is *S. plumieri* (Pammenter 1983). The tufted composite species, *Arctotheca populifolia* and *Gazania rigens* var. *uniflora*, and procumbent *Tetragonia decumbens* form small hummock dunes that are not easily invaded by other dune colonizing species (Chapter 1). Moreover, hummock dunes are often unstable (Wiedemann 1984). The other dune colonizing species, such as *Hebenstretia cordata*, penetrated into the *Scaevola* zone (Plate 2.1 & Fig. 2.5), resulting in an observable change in species diversity and dominance over the five-year period (Table 2.5). *Ipomoea pes-caprae* is also cosmopolitan and produces distinct vegetation zones behind the pioneer zone in Barbados (Gooding 1947). Van Tooren *et al.* (1983) found that life form is important in succession, but these dune species do not conform to any life form-habitat pattern, as each stage is composed of a variety of life forms.

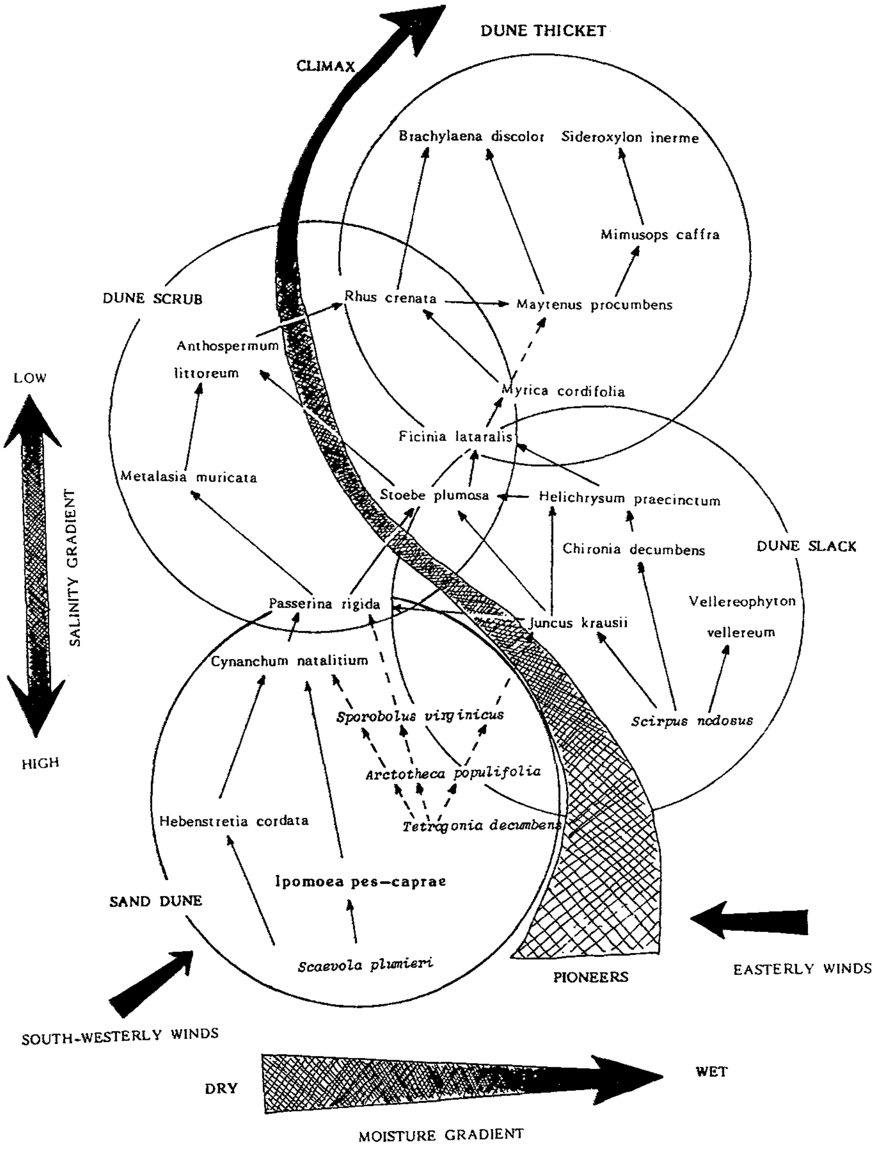


Figure 2.9 A model of plant succession in the dunefields of the Eastern Cape. Solid lines show the common and dashed lines the less common successional pathways. Not all species found at Kleinemonde are included in the diagram, and additional species not found in the study area are added for completeness of the successional model.

Salt spray may be a limiting factor on the foredunes, since it affects the growth of seedlings (van der Valk 1974; Lubke & Avis 1982b). However, the foredune species are more resistant to salt spray, and it has proven difficult to correlate salt spray with vegetation zonation (Donnelly & Pammenter 1983). Van der Valk (1974) found that salt spray played a secondary role to sand movement in eliminating forbs from the foredunes. However, salt spray is also important in the supply of nutrients to the sand, but rapid leaching of nutrients by rain results in a low cation exchange capacity of dune sands (van der Valk 1974). This tends to limit the growth of species on dunes (Willis 1963; Willis & Yemm 1961; Onyekwelu 1972). There must therefore be a balance between nutrient supply from salt spray and the ability of the foredune species to withstand salt damage.

Although moisture is unlikely to be a factor limiting the growth of mature plants such as *Scaevola plumieri* on the foredunes (van der Valk 1974; Pammenter 1983), data from this and the previous study reveal that it is of much greater consequence in the dune slacks. The loss of species such as *Vellereophyton vellereum* in the study area during a dry cycle (Table 2.4; Fig. 2.1) has been noted as a periodicity of species fluctuation in the beach plain of the Netherlands by van Tooren *et al.* (1983), whose study extended over a longer (10-year) period. The most important factor controlling dune slack vegetation at Kenfig, South Wales is the fluctuating water table, which is dependant on the location of the slack within the groundwater system and the morphology and size of the slack. Consequently, vegetation succession and species composition were found to be dependant on the prevailing water regime (Jones & Etherington 1989). It is possible to predict that with the return of wetter conditions, these slack species will reappear, since the wet periods are important in the establishment of a more diverse slack flora. With higher soil moisture (Fig. 2.3) successful seedling establishment of *Scirpus nodosus* was achieved (Fig. 2.6; Plate 2.3) and under these conditions the diversity (Fig. 2.7) and abundance of other species (Fig. 2.8) increased. In contrast, during drier periods and in drier regions of the slack, for example to the north of the study slack (Fig. 2.6), *Sporobolus virginicus* and *Arctotheca populifolia* may colonize the sands but the diversity of species will not increase. This dependancy on soil moisture variability lends support to the reason given for the disjunct location of dune slacks in the ordination diagrams discussed earlier (Figs. 1.7 & 1.8, Chapter 1). The model (Fig. 2.9) therefore shows that the greatest diversity of slack species is most likely to occur when *Scirpus nodosus* is the pioneer of a wet slack (clockwise arrow, Fig. 2.8) and not via dry slacks colonized by the latter two species (counterclockwise arrow).

Other soil factors such as conductivity and pH (Table 1.3; Fig. 2.3) do not appear to be correlated with vegetational development. However, the buildup of nutrients as a result of humus decomposition (van der Valk 1974; Guevara 1982) must be an important factor in the successful invasion and establishment of other species in the dune slack. Nutrient levels have not been measured in this area, and studies of this nature would be important in substantiating this conclusion (see Chapter 4). Air temperatures and consequently soil temperatures vary according to the site and aspect (Oosting & Billings 1942). They are lower or less extreme in the slacks (Lubke 1983) and since seedling establishment occurs during the cooler periods, it is not a factor that is likely to be of paramount importance in pioneer vegetation establishment, either on the dunes or in the slacks. However, once the *Scirpus-Juncus* stage in the slack or the *Scaevola* stage on the dunes is achieved, a favourable microclimate has been created for seeds of other species to germinate and young plants to become established.

Of the Dune Scrub woody plants, *Passerina rigida* is the first to invade the dunes (Figs. 2.4 & 2.5) and the dune slacks (Figs. 2.6 & 2.8), as it can tolerate a variety of soil moisture and sand movement regimes. Other shrub species rapidly invade, and the study slack has now reached the Dune Scrub stage in the model (Fig. 2.9), as these shrubs have matured and become successful colonizers of the dune slack (see Plate 4.3, pg 133). *Rhus crenata* links the observed succession (Fig. 2.8) to the successional model (Fig.

2.9), as it is a common dominant in Dune Scrub (Chapter 1). The climax trees of Dune Thicket (Chapter 1) are the milkwoods *Sideroxylon inerme* and *Mimusops cafra*, and *Brachylaena discolor*, depending on locality and prevailing conditions. *Myrica cordifolia* is common on pebble beaches and in blowout areas of the Dune Thicket and has been recorded as dominant in bushpockets (McLachlan *et al.* 1982; Young 1987; Talbot & Bate 1991; Chapter 1) in the Alexandria dunefields. The accumulation of humus and the development of a soil profile is important in the succession of large woody shrubs and trees on drift sands (Moll 1969). Lubke (1983) recorded a lowering of pH and an increase in conductivity related to a build up of organic matter in the soils of rocky promontories where Dune Thicket occurs and Burns (1986) recorded similar results for the dune forests near East London. These and other aspects relating to edaphic changes are discussed in more detail in Chapter Four. The physical effect of wind and salt spray are important additional factors throughout the dune environment and may be a cause of shrub and tree pruning on the rear dunes (Parsons & Gill 1968; Moll 1969).

Once vegetation has become established on the foredunes, it does not mean that succession will continue in the direction indicated on the model (Fig. 2.9). In some areas foredunes may be colonized, but extensive unvegetated dunefields between these foredunes and the climax Dune Thicket can occur (Lubke 1983; McLachlan *et al.* 1987; Chapter 1). The critical stage is thus for dune slacks to become colonized and stable. Under the present rainfall conditions it is unlikely that the dunefields of Alexandria or at Kleinemonde will be naturally stabilized. Should the rainfall become more consistent and exceed 1 000 mm per annum, succession will be speeded up, resulting in rapid vegetational changes similar to those observed near Richards Bay (Weisser 1978a; 1978b; Chapter 3). With an erratic cycle of wet and dry periods (Table 2.1; Fig. 2.1) and rainfall never exceeding 600 mm per annum, slack vegetation will never develop much further than the stages observed at present. The occurrence of isolated scrub remnants (Plate 2.3) and a retreating Dune Thicket margin (Plate 2.4) are evidence of a moister, more equitable climate in prehistoric times.

The controlling environmental factor thus appears to be rainfall and soil moisture, for only under moist conditions will a more diverse slack community develop. However, the strong winds (Fig. 2.2) of this area are the major factor reducing growth of the slack vegetation. Under dry, windy conditions sand movement is sufficient to cause burial of seedlings; adult plants and utimately the whole slack community disappears. The dimishing size of the slack at Kleinemonde (Plate 2.2a-d) is due to these causes, and similar observations have been made along the whole of this coastline during dry cycles. When moister conditions return, the slack communities will increase in size but will never attain the climax situation illustrated in the model (Fig. 2.9), except in a few localized or protected areas.

CONCLUSIONS

The major factor controlling the establishment and growth of plants on the mobile dunes is the climate. Under high rainfall and cool conditions, seedlings become established on the foredunes and dune slacks. Even if the foredunes are well colonized, it is only when the slacks become stabilized that succession will proceed to climax coastal scrub or forest. Under the present dry rainfall regime, the coastal slacks are contracting as dry sands are highly mobile and the prevailing winds predominantly from the southwest deposit large amounts of sand on the existing plant communities. When higher rainfall conditions return, a more diverse slack flora should develop, resulting in an expansion of the vegetation in these regions. Salt spray and soil factors appear to be secondary in the complete successional scheme, but locally or periodically these may be decisive factors in determining the successional pathway. There is evidence that the Dune Thicket vegetation has been contracting over a long period of time (hundreds of years - Tinley 1985; Burns 1986). Unless the rainfall increases to over 1 000 mm per annum, it is unlikely that the present dunefields in the Eastern Cape will ever be fully colonized and a climax vegetation attained.

CHAPTER THREE

EVIDENCE FOR A CLEMENTSIAN VIEW OF SUCCESSION IN THE DUNEFIELDS AT MTUNZINI, NATAL

INTRODUCTION

Since the turn of the century, plant succession has been extensively studied by plant ecologists, who have been unable to reach agreement on the nature of the process. Although originally proposed by Cowles (1899) successional theory was developed and clearly explained by Clements (1916) to whom most credit is given. From his organismic ecosystem theory an opposing individualistic population-centered theory was developed by Gleason (1926). Ecologists have tended to support either of these main viewpoints, and a number of theories have appeared in the literature. Of note is the work of Lindeman (1942), Whittaker (1953; 1975), Tansley (1935), Egler (1954), Margalef (1968), Odum (1969), Horn (1974; 1976; 1981) and Peet & Christensen (1980). These concepts have also been criticized by, amongst others, Drury & Nisbet (1973), Shipley & Keddy (1987) and Noy-Meir & van der Maarel (1987), leading to further new theories concerning community change or succession. Connell & Slatyer (1977) considered the mechanisms which determine the changes during succession and the relationship between succession, community stability and organization. They proposed three models, the Facilitation, Tolerance and Inhibition Models (see Fig. 1, General Introduction). Noble & Slatyer (1980) emphasized the importance of vital attributes in secondary succession, and recently Picket *et al.* (1987) discussed succession in terms of three fundamental concepts, namely, pathways, mechanisms and models.

From the pioneering studies of Cowles (1899) on the Lake Michigan sand dunes, studies on dune systems have played an important role in the formulation of successional theories (Olson 1958; Morrison & Yarranton 1973; 1974). Dune systems have a number of advantages for this type of study. They afford a convenient example since environmental conditions at their initiation are generally uniform over a relatively large area; they are considered good examples of spatial sequences, representing temporal sequences (Salisbury 1925); and they have relatively simple, well defined communities.

A number of broad vegetation surveys have been undertaken along the Natal and Zululand coast (Bews 1920; Bayer 1938; Edwards 1967; Weisser & Marques 1979; Ward 1980; Tinley 1985), but only a few detailed studies have been undertaken in the Mlalazi Nature Reserve. Moll (1969) presented an account of the structure, distribution and ecology of the various dune communities. Weisser and his colleagues have studied the area with regard to dune advancement and vegetation changes using air-photo interpretation. They presented a rough vegetation-succession chronology for the area (Weisser *et al.* 1982; Weisser & Backer 1983; Weisser & Muller 1983; Weisser *et al.* in prep.). More recently, members of the South African Forest Biome workgroup undertook a rapid survey of forest advancement along the successional gradient (van Daarlen *et al.* 1986).

The studies in this region have not been quantitative or specific enough to clearly elucidate the pathway of succession in this dune system. Consequently, field and laboratory studies were carried out to provide information on this unique region. The aim was to objectively determine and accurately describe the various dune communities along a chronosequence, and to present quantitative data of vegetative and edaphic changes along this dune sequence, the hypothesis being that the classical concept of succession (Facilitation model) may apply in this specific situation.

THE STUDY AREA

The Mlalazi Nature Reserve at Mtunzini, Natal, lies approximately 130km north east of Durban within a 42km long dunefield between the Tugela River in the south (lat. 29° 3'S; long. 30° 30'E) and the Mlalazi estuary in the north (lat 28° 57'S; long 31° 48'E; Fig. 3.1). The Holocene beach ridges are parallel to the coast and form a prograding shoreline, which has advanced at least 120m in the last 40 years, mainly due to sand loads deposited into the sea by the Tugela River. This sand is transported northwards by longshore drift associated with an inshore counter current and deposited on the beaches (Weisser & Backer 1983; Fig. 3.1). Windborne sand is moved from the beach landwards where it accumulates around pioneer dune-forming plants. The net result is a series of parallel beach ridge hummocks which are distinctive of accreting shorelines (Tinley 1985; Plates 3.1 & 3.2). The vegetation of the study area has been described in some detail by Moll (1969) and Weisser & Baker (1983). The vegetation on the sixteen dune ridges sampled in this study ranges from recent (last 15 years) pioneer stages to mature dune forest (older than 150 years) along a successional gradient.

The climate can be described as being subtropical, with humid and warm to hot days. Mean annual daily maximum temperature is 26.6°C and minimum of 16.3°C. Extremes range from a maximum of 43.9°C in December, and minimum of 5.0°C in June (Schultz 1985). The mean annual rainfall recorded at Mtunzini over a 53 year period is 1204.5mm (Weather Bureau 1954). July is the only month that could be described as dry, and the growing season from October to May receives in excess of 100 mm rainfall per month (Fig. 3.1). Consequently, no soil water deficit occurs, and conditions for plant growth are favourable. The prevailing northeasterly and southwesterly surface winds blow roughly parallel to the coastline. The southwesterlies tend to be stronger and play a greater role in dune formation than the northeasterly winds (Fig. 3.1).

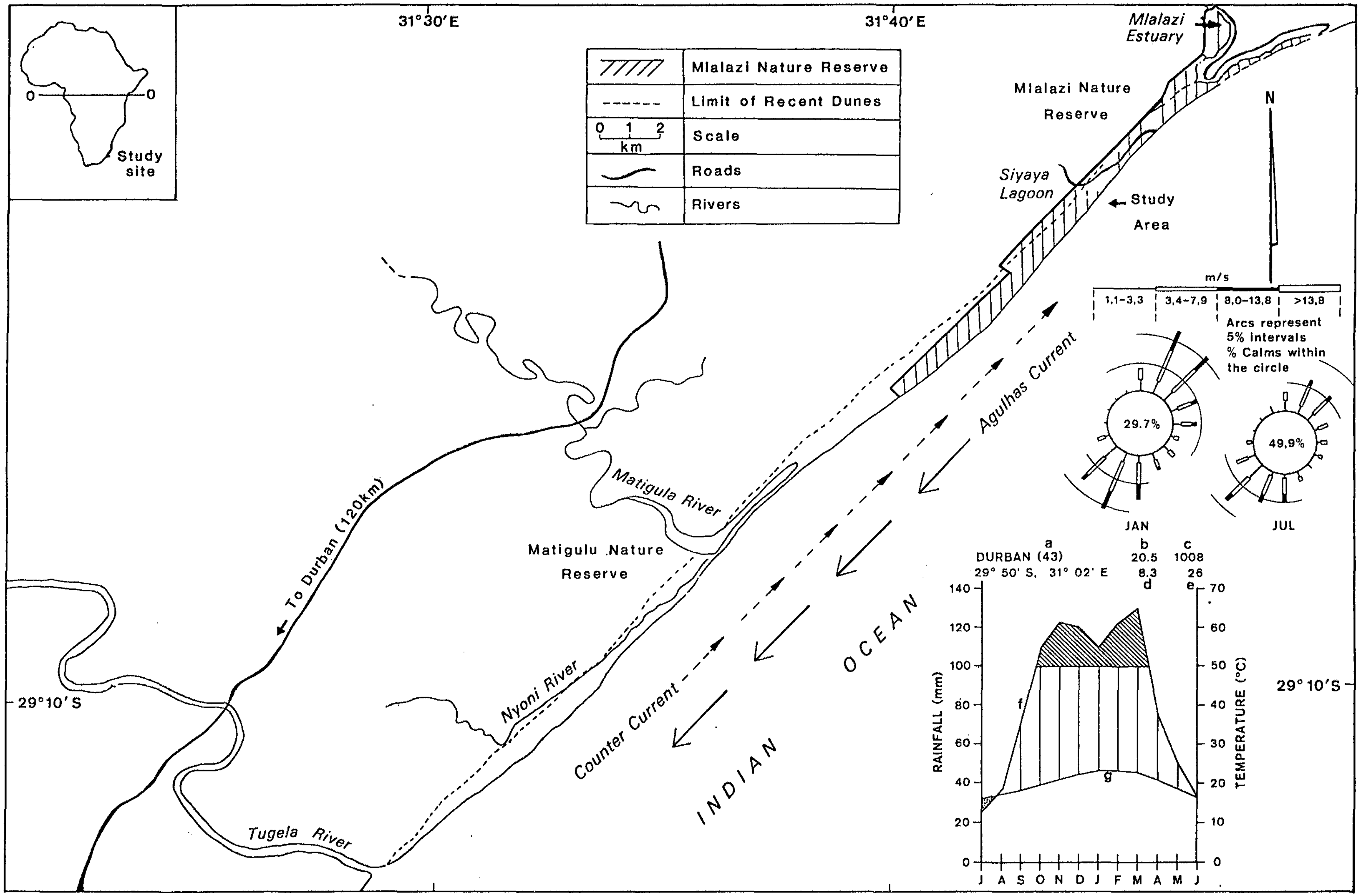


Figure 3.1 Location of the study site showing the extent of the Mlalazi Nature Reserve and limit of recent dunes. Wind roses of Durban for January and July show dominant wind directions in relation to the orientation of the coastline. Rainfall and temperature data for Durban have been summarized in a Walter-Leith Climate Diagram (a - elevation in metres; b - mean annual temperature; c - total annual precipitation; d - mean diurnal range in temperature; e - mean annual temperature; f - rainfall curve; g - temperature curve.

METHODS

VEGETATION SAMPLING

Three transects running perpendicular to the coast in a north - north-westerly direction were surveyed using an Abney Level and staff to determine topographical variation of the dune morphology (Figs. 3.2 & 3.3). Along the length of these transects ten to thirteen 10 x 10m relevés were randomly located (Fig. 3.2). Seven vegetation types (seral stages) were identified in the field based on dominant species and vegetation structure, and after sampling relevés were allocated to one of these communities (Table 3.1).

Table 3.1 Relevé numbers and total number of samples for each of the seral zones.

	Pioneer	Enriched Pioneer	Open Dune Scrub	Closed Dune	Bushclumps	Forest Margin	Forest
Transect 1 Relevé No.	1	2, 3	4, 5	6, 7, 8	9	10, 11	12, 13
Transect 2 Relevé No.	14	15, 16	17, 18	19	20	21	22, 23
Transect 3 Relevé No.	24	25, 26	27	28, 29	30, 31	32, 33	34
TOTAL	3	6	5	6	4	5	5

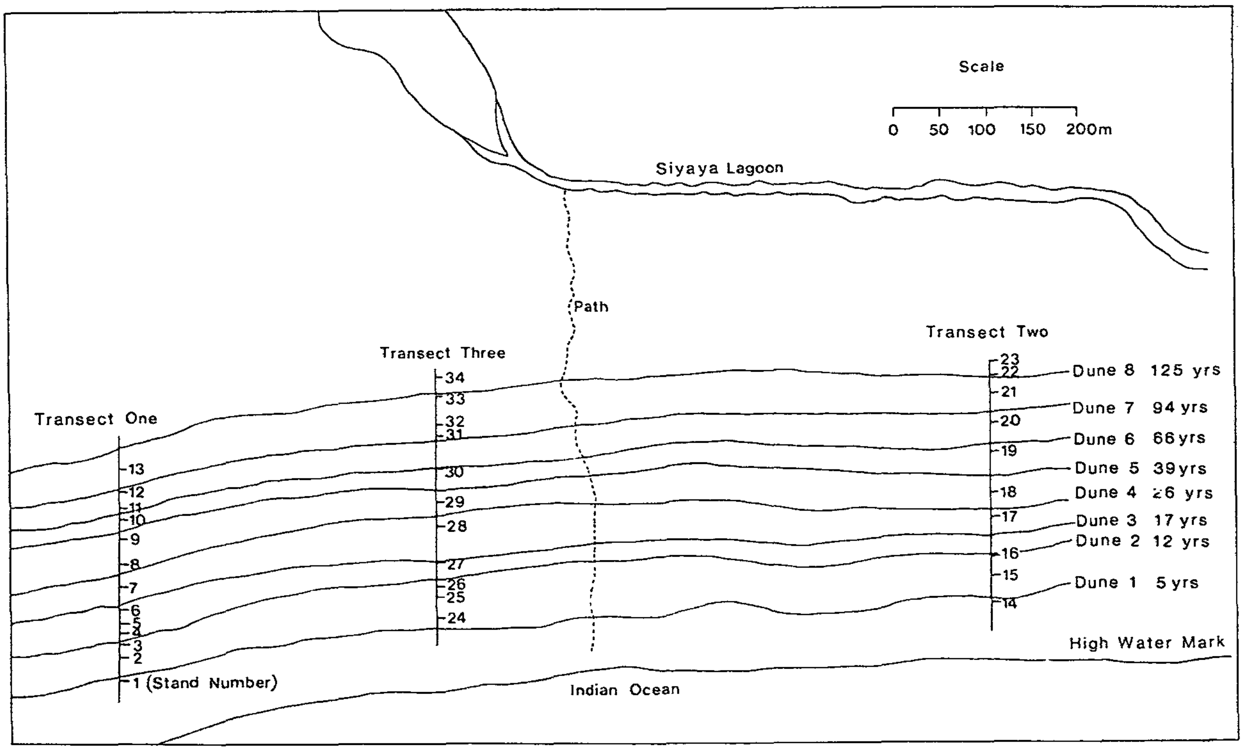


Figure 3.2 Location of transects and relevés sampled, relative to eight aged dune ridges at Mtunzini. Note the chronological sequence of the dune ridges, as determined at the time of the study in 1987.

To enable the direct comparison of data from the various vegetation types, the same relevé size and sampling technique was used in each community. Within each relevé 25 one metre square sub-samples were randomly selected by locating each quadrat on a grid system using random numbers (1 - 100). In each quadrat the number of individuals (not always rooted) and percentage aerial cover of each species was recorded. This technique ensured that rare and/or inconspicuous species were recorded, these species being very important as they indicate changes in the continuum (indicator species of Clements 1916). This method was also the most appropriate as direct comparison of data using Detrended Correspondence Analysis (DECORANA) requires a constant quadrat size (Gauch 1982).

The major disadvantage of using a constant sample size of $100m^2$ is that relevés are too small for sampling in forests, but Cambell *et al.* (1988) also used 100 m^2 samples in a similar study. Van Daarlen *et al.* (1986) showed that the minimum relevé size for the forest margin at Mtunzini was $160m^2$, and for forest $170m^2$. Subsampling can also result in the cover and density estimates of the larger trees being overestimated. However, the multivariate techniques used for data analysis place more importance on the similarities than on the differences between samples. For example, if the same species has a cover of 18% in one relevé and 36% in another, it contains 2 pseudospecies in the former, and three in the latter. Thus, the samples are registered as having more in common than by way of difference (Hill 1979a). Consequently, the resultant overestimate of cover and abundance for larger species is less significant than the potential underestimate of rare species and seedlings.

SOIL SAMPLING AND ANALYSIS

Within each relevé three random soil samples were taken with a barrel auger up to 15cm depth. In the forested areas (Table 3.1) an additional sample was taken between 15-30cm. Samples were sealed in plastic bags for laboratory analysis. Percentage organic matter was estimated as the percentage loss on combustion of air dried soil placed in a muffle furnace for 8 hrs at 450°C. The reaction of the soil was determined by measuring the pH of 20 grams of soil in 50ml of deionized water using a DDS 200 pH/Conductivity meter. For conductivity, the solution was left to stand for 24 hrs, reagitated, filtered and measured with the same instrument using a conductivity probe.

Soil cations were determined by extraction, following the methods developed by Bray & Kurtz (1954). Five grams of soil was agitated for 15 mins with 50ml of a 1 mol/litre ammonium acetate solution, pH 7, at a soil/extractant ratio of 1:10g/ml. The suspension was then filtered and 0.5ml LA stock solution added to each bottle. The amount of Ca, Mg, K and Na in the filtrate was then measured by atomic absorption with a Varian AA - 12 75 series Atomic Absorption Spectrophotometer. For soil phosphate 6g of soil was extracted in 45ml of Bray 1 solution by shaking for 1 min, and then adding 0.55ml flocculent solution. The filtrate was then measured with a Phillips PU 8620 series Spectrophotometer at 680 and 882 nm.

DUNE AGES

The rate of dune advancement along this prograding coastline was assessed from aerial photographs by Weisser *et al.* (1982) and Weisser & Backer (1983). These studies showed that dune advancement was not a linear process, but occurred in pulses. The advancement rate measured by Weisser & Backer (1983) showed an increase from 1.2m yr^{-1} (1937 - 1957), to 3.56m yr^{-1} (1957-1965) to 5.67m yr^{-1} (1965-1977). This increase is probably a consequence of increased soil erosion in the catchment of the Tugela River. They concluded that it would take 5 years for a dune ridge to be formed under present conditions.

Using these data the age of the eight dune ridges sampled could be estimated. The first dune ridge was assumed to be 5 years old. The mean horizontal distance between successive dune ridges was calculated from the three transects. The age of each ridge was then estimated by dividing the mean distance between ridges by the rate of sand movement for that time period. If the estimated age straddled two time period rates, (for example ridge 4, age falls between 1961 to 1970; Table 3.2) a mean advancement rate for that period was calculated by multiplying the two rates with their estimated time periods (years), and dividing by the total number of years. In this way a fairly accurate estimate of dune age was obtained (Table 3.2; Fig. 3.2).

DATA ANALYSIS

Importance Values

Using percentage cover, density and occurrence of each species in each $1m^2$ quadrat, the total and mean percentage cover and density, and frequency of species were calculated for each relevé. Relative values were calculated by expressing mean values as percentages of the respective totals and the importance value was calculated as the sum of the relative density, cover and frequency values (Lubke 1983).

Continuum Index

A simple technique of ordinating stands in relation to an environmental gradient, as developed by Cottam (1949) and Curtis & McIntosh (1951), was applied to the data to determine whether the chronosequence of vegetation was organised as a continuum, and if not, to show where various indicator species appeared and disappeared along the transect. Climax adaptive numbers, ranging from 1 to 10, were assigned to each species based on the order of the leading dominants and the position of each species in the chronosequence. The continuum index (CI) is regarded as a measure of the total environment of a relevé expressed in terms of species composition and relative abundance. It is calculated as follows:

$$CI = \sum_{i=1}^{t} IV_i a_i$$

where t = total number of species,

IV = the importance value of each species,

a = the climax adaptive number of the species.

Ordination of the species is illustrated by plotting individual importance values against continuum index values. A line of best fit was then calculated using the Harvard Presentation Graphics (HPG) computer programme.

Ordination

The data matrix of 34 relevés and importance values of 74 species was also analyzed using Detrended Correspondence Analysis (DECORANA; Hill 1979b), which is a more reliable method than reciprocal averaging and principal components analysis. The merits of this technique have already been discussed (Chapter 1), and Peet *et al.* (1988) state that DCA is a powerful tool for presenting pattern along compositional gradients, and Austin (1977) has encouraged the use of ordination in successional studies. The use of the above two ordination techniques is in line with van der Maarel's (1982) suggestion to apply at least two conceptually different techniques.

Classification

Classification of species and relevés was achieved using Two Way Indicator Species Analysis (TWINSPAN; Hill 1979a). TWINSPAN constructs a classification of the samples, and then uses this classification to obtain a classification of the species according to their ecological preferences. These techniques have been used successfully in a number of similar studies (Williams *et al.* 1969; Onyekwelu 1972; Kachi & Hirose 1979; Kirkpatrick & Hassal 1981; van der Maarel 1982; Moreno-Casasola & Espejel 1986; Lubke & Strong 1988).

Species Diversity and Life Forms

The species richness value (S), namely the number of species per site (Cowling 1984), was calculated by totalling the number of species recorded in each of the seven communities defined by the TWINSPAN classification. The alpha diversity, the within-habitat or intra-community diversity (Whittaker 1975) was calculated for each community (Brower & Zar 1984). Simpsons' diversity (Ds) is an expression of the number of times one would have to take pairs of individuals at random from the entire aggregation to find a pair from the same species. This, and the inverse, Simpsons' dominance (ℓ) was calculated using the density values for each community (Brower & Zar 1984). The mean number of species and the relative importance value of the life forms in each community were also calculated. Beta diversity was assessed using Sorenson's (1948) co-efficient of community (CC) given by:

$$CC = 2S_s/(Sj + Sk)$$

Where S_s is the number of species shared by two samples; Sj is the number in the first and Sk the number in the second sample. It must be noted that this is a measure of similarity between communities, and a high CC value indicates a large degree of similarity between the communities under consideration. A low CC means the two communities are dissimilar, and by inference the Beta diversity (species turnover) is high.

Soil Data Analysis

A mean value for each soil factor was calculated from the three soil samples taken in each relevé. The data were standardized for the multivariate analyses by converting into percentages on the basis of the highest value for each variable. Pseudospecies cut levels for DECORANA and TWINSPAN were modified to encompass the full range of percentage values, and soil data were analyzed using these two techniques.

RESULTS

DUNE MORPHOLOGY AND CHRONOLOGY

Interpolation of the dune advancement rates calculated by Weisser & Backer (1983) gave a congruous assessment of dune age (Table 3.2). Dune ridge eight, furthest from the sea, is 115 years older than the first ridge. Since sand deposition is not uniform, the time period between ridges is not equal and varies from 31 years between ridges 7 and 8, to 4.5 years between ridges 2 and 3 (Table 3.2; Fig. 3.2). The topographical variation in dune morphology and position of sample sites is shown in the profile diagrams of the three transects sampled (Fig. 3.3). Dune ridges have been numbered to clarify their position since they vary spatially due to fluctuating environmental factors such as wind, which plays an important role in their development. This variability may also be due to different rates of "autogenic" change (plant growth, enhancement of soil conditions .

Table 3.2 Rate of sand movement (from Weisser & Backer 1983), mean distance between dune ridges and approximate dune ages, when the study was carried out in 1987.

Dune ridge	Mean rate of sand movement ($m\ yr^{-1}$)	Mean distance from previous ridge (m)	Age (yrs) from previous ridge	Approximate accumulative age (yrs)
1	5.67	5	5	5
2	5.67	39.3 ± 5.6	39.5/5.67 = 6.9	12
3	5.67	25.3 ± 5.5	25.3/5.67 = 4.5	17
4	4.5	41.3 ± 5.8	41.3/4.5 = 9.2	26
5	2.4	30.7 ± 3.7	30.7/2.4 = 12.8	39
6	1.25	27.3 ± 1.76	27.3/1.25 = 27.8	61
7	1.25	34.7 ± 4.4	34.7/1.25 = 27.8	89
8	1.25	39.3 ± 1.8	39.3/1.25 = 31.4	120

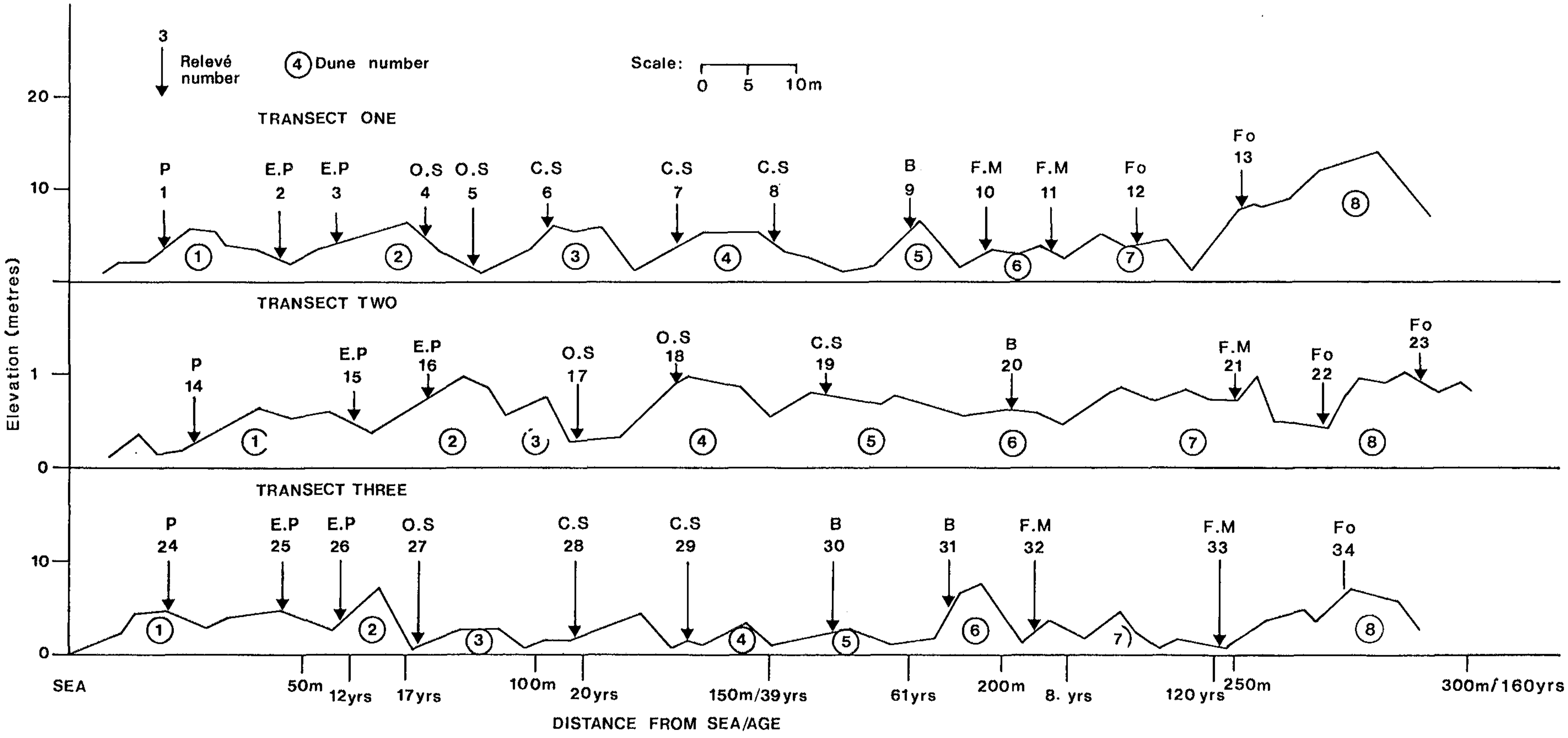


Figure 3.3 Profile diagrams of the three transects sampled, showing position of sample sites in relation to topographical variation and community type recognized in the field, and the position of the eight dune ridges. The x axis is both distance from the sea and age (inferred from Table 3.2). P - Pioneer; EP - Enriched Pioneer; OS - Open Dune Scrub; CS - Closed Dune Scrub; B - Bushclump; FM - Forest Margin; Fo - Forest.

PLANT COMMUNITIES - CLASSIFICATION AND DESCRIPTION

Classification of the relevés using TWINSPAN produced eight plant communities, and the species classification resulted in six groups, both at the third level of division. The phytosociological table so generated revealed species dominance in each community (Table 3.3). The quantitative characteristics (species richness, etc.) of these eight plant communities are recorded in Table 3.4 and they are briefly described below:

Pioneer Community

The differential species of this young pioneer community (up to 5 years old) are *Scaevola plumieri* and *Ipomoea pes-caprae* (Table 3.3). These low plants (less than 0.5m) are creeping evergreen colonizers of bare sand with low percentage cover and species diversity (Table 3.4). The most striking feature is the overall dominance of *S. plumieri*, which is capable of continuous stem elongation and adventitious root production from buried stems (Plate 3.1). It appears to be stimulated by sand movement, and has been the subject of detailed ecophysiological studies (Pammenter 1983; 1985).

Plate 3.1 View of the Mtunzini study area looking west. Note the parallel dune ridges and the new incipient foredune developing in the background, and the *Scaevola plumieri* dominated foredune in the foreground.

Enriched Pioneer Community

Relevés from the trough between dunes 1 and 2 and the seaward side and crest of dune 2 were grouped in this community (Fig. 3.3). Differential species are *Launaea sarmentosa*, *Gazania rigens* and *Helichrysum asperum* and dominants include *S. plumieri*, *Ipomoea pes-caprae* and *Senecio litorosus*. The presence of species such as *Helichrysum kraussii* and *Stipagrostis zeyheri* indicate that the community is older, and the estimated age is about 12 years (Table 3.2). This community is dominated by herbs with values of percentage cover, species richness and diversity greater than those recorded on foredunes (Table 3.4), and with a greater variety of life forms (Fig. 3.4; Plate 3.2).

Plate 3.2 Looking east along the second dune ridge, with the Enriched Pioneer community in the centre. The grass is *Stipagrostis zeyheri* and occasional shrub *Passerina rigida*. On the left is the Open Dune Scrub community. The large tree in the background is the invasive *Casuarina equisetifolia*. Note the increase in woody species and the parallel dune ridges.

Open Dune Scrub

All relevés (except 4) sampled in the field as this community were grouped together (Table 3.1 & 3.3). Open dune scrub occurs in troughs between ridges 2 to 4 (Fig. 3.3) and is estimated to be between 15 and 24 years old (Table 3.2). Differential species are *Chrysanthemoides monilifera* subsp. *rotundifolia* and *Mariscus capensis,* with the woody shrub, *Passerina rigida*, the grass, *Stipagrostis zeyheri* and the herbs, *Carpobrotus dimidiatus* and *Helichrysum asperum* being dominants (Plate 3.2). This community is protected from onshore winds by the seaward dune ridges and is structurally and floristically more complex, with two strata and relatively high values of abundance and diversity (Table 3.4).

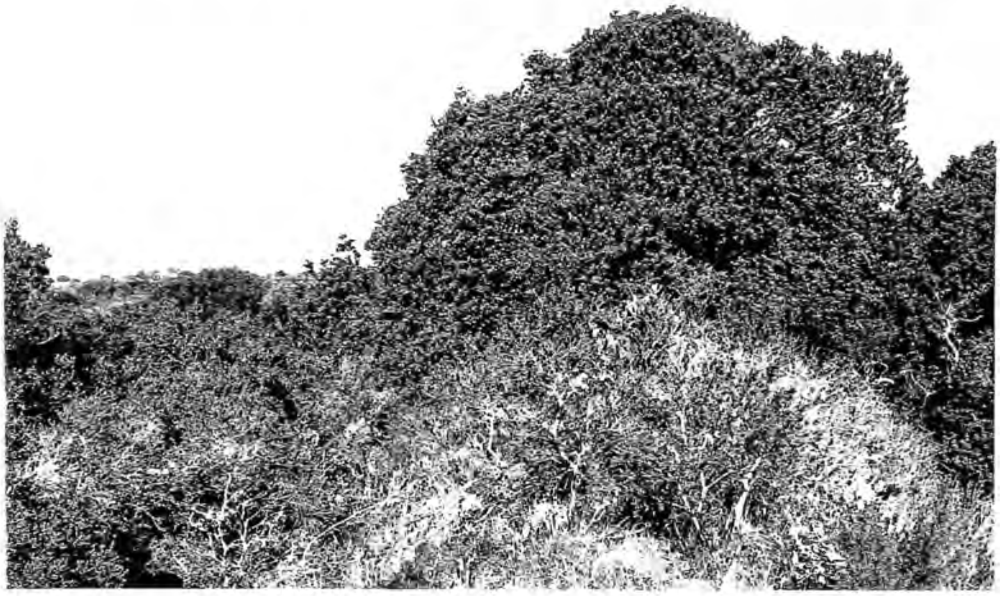


Plate 3.3 The Bushclump community has three strata. Field layer is *Imperata cylindrica*, and the large tree *Mimusops caffra*. On the left is the Closed Dune Scrub community.

Closed Dune Scrub

This community is represented by only three relevés (Table 3.3), two between dunes 3 and 4 and one on dune 3 (Fig. 3) and is estimated to be between 20 and 30 years old (Table 3.2). Differential species are *Helichrysum apendiculatum* and *Eugenia capensis* and these species, together with *Colpoon compressum* and the grasses, *Stipagrostis zeyheri* and *Imperata cylindrica* dominant (Table 3.3; Plates 3.3 & 3.4).

	SPECIES NAME	F	FM	BM	B	CDS	ODS	EP	P
Relevé		233 334	12123 32212	112 -1-	--133 989-1	--2 679	22-11 78578	-1--12 462356	-122 1445
Forest Margin and Forest Species	*Oplisminus hirtilus*	354	222-3	---	-----	---	-----	------	----
	Scadoxus sp.	445	5-1-2	---	---2-	---	1----	------	----
	Crocosmia aurea	321	1-1--	---	-----	---	-----	------	----
	Mimusops caffra	-34	1----	---	-----	---	-----	------	----
	Ekebergia capensis	--4	-1---	--1	-----	---	-----	------	----
	Maytenus nemorosa	--4	----2	--2	-----	---	-----	------	----
	Allophyllus natalensis	231	23542	221	1--2-	---	-----	------	----
	Rhoicissus rhomboidea	554	553-4	1-4	2----	---	-----	------	----
	Scolopia zeyheri	--2	1----	-1-	-----	---	-----	------	----
	Peddia africana	433	432-3	-3-	---1-	---	-----	------	----
	Kraussia floribunda	-23	41--2	-2-	-----	---	-----	------	----
	Dioscorea sylvatica	121	32--3	-22	----1	---	-----	------	----
	Dalbergia armata	--3	5112-	24-	-1---	---	-----	------	----
	Maytenus procumbens	223	-4553	532	2----	---	-----	------	----
	Apodytes dimidiata	-3-	34-55	114	2----	---	-----	------	----
	Euclea natalensis	3-4	2431-	223	1--1-	---	-----	------	----
	Sideroxylon inerme	11-	5513-	---	-----	---	-----	------	----
	Carissa bispinosa	-1-	12---	---	-----	---	-----	------	----
	Canthium obovatum	1--	55534	---	--223	---	-----	------	----
	Protasparagus sp.	--2	2-3-2	-1-	-1-2-	---	-----	------	----
	Scutia myrtini	-1-	2--4-	13-	----2	---	-----	------	----
	Tricalysia sonderana	---	--44-	-23	-----	---	-----	------	----
Bushclump/ Forest Margin	*Cyrtorchis arcuata*	--15	--1-1	13-	-----	---	-----	------	----
	Maytenus heterophylla	-	43-35	552	4345	---	-----	------	----
	Minusops caffra	555	311-4	445	5-453	---	-----	------	----
	Secamone alpinii	122	---13	554	41-21	---	-----	------	----
	Microsorium scolopendrium	555	55555	555	54555	314	---5-	------	----
	Brachylaena discolor	-3-	3-354	43-	234-1	--1	2----	-2----	----
Shrubs and Graminoids of Closed Scrub	*Colpoon compressum*	---	-----	-12	3-5-4	-4-	----2	------	----
	Rhus nebulosa	---	1---2	23-	4---2	--2	-----	------	----
	Rhoicissus digitata	--1	---34	-3-	--423	--3	-----	-2----	----
	Eugenia capensis	---	--144	555	55555	425	24-55	32----	----
	Imperata cylindrica	---	-----	355	55455	555	-52-3	------	----
	Mariscus dregeanus	---	-----	--3	1--23	-21	23---	------	----
	Kalanchoe rotundiflora	---	-----	---	11-1-	-13	-----	------	----
	Helichrysum appendiculatum	---	-----	---	13-31	254	-1---	------	----
Shrubs and Graminoids of Open Scrub	*Stipagrostis zeyheri*	---	-----	125	45555	555	55555	534212	----
	Mariscus capensis	---	-----	--2	--3--	3--	-233-	------	----
	Passerina rigida	---	-----	--3	13442	555	55555	42-1--	----
	Chironia baccifera	---	-----	---	---22	422	22-2-	------	----
	Carpobrotus dimidiatus	---	-----	---	-414-	544	35555	44---1	----
	Helichrysum kraussii	---	-----	---	1----	-34	-1---	------	----
	Chrysanthyemoides monilifera	---	-----	---	-----	-2-	33243	3-----	----
Pioneer Species	*Helichrysum asperum*	---	-----	--1	22342	--2	55543	555555	--25
	Senecio litorosus	---	-----	---	-2---	242	23544	443335	---1
	Tephrosia purpurea	---	-----	---	-----	21-	533-2	555555	---5
	Canavalia maritima	---	-----	---	-----	---	-1---	-1---1	--44
	Ipomoea pes-caprae	---	-----	---	-----	---	--41-	445543	2555
	Scaevola plumieri	---	-----	---	-----	---	2-53-	555555	5555
	Gazania rigens	---	-----	---	-----	---	-----	-55555	---2
	Launeae sarmentosa	---	-----	---	-----	---	2--4-	454545	---3
Relevé	SPECIES NAME	233 334	12123 32212	112 010	00133 98901	002 679	22011 78578	010012 462356	0122 1445
		F	FM	BM	B	CDS	ODS	EP	P

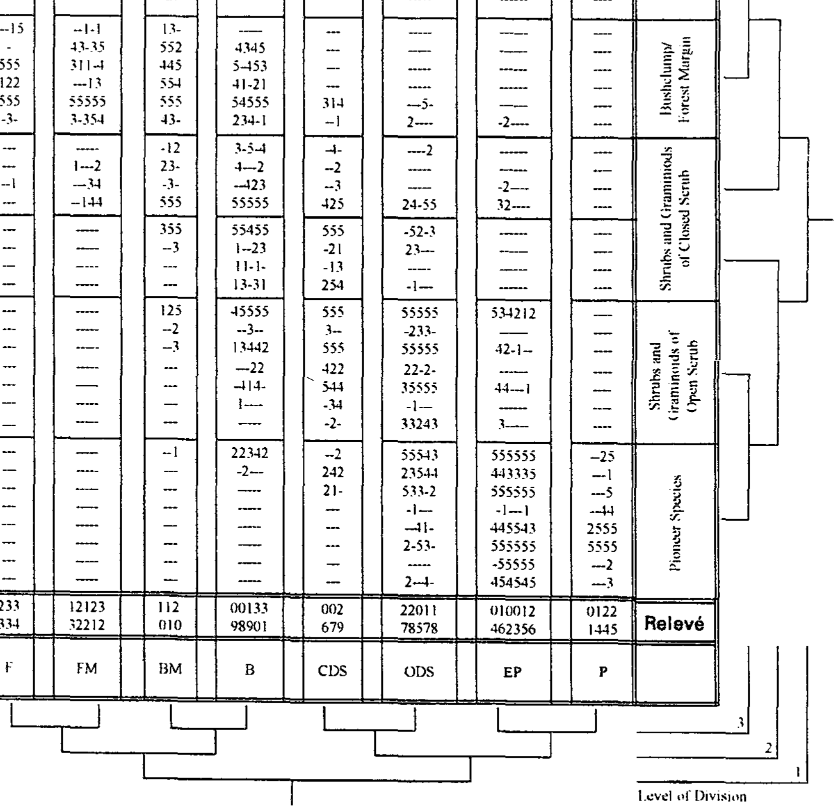


Table 3.3 Phytosociological table and dendrograms generated by TWINSPAN classification from Importance Value data. The dendrogram of relevé classification is shown at the bottom of the table, and for species classification on the right. Species and species groups are listed on the left and right of the table, and relevé numbers and relevé groups at the top and bottom. The position of relevés is given in Table 3.1 (pg 93) and shown on Figs. 3.2 (pg 93) and 3.3 (pg 98). Groups correspond to those used for Figures 3.5 and 3.6. The table has had limited reordering, and numbers in the table indicate TWINSPAN scores of abundance. F-Forest; FM-Forest Margin; BM-Bushclump/Forest Margin; B-Bushclumps; CDS-Closed Dune Scrub; ODS-Open Dune Scrub; EP-Enriched Pioneer; P-Pioneer.

The relative importance of woody life forms is less than in the previous community due to the overall dominance of the two grass species (Fig. 3.4). This is reflected by a relatively high dominance value and correspondingly low diversity (Table 3.4).

Bushclump Community

The bushclump and other woody communities were separated from the previous four communities at the first (primary) level of division (Table 3.3). This indicates the stage at which colonization by forest species begins, and where almost all pioneer species disappear (Plate 3.3). Bushclumps develop in more sheltered areas where later successional species can survive (Tinley 1985), and 5 relevés on dunes 4, 5 and 6 fall into this community (Fig. 3.3), which has been estimated to be between 30 and 60 years old (Table 3.2). Since it is transitional between the non-woody and woody communities, individuals from all six species groups are represented (Table 3.3). The community has three strata, and the field layer (less than 0.8m) is dominated by the grasses *Imperata cylindrica* and *Stipagrostis zeyheri* in open areas and the fern, *Microsorium scolopendrium* under trees and shrubs. The shrub layer (1 to 2.5m) is dominated by *Maytenus heterophylla* and *Eugenia capensis,* and the tall shrub/tree layer (2.5 to 4m) by *Canthium obovatum* and *Mimusops caffra.*

Table 3.4 Abundance, species richness and diversity (mean ± s.e.) for the eight plant communities classified by TWINSPAN.

COMMUNITIES	Pioneer	Enriched Pioneer	Open Dune Scrub	Closed Dune Scrub	Bushclumps	Bushclump /Forest Margins	Forest Margin	Forest
Relevé Nos.	1;14;24;25	2;3;4;15; 16;26	5;17;18;27; 28;	6; 7;29	8;9;19;30;31	10;11; 20	12;13;21 22;32	23;33;34
Total mean of cover (%)	30.5 ± 4.06	48.15 ±4.96	67.50 ±5.18	73.59 ±13.56	99.72 ±5.74	131.52 ±4.12	169.17 ±7.31	199.91 +5.99
Species richness value	9.0	15.0	24	23	35	36	34	37
Mean number of species per relevé	4.0 ± 1.42	10.0 ±0.93	13.0 ±1.00	15.0 ±1.53	18.4 ±1.47	22.3 ±2.59	19.4 ± 1.18	22.67 ±2.66
Simpson diversity	0.292 ± 0.145	0.791 ±0.02	0.800 ±0.02	0.685 ±0.05	0.791 ±0.04	0.791 ±0.03	0.724 ±0.03	0.815 ±0.05
Simpson dominance	0.708 ± 0.14	0.209 ±0.02	0.200 ±0.02	0.315 ±0.04	0.209 ±0.04	0.209 ±0.04	0.276 ±0.03	0.185 ±0.05

Bushclump/Forest Margin Transitional Community

This community was not recognized in the field, but was separated by TWINSPAN from the Bushclump and Forest Margin communities (Table 3.3). The three relevés which make up this community are all found on dune 6, which has an estimated age of 60 to 80 years (Figs. 3.2 & 3.3; Table 3.2). No individual differential species can be isolated, but it is distinct from Bushclumps due to the presence of more Forest Margin and Forest species and from Forests due to a lack of dominance by typical forest species such as

Sideroxylon inerme. It is therefore transitional between the Bushclump and Forest Margin communities, and also has three strata. The field layer (less than 0.8m) is dominated by *Microsorium scolopendrium* and *Imperata cylindrica*, the shrub layer (1-3m) by *Eugenia capensis*, *Maytenus heterophylla* and *M. procumbens* and the tree layer (3-5m) by *Mimusops caffra* and *Apodytes dimidiata* (Table 3.3). The relative importance of herbs and grasses decreases, but the importance of shrubs, geophytes, ferns, trees and vines increases (Fig. 3.4; Table 3.4).

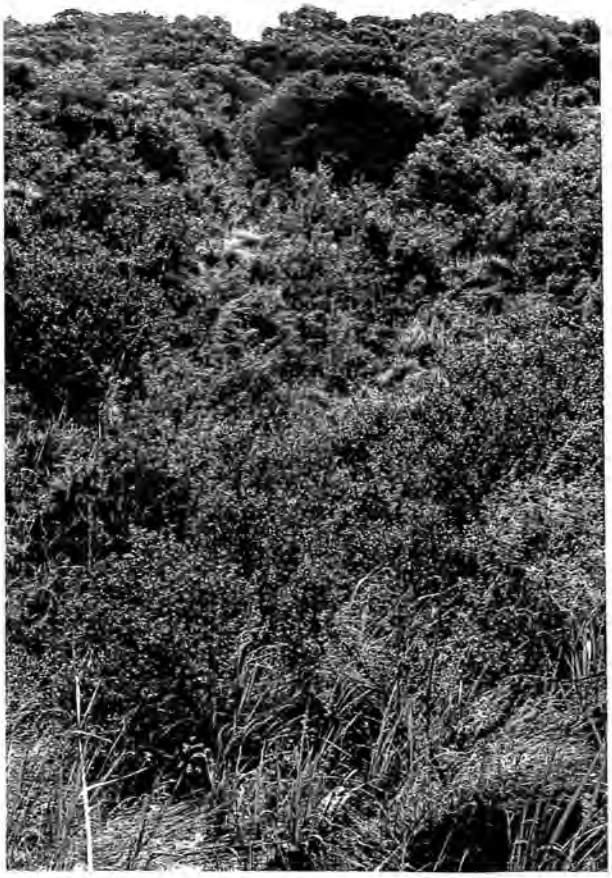


Plate 3.4 View of one of the transect lines looking landward, with the Closed Dune Scrub in the foreground, grading into Bushclump and Forest Margin in the background, showing an increase in woody shrubs and the presence of two strata. The dominant shrub in the foreground is *Eugenia capensis*, and the field layer is dominated by *Imperata cylindrica*, both typical of the Closed Dune Scrub community.

Forest Margin Community

These relevés are found on dune 7 and the seaward slope of dune 8 (Fig. 3.3), and age is estimated to be between 80 and 120 years (Table 3.2; Fig.3.2). Pioneer plants of the first three species groups are now completely absent, and species from the Forest Margin and Forest groups predominate (Table 3.3). Differential species are the trees, *Canthium obovatum* and *Sideroxylon inerme*. This community has a closed woodland physiognomy, with three strata (Plate 3.5). The field layer is dominated by *Microsorium scolopendrium* but the forest grass, *Oplisminus hirtillus* is also common. The sub-canopy layer (0.8 - 3m) is dominated by *Allophylus natalensis* and *Maytenus procumbens*, and the canopy layer (3 - 6m) by the differential species of trees. The relative importance of life forms has changed, with shrubs, ferns and trees being most common (Fig. 3.4).

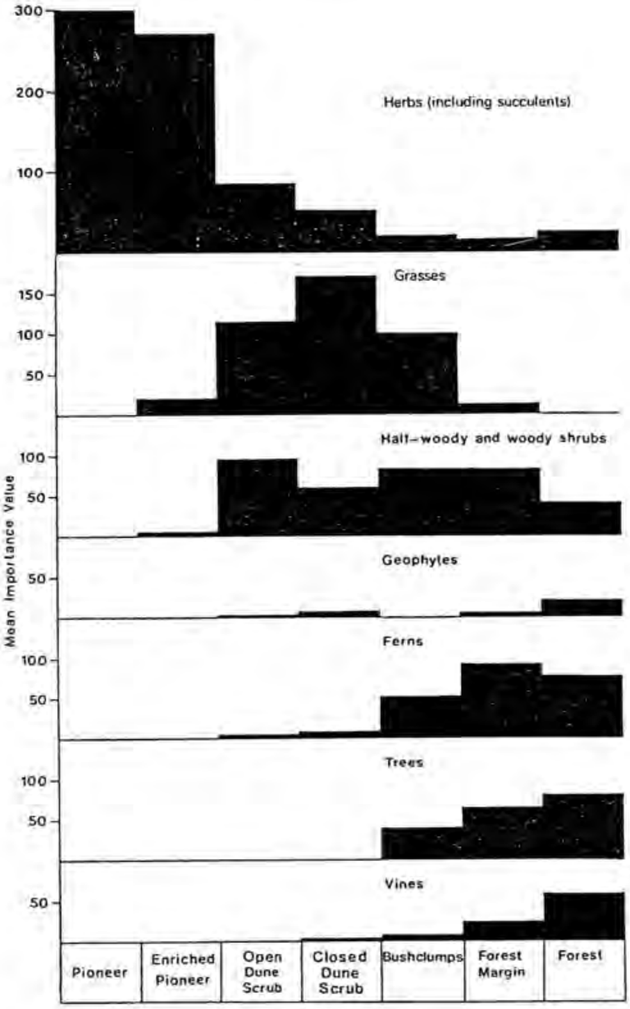


Figure 3.4 Histogram showing the relative importance value of the dominant life forms in the eight plant communities.

Forest Community

Relevés 23, 33 and 34 were sampled on dune eight, which is older than 120 years, and represent the Forest community (Figs. 3.2 & 3.3; Table 3.3). Differential species include *Mimusops caffra, Peddia africana* and *Oplisminus hirtillus*. Only species from the woody communities were recorded in the Forest, species from pioneer and herbaceous communities now being completely absent. The physiognomy differs from the previous community due to the presence of a true canopy (Plate 3.6). The field layer is taller (0 - 2m) and denser but still dominated by *Microsorium scolopendrium*. However, herbs, geophytes and grasses such as *Scadoxus puniceus, Crocosmia aurea* and *O. hirtillus* become more abundant. The sub-canopy layer (2 - 6m) is poorly defined and dominated by *P. africana* and *Kraussia floribunda*, but species such as *Monanthotaxis caffra* and *Carissa bispinosa* can also be fairly abundant. The tree canopy ranges in height from 5 to 20m and is dominated by *M. caffra, Sideroxylon inerme* and *Allophylus natalensis*. Trees are the dominant life form, and values of percentage cover, and species richness (Table 3.4) are greatest for this community.

Plate 3.5 The Forest Margin community has a closed woodland physiognomy. The dominant field layer is the fern, ***Microsorium scolopendrium***, and woody species include ***Maytenus procumbens*** and ***Canthium obovatum***.

Plate 3.6 The Forest community has a true canopy, and the field layer is taller. Note the increased density of all species.

With increasing distance from the sea the forest becomes older and more complex in structure and composition. Here canopy trees include *Dovyalis longispina* and *Scolopia zeyheri* and the shrub layer becomes less defined with scattered individuals of *Peddia africana* and *Carissa bispinosa* (Moll 1969). The field layer becomes dominated by the densely growing herb, *Isoglossa woodii* (Weisser & Backer 1983). The transects were not continued into the older forests in this study as the objective was to examine early succession from the pioneer to forest communities, not changes in forest types, which are much slower successional changes.

FLORISTIC AND VEGETATIONAL CHANGES ALONG THE SUCCESSIONAL GRADIENT

Scatter diagrams produced by the ordination of the data using DECORANA are presented in Figures 3.5 & 3.6. Species and relevé groups are based on the TWINSPAN classification (Table 3.3). The analysis showed that axes 1 & 2 (eigenvalues of 0.8868 & 0.2078) expressed the desired information better than 3 & 4 (eigenvalues of 0.0889 & 0.0664).

Distribution of relevés on axis 1 corresponds to an increasing distance from the sea and therefore age of dunes and possibly community complexity. The Pioneer community on the left is young (ca. 5 years), whereas the Forest Margin and Forest communities are much older (over 120 years). The gradient on axis 2 is due to an increase in the differences between relevés within each community. For example, foredune relevés are almost identical to each other in terms of species composition and show little dispersion on axis 2, whereas within the more complex Forest Margin and Forest communities relevés are very different from each other and widely dispersed on this axis (Fig. 3.5).

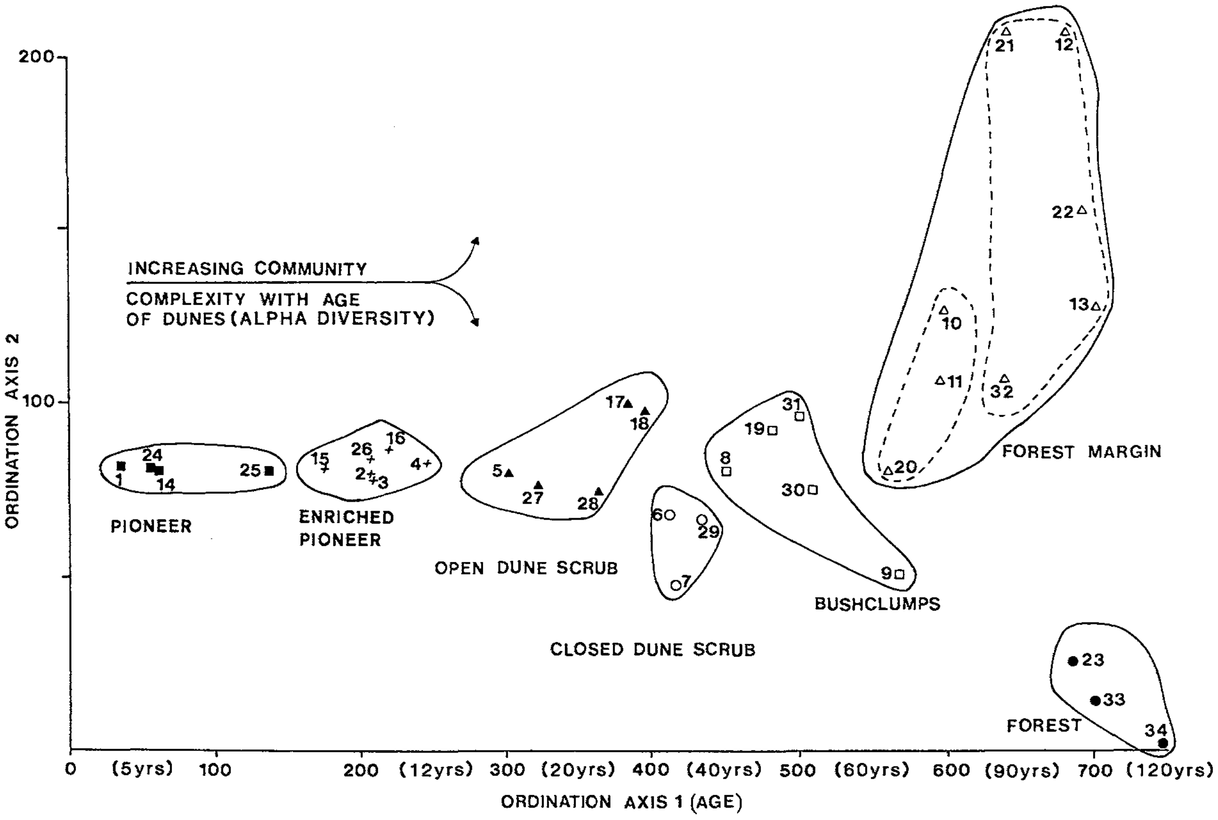


Figure 3.5 Relevé ordination of the data set, showing distribution of plant communities isolated by TWINSPAN. . ■ - Pioneer Community; + - Enriched Pioneer; . ▲ - Open Dune Scrub; ○ - Closed Dune Scrub; . □ - Bushclumps; . △ - Forest Margin; ● - Forest. Relevé numbers are as indicated in Table 3.1 (pg 93) and their position is shown on Figs. 3.2 (pg 93) and 3.3 (pg 98)

Species ordination revealed a similar trend, with axis 1 corresponding to species distribution from young to older dunes moving from left to right (Fig. 3.6). A total of six species groups were recognized (Table 3.3), which were not as distinct as the relevé groups. Species diagnostic of Pioneer and Enriched Pioneer communities were clustered together, whereas species of the Open Dune Scrub community formed a unique group. These two groups differ from the other four groups in that they do not contain many woody species. On axis 2 a greater differentiation within the more mature species groups is revealed, and this is related to an increase in variety of life forms present in each group. On the foredunes, herbs are dominant, grasses fairly common, shrubs almost absent and all other life forms absent. However, in the Forest Margin and Forest species groups, life forms are present in almost equal numbers (Fig. 3.4).

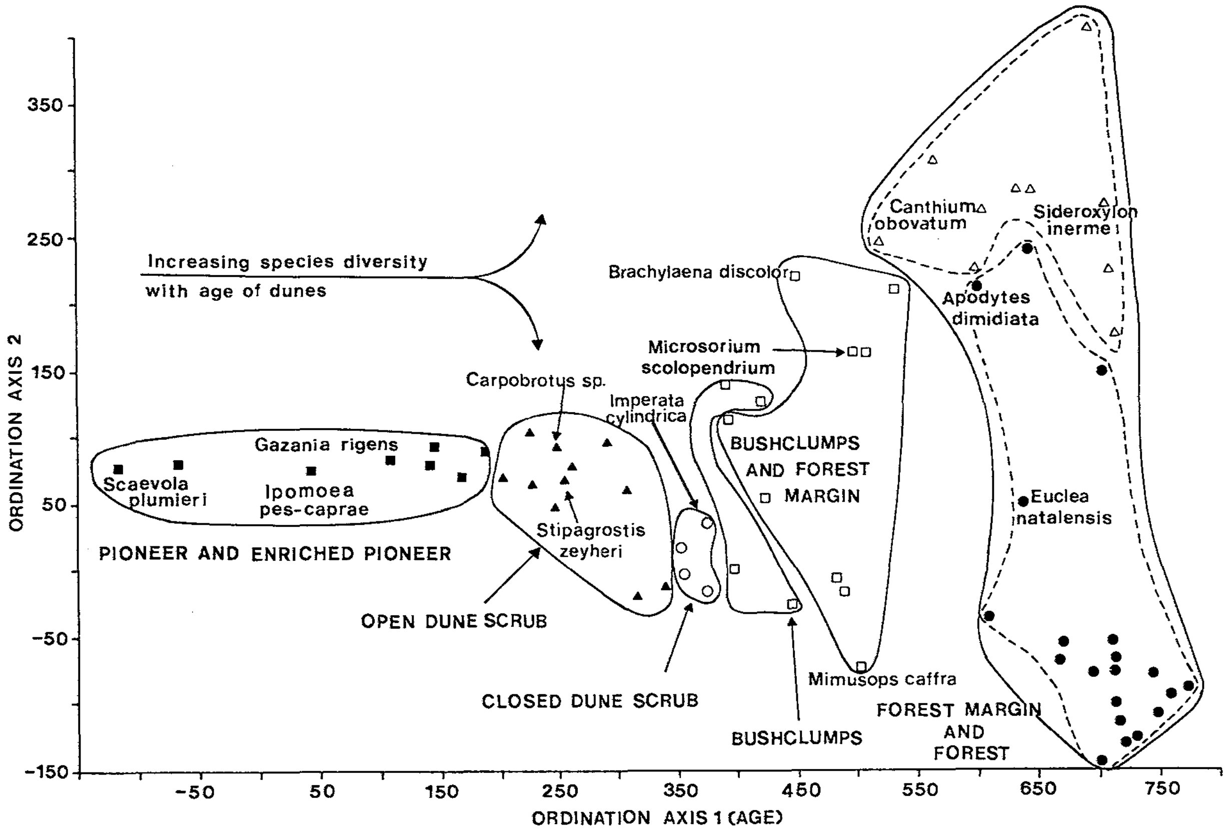


Figure 3.6 Species ordination of the data set, showing the distribution of species groups isolated by TWINSPAN, and position of key species on the scatter diagram. ■ - Pioneer and Enriched Pioneer; ▲ - Open Dune Scrub; o - Closed Dune Scrub; . □ - Bushclumps and Forest Margin; .● & △ - Forest Margin and Forest.

As succession progresses, species diversity increases, but sometimes reaches a maximum value prior to the climax community, whereafter it decreases (Margalef 1968). The Simpson Diversity Index (Ds) calculated from the density data (Table 3.4) shows an initial sharp increase from the Pioneer to the Enriched Pioneer community, whereafter it remains fairly constant except for decreases in the Closed Dune Scrub and Forest Margin communities (Fig. 3.7). As expected, Simpson's Dominance (ℓ), the inverse to diversity mirrors these results. This variability in the alpha diversity along the chronosequence supports Drury & Nisbet's (1973) statement that diversity is a result of microtopographic and other influences, and that it is not uniformly expressed in all parts of the community. However, the species richness does increase with increasing community complexity.

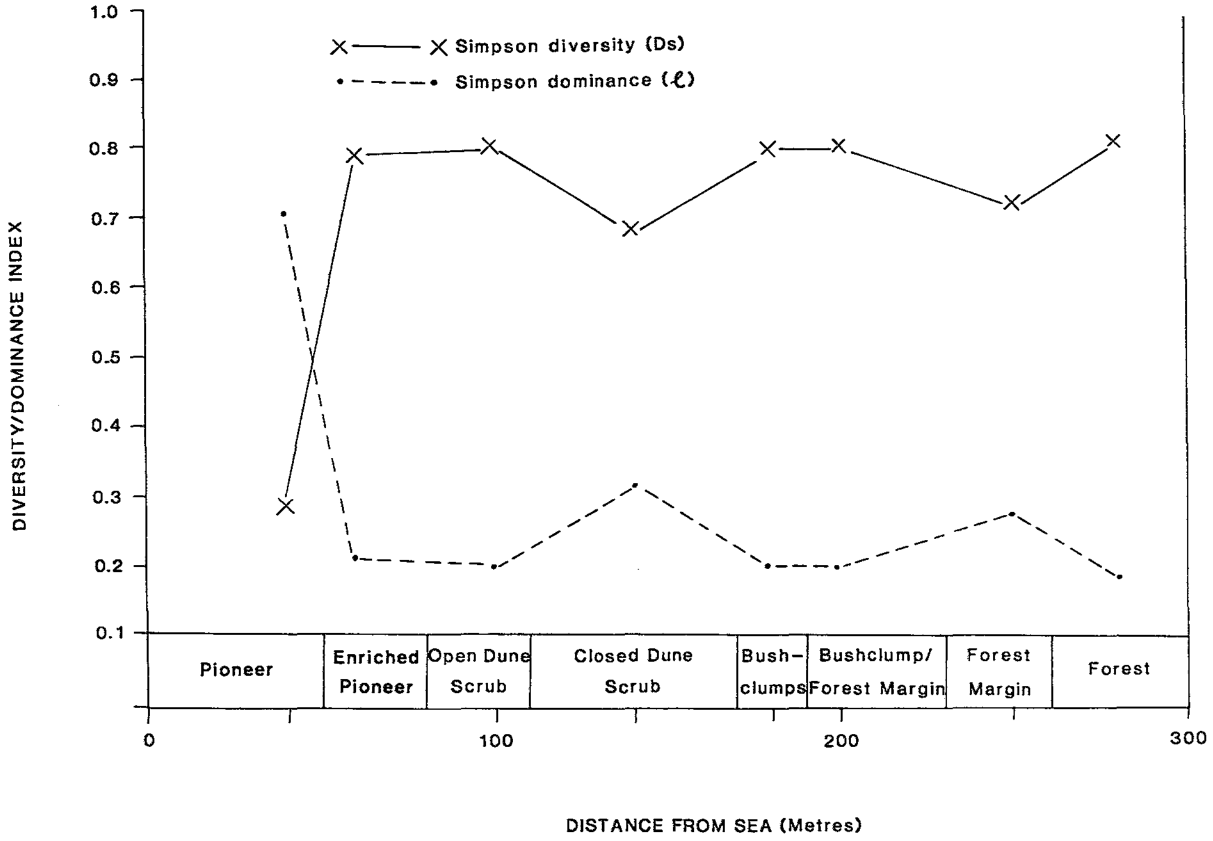


Figure 3.7 Changes in Simpson's diversity and dominance in communities with increasing distance from the sea.

One would expect Beta diversity to be highest and the co-efficient of community (CC) lowest, for communities furthest apart, since they do not have many shared species. This trend is clearly evident, with highest CC values always recorded for spatially linked communities (Table 3.5). The CC value decreases steadily as communities become more disjunct. The Pioneer community has no similarity with Forest Margin and Forest communities, since they have no shared species. Likewise, Open Dune Scrub has a lower CC value with Forest Margin and Forest than Closed Dune Scrub, and values for the latter are lower than for Bushclumps (Table 3.5). The number of shared species also decreases steadily from Pioneer to Forest communities for all pairwise comparisons, and this suggests that species turnover is very rapid along this 300 m successional gradient.

Table 3.5 Matrix showing the number of species shared by the eight communities (shaded), the species richness in each community (bold) and the Sorenson's Co-efficient of Community (CC).

COMMUNITY	Pioneer	Enriched Pioneer	Open Dune Scrub	Closed Dune Scrub	Bushclump	Bushclump Forest Margin	Forest Margin	Forest
Pioneer	**8**	0.695	0.516	0.139	0.093	0.045	0	0
Enriched Pioneer	8	**15**	0.666	0.526	0.320	0.235	0.122	0.076
Open Dune Scrub	7	13	**24**	0.765	0.508	0.333	0.103	0.065
Closed Dune Scrub	3	10	18	**23**	0.620	0.406	0.175	0.100
Bushclump	2	8	15	18	**35**	0.732	0.579	0.500
B/Forest Margin	1	6	10	12	26	**36**	0.685	0.547
Forest Margin	0	3	3	5	20	24	**34**	0.845
Forest	0	2	2	3	18	21	30	**37**

The changes in importance of 13 diagnostic species along the successional gradient (Fig. 3.8) shows how the species are grouped into discrete and recognizable associations as suggested by the multivariate analyses (Figs. 3.5 & 3.6). This is further supported when the importance values of most of these species are plotted along a continuum index following the methods of Cottam (1949). This community concept is contrary to the more commonly accepted continuum concept (Austin 1985). Although environmental gradients are abstract dimensions of ecological space, in this example the position along the environmental gradient can be equated with physical location in the dunefield.

Scaevola plumieri and *Tephrosia purpurea* are dominant on dunes closer than 100 metres from the sea in all three transects (Fig. 3.8), and disappear from the chronosequence at a low Continuum Index Value (CI=1700; Fig. 3.8a). This is reflected in the overall dominance of herbs in the Pioneer and Enriched Pioneer communities (Fig. 3.4). Dominant species of the Open and Closed Dune Scrub communities, namely *Stipagrostis zeyheri*, *Passerina rigida* and *Carpobrotus dimidiatus* are restricted to the central portions of the transects. They first appear at 60m from the sea, and dominate between 100 and 150m. No Open and Closed Dune Scrub species are found more than 260m from the sea (Fig. 3.8) and all disappear at a CI value of 2200 (Fig. 3.9a&b). Grasses and shrubs are therefore the dominant life forms in these communities (Fig. 3.4). *Imperata cylindrica* is restricted to a narrow zone along the successional gradient between 125 and 250m from the sea (Fig. 3.8) and it shows a distinctive peak along the continuum, between 1560 and 2350 (Fig. 3.9b). It is more common in transects one and three, where it dominates the Closed Dune Scrub communities and is the main contributor to the high importance value of grasses in this community (Fig. 3.4). The woody shrub *Eugenia capensis*, on the other hand, has a wider distribution (CI value = 700 to 2520; Fig. 3.9b) and first appears in the Open Dune Scrub, 100m from the sea. However, it never dominates but contributes to the fairly broad distribution of shrubs (Fig. 3.4).

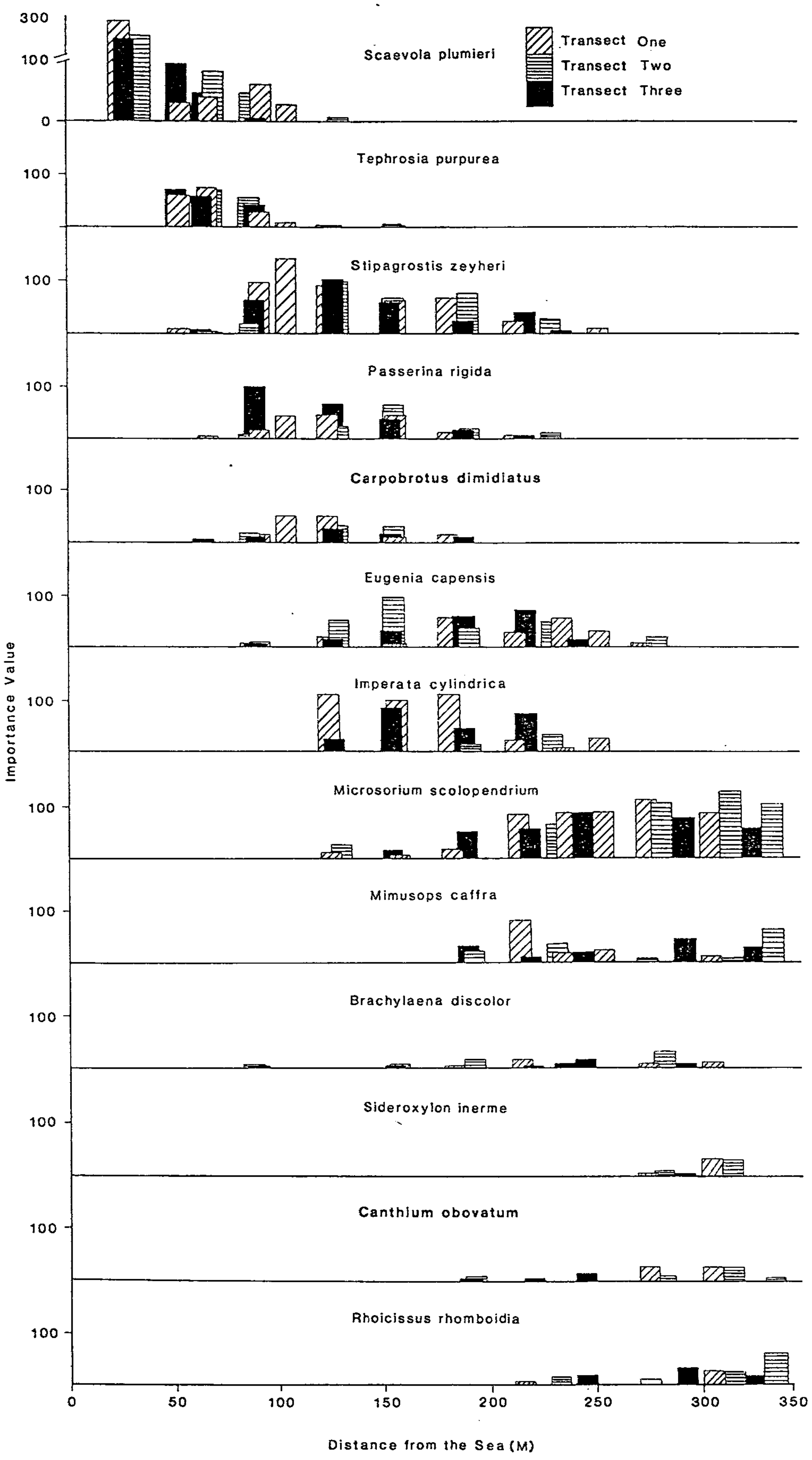


Figure 3.8 Histogram showing the relative importance values of 13 diagnostic species with increasing distance (age) from the sea for all three transects.

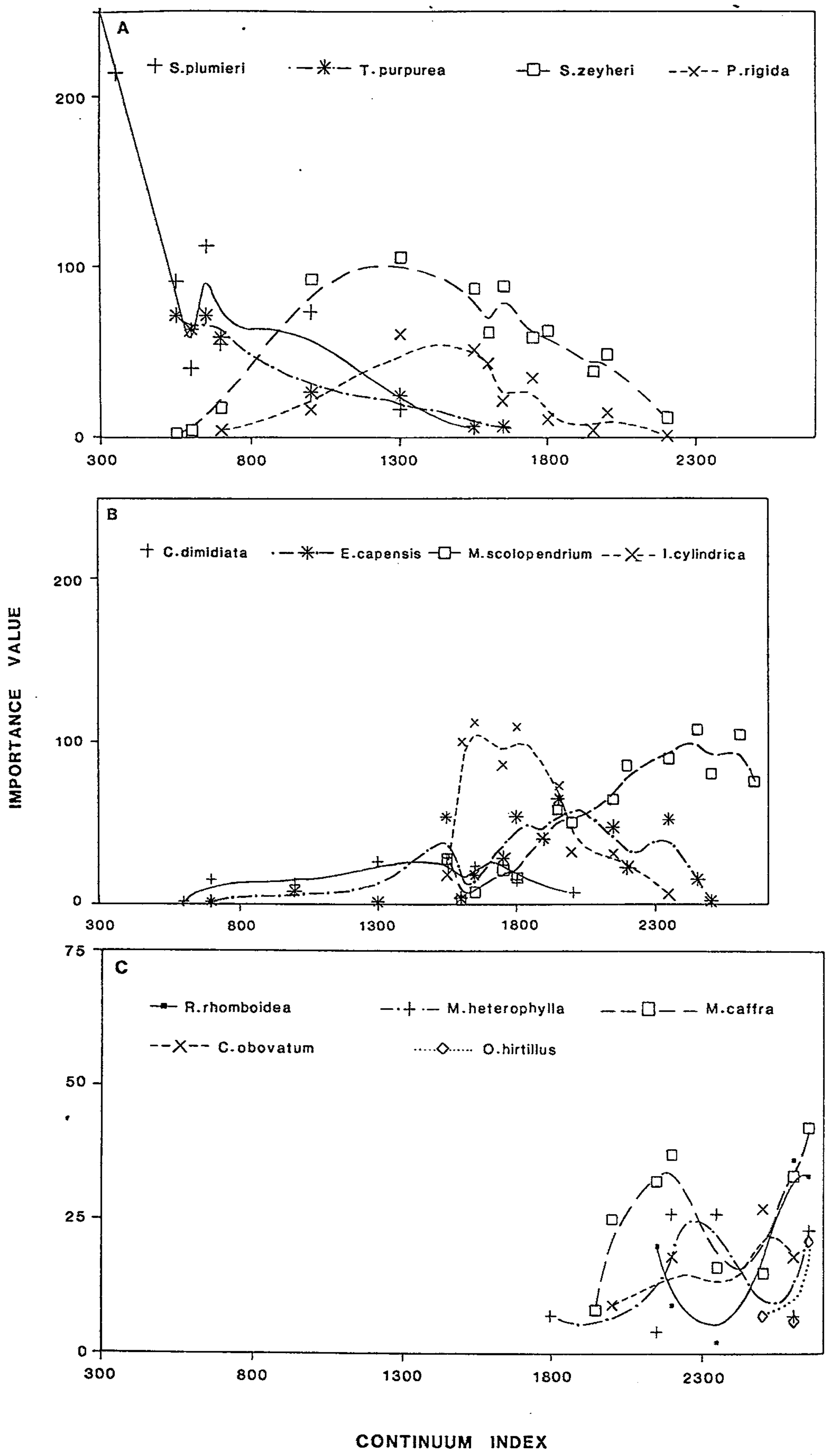
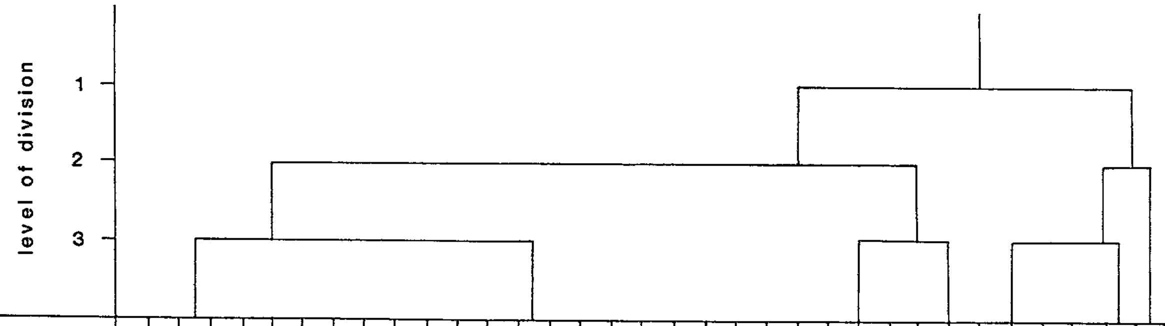


Figure 3.9 Importance value curves for thirteen diagnostic species in the dunefield, plotted along a Continuum Index ranging from 300 to 2700. A-Pioneer and early successional species. B-Secondary Dune Scrub and primary forest species. C-Secondary and climax forest species (note change in scale of importance value units).

The fern, *Microsorium scolopendrium*, is the dominant ground cover species under woody plants and first appears at a CI value of 1550 (Fig. 3.9b), whereafter it dominates. This trend is reflected as an increase in abundance from 200 m onward (Fig. 3.8) and the increase in ferns from the Bushclump community is clearly illustrated in Figure 3.4. Of the woody shrub species, *Brachylaena discolor* and *Eugenia capensis* are the first to appear. Like *E. capensis, B. discolor* never becomes dominant, but this hardy shrub is widespread along the South African coastline (Chapter 1), and is very suitable for dune stabilization (Chapter 8). It is of note that this species was not recorded in the oldest communities. *Mimusops caffra* is the first tree species to appear, and is prominent from 200 m inland. Typical forest trees such as *Sideroxylon inerme* have a more limited distribution, and first appear about 250 m from the sea. Although not recorded at 350 m, this species is prominent in the forest. Vines, such as *Rhoicissus rhomboidia* first appear in the Closed Dune Scrub, but are only common in the forest community (Figs. 3.4 & 3.8). Species which dominate the woody communities first appear at a CI value of 1800, and increase in importance along the rest of the chronosequence (Fig. 3.9c). Their distribution is far more distinct and restricted when compared to species in Figure 3.9b.

SOIL CLASSIFICATION

The TWINSPAN classification of relevés using the soil data resulted in seven groups at the third level of division (Fig. 3.10). The primary division is between soils from forest plant communities and soils from relevés of pioneer and non-forest communities, indicating the important change in forest soil formation. In the second division soils from pioneer relevés dominated by non-woody species are separated from soils from older relevés dominated by woody species. At level three the large group of relevés from pioneer communities with predominantly non-woody species split into two groups on the basis of their soil characteristics. In these young soils the samples cannot be accurately related to the pioneer or more mature dune communities. This indicates that soil development may be relatively unimportant, slow or difficult to detect in the early stages (first 50-75 years) of succession.



Relevé No.	1	24	26	27	31	2	3	4	5	7	8	14	15	16	17	18	19	20	25	28	29	30	9	11	21	32	6	10	22	23	33	34	12	13
Group	1					2																	3				4		5				6	7
Vegetation	Predominantly Non-Woody																						Bushclump, Forest Margin & Forest											

Figure 3.10 Dendrogram produced by TWINSPAN showing the classification of relevés based on their soil characteristics. Relevé numbers are as indicated in Table 3.1 (pg 93) and their position is shown on Figs. 3.2 (pg 93) and 3.3 (pg 98).

In group 1 (Fig. 3.10) the concentration of phosphate and the exchangeable bases (K, Na, Ca & Mg) is low, and the pH is relatively high (Table 3.6). In group 2 soil properties are very similar to group 1, with relatively high potassium and calcium values and a higher pH indicative of younger dune sands. Soils within the forest margin (Group 3) have a relatively low phosphate concentration and the pH is also lower. Concentrations of the other exchangeable bases are greater than in the previous two communities, as is the conductivity and organic matter (Table 3.6). The soils of the bushclump community (Group 4) differ from those of the forest margin in having a very high phosphate level and greater organic matter. The high phosphate level in soils of these two bushclump relevés is difficult to explain but must merely be a local variation in soil development. Soils sampled within the forest (Groups 5-7) have a slightly higher phosphate level than the other communities (except the bushclumps), and the pH has decreased as is characteristic of forest soils. Likewise, as expected, the high organic content of forest soils is associated with an increase in all the exchangeable bases and the conductivity. Groups 6 and 7 (relevés 12 & 13) are soil types separated from the other forest soils due to low sodium concentration, and very high organic matter content respectively (Table 3.6).

Table 3.6 Mean values (±s.e.) of the soil properties in the seven groups defined by TWINSPAN at the third level of division (Fig. 3.10).

Soil Property	1 Pioneer Community, predominantly non-woody	2 Pioneer community predominantly non-woody	3 Forest Margin	4 Bushclump	5 Forest	6 Forest	7 Forest
Relevés	1;24;26;27;31	2-5;7;8;14-20;25;28-30	9;11;21;32	6;10	22;23;33;34	12	13
pH	8.23 ± 0.09	8.45 ± 0.06	7.24 ± 0.22	7.75 ± 0.24	7.30 ± 0.24	7.71	7.38
Conductivity (uS/cm)	67.4 ± 4.4	73.9 ± 9.41	115.4 ± 6.5	121.1 ± 3.39	204.5 ± 12.0	201.5	225.7
% Organic matter	0.46 ± 0.04	0.51 ± 0.09	1.37 ± 0.25	1.93 ± 1.03	2.73 ± 0.32	2.66	6.0
Phosphate (mg/kg)	3.81 ± 0.35	3.44 ± 0.64	3.45 ± 0.67	9.0 ± 1.41	4.15 ± 0.32	4.1	5.1
Potassium (ppm)	171.76 ± 11.83	701.0 ± 104.73	310 ± 27.0	294 ± 8.99	395 ± 15.0	450	670
Sodium (ppm)	275 ± 12.5	318 ± 76.22	321.24 ± 30.3	237.5 ± 37.5	601.2 ± 6.57	325	630
Calcium (ppm)	5499 ± 604	9645 ± 636	5715 ± 776.7	5222 ± 647	12537 ± 1254	12970	10120
Magnesium (ppm)	375.9 ± 22.8	574 ± 49.81	805 ± 42.2	862.5 ± 187.5	1910 ± 127.7	1080	1990

EDAPHIC CHANGES ALONG THE SUCCESSIONAL GRADIENT

The DECORANA ordination of relevés using their soil properties (Fig. 3.11) shows groups based on the TWINSPAN classification (Fig. 3.10). Axis 1 corresponds to an increasing distance from the sea and therefore represents soil development, since this axis reflects age of the dunes and community complexity. Axis 2 is more difficult to interpret. Relevés within groups one and two mainly belong to soils of the pioneer plant communities with non-woody components. Within group 3, relevé 9 is soil from a bushclump, and within Group 4, relevé 6 is soil from the Closed Dune Scrub community. However, the three groups which represent forest soil types (5, 6 and 7) are very distinct.

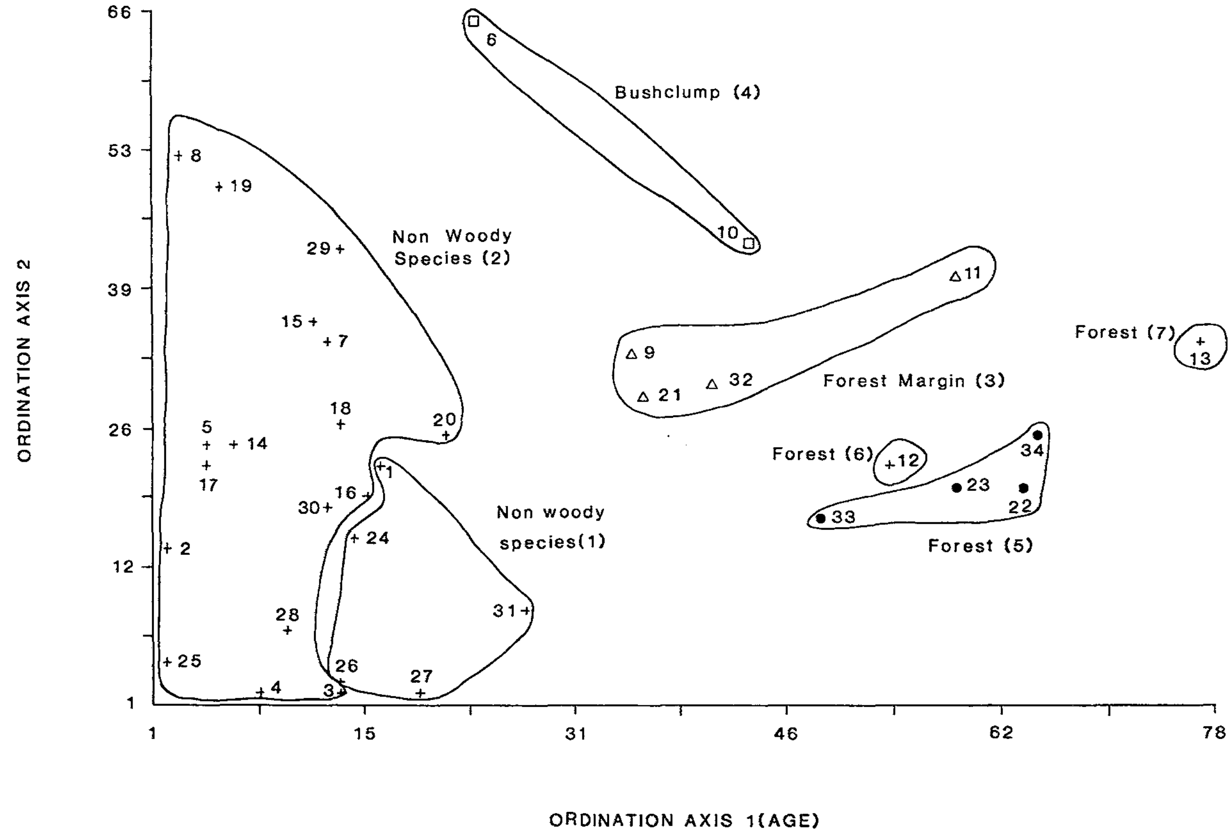


Figure 3.11 Relevé ordination of the soil data, showing the distribution of groups based on soil properties. Groups were isolated by TWINSPAN (Fig. 3.10). The number in parentheses refers to communities shown in Table 3.6.

Figure 3.11 suggested a relationship between the soil properties and the increase in community complexity, and to demonstrate this more clearly, isolines for soil pH, percentage organic matter and exchangeable bases (Ca, Mg, K, Na) were plotted on the scatter diagram of the relevé ordination (Fig. 3.12a-c respectively). The soil pH shows a decrease from the Pioneer community to the Forest Margin. From the Forest Margin to Forest, the pH decreases further from 7.2 to 6.8 (Fig. 3.12a). Conversely, percentage organic matter of the soil shows an increase from foredunes to forest. Soils of most of the foredune communities have an organic content of less than 0.5%. Values of between 0.5 and 1.0% occur in soils of Closed Dune Scrub and Bushclumps, whereas the woody communities (Forest Margin & Forest) have soils with organic matter between 1.0 and 3.0%. Only relevés 22 and 13 have values exceeding 3% (Fig. 3.12b).

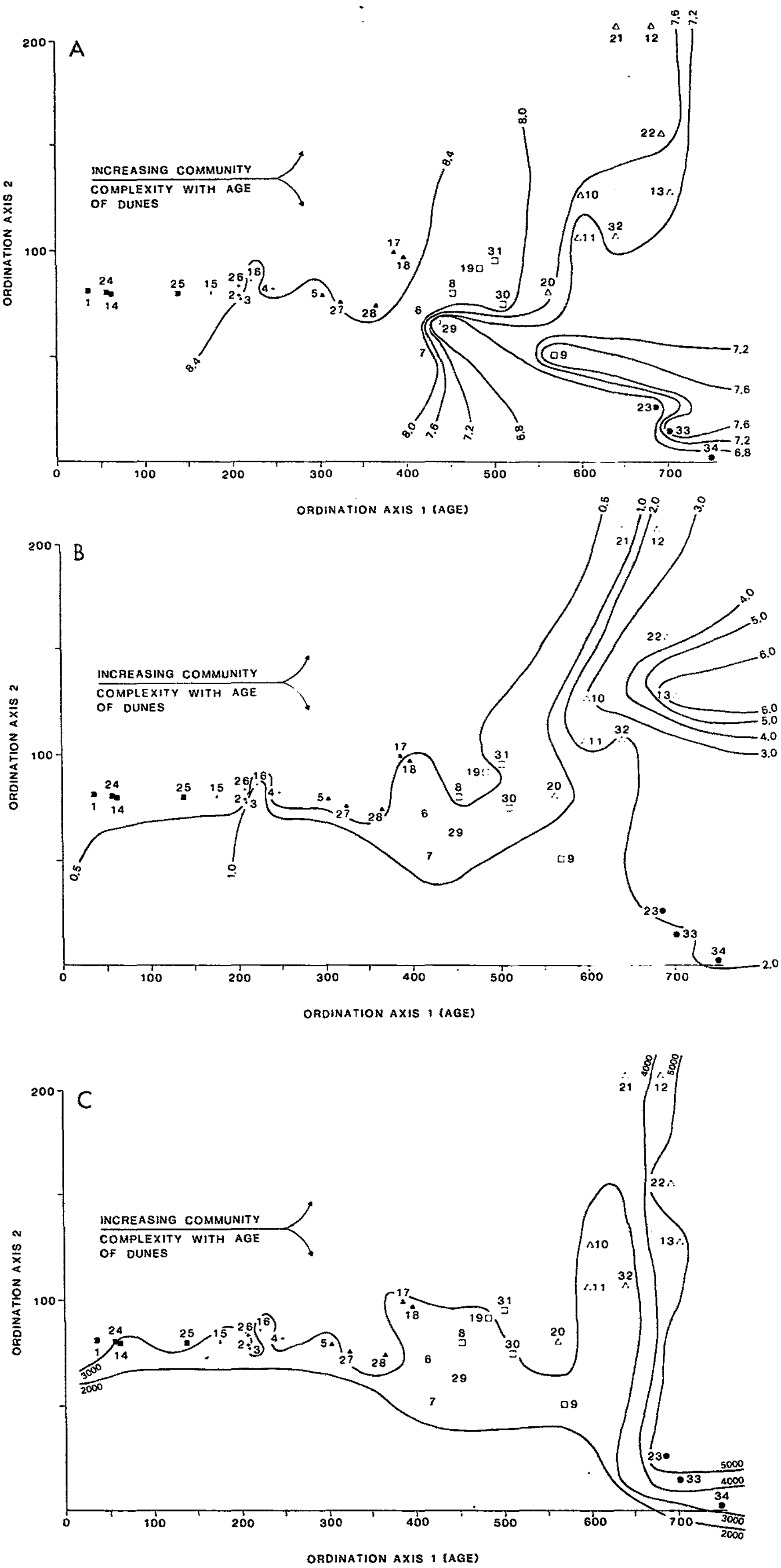


Figure 3.12 Isolines for a - pH; b - Percentage organic matter, and c - Exchangeable bases (Ca, Mg, K & Na) plotted on the relevé ordination diagram (Fig. 3.5).

The mean value of exchangeable bases was calculated for each relevé and isolines ranging from 2000 to 5000 ppm plotted (Fig. 3.12c). The gradient of increasing values along axis 1 is not as clear as for the other soil factors. Values for soils of the Pioneer and intermediate groups ranged between 2000 and 4000 ppm and only a few Forest Margin and Forest relevés had values greater than 4000 ppm. However, the general trend of increasing soil complexity along axis 1 (i.e with age) is shown, indicating changes along a successional gradient.

DISCUSSION

Very few detailed quantitative studies have been made of even short-term changes in vegetation, and observations of genuine primary succession which show a complete sequence of stages are very rare (Drury & Nisbet 1973; Colinvaux 1986). More recently, numerical techniques have been applied to studies of succession (Williams *et al.* 1969; Morrison & Yarranton 1973; Austin 1977; Persson 1980; Regnell 1980; Kirkpatrick & Hassal 1981; Sacheti & Scott 1986), and the suitability of these techniques, particularly multivariate analyses such as ordination, have been found to be most useful for studies on succession (see Austin 1977; van der Maarel & Werger 1978). Canonical correlation analysis was not used as it has been found to be ineffective due to its linearity requirements being too stringent to accommodate most ecological data (Gauch & Wentworth in Gauch 1982).

The importance of the Mtunzini dunefield for studies on vegetation dynamics and community change have been discussed by Weisser *et al.* (in prep.), Moll (1969) and van Daarlen *et al.* (1986). Despite this, few quantitative studies have been undertaken in sufficient detail to accurately describe the succession taking place. Although mostly qualitative, all the above studies noted that the area supports a classical example of primary succession. It provides one of the finest opportunities to study the relative importance of soil development, changes in nutrient supply, exposure to environmental stress, seed immigration and biotic interaction in controlling the rate and direction of vegetation development (see for example, van Daarlen *et al.* 1986). This study represents the first detailed quantitative investigation relating changes in vegetation and floristics to changes in soil properties. Furthermore, the various dune ridges have been dated from aerial photographs and published data, making it possible to link spatial changes with temporal ones.

PLANT COMMUNITIES RELATED TO THE CHRONOSEQUENCE

The Mtunzini area was most suitable for a comparative study on plant succession, since the age of the dunes could be determined and it appeared that these communities were related to a chronosequence. Similar results were found by Olson (1958) and Morrison & Yarranton (1973), but in both cases dunes were much older (thousands of years). The rate of succession at Mtunzini is rapid due to the high rainfall (Fig. 3.1) and rapid accretion of sand along this coastline.

The application of TWINSPAN to the 34 relevés sampled in the dunefield produced eight distinct plant communities (Table 3.3). Distinct changes in both species composition and physiognomy of the communities have been demonstrated. The youngest community, dominated by *Scaevola plumieri*, was structurally and floristically simple. With increasing distance from the edge of the prograding shoreline, many changes associated with succession (Odum 1969) were noted. Species diversity increased (Table 3.4), spatial heterogeneity and plant size increased and development of strata was noted. Generally the communities became more complex, and an increase in type and size of life forms (Fig. 3.4) and species richness (Table 3.4) was recorded.

The increase in species diversity during succession noted here was more rapid in the initial five years (Fig. 3.7). This is similar to the observations made at Kleinemonde (see Fig. 2.7, pg 81), where diversity did not increase significantly after four years. An increase in diversity has also been observed by Morrison & Yarranton (1973) at Lake Huron in Canada and by Mun & Kim (1985) in Korea. Morrison & Yarranton related the increase in species richness to the immigration of new species. They attributed low diversity in the early stages of the succession to the variable or even unstable environment, which also explains the initially low diversity recorded here (Table 3.4; Fig. 3.7). A relationship between diversity and structural type has been shown to exist in dune grassland (van der Maarel 1978) and it is possible that a similar relationship exists at Mtunzini.

In a similar study on the Oregon coast, Kumler (1969) isolated nine communities which ranged from pioneer species to near climax dune forest on a parabolic dune. He noted that many of the earlier shrubs persisted as part of the understory in the tree communities, and concluded that the communities were related to a chronosequence. A multiple pathway succession with three principle trajectories of succession from pioneer to woodland vegetation was described by van Dorp *et al.* (1985) in the Netherlands. A general feature of this succession was the occurrence of a number of triangular relations between the various pathways of succession. Multiple pathways of community change were not observed at Mtunzini, but they cannot be excluded since this study is spatial, whereas that of van Dorp *et al.* was temporal over a 10-15 year period.

The succession at Mtunzini is probably along a single pathway, at least in the early stages when pioneer communities are very similar, as indicated by their relative distribution along the median of axis 2 of Figure 3.5. The position of relevés from Forest Margin and Forest groups on the outer edges of axis 2 suggests that multiple pathways may occur at this stage. In this regard the successional pathway at Mtunzini is similar to that reported by Cambell *et al.* (1988) at Inhaca Island, Mozambique. Detrended Correspondence Analysis of the vegetation data supported the hypothesis that this increase in community complexity is related to an increase in the age of dunes, and species with similar environmental requirements appeared to be grouped together along the gradient (Figs. 3.5 & 3.6). Despite being sampled randomly along transects, groups of relevés represent distinct communities, and therefore species appeared to be grouped along the chronosequence (Fig. 3.9), rather than evenly along a continuum. In all but one instance, it was possible to identify distinct communities in the field, based on visual observations of species composition.

Changes in individual species are shown along the chronosequence (Fig. 3.8 & 3.9), but in order to understand species change we need to know if species associations replace each other as groups; whether later communities replace early stages; or if many of the final and climax species are present on the site from the start. Also, do the species of the early stages facilitate or inhibit the establishment of later succession species? Finally, do successions always go in one direction? (Drury & Nisbet 1973). These results show that the early successional stage was made up almost exclusively of species of lower stature and herbaceous life forms (Figs. 3.4 & 3.8) and that none of the "climax" species were present at the start (Table 3.3). The results also suggest that species associations replace each other as groups, but there is an overlap between groups (Fig. 3.9). Also, the earlier species facilitate the establishment of species of later stages by stabilizing the substratum, trapping moving sand and salt spray, and increasing the organic content of the soil (Table 3.6). No evidence of some species inhibiting others, as shown by Olson (1958) was found, but knowledge of the ecophysiology and demographic responses of these species is limited, and it is not possible to draw sound conclusions in this regard. However, results seem to indicate that the succession is unidirectional since no evidence of retrogression was found, but more data needs to be collected from the climax forest communities to substantiate this, as gap-phase replacement is likely to occur.

EDAPHIC CHANGES RELATED TO THE CHRONOSEQUENCE

The edaphic factors also showed changes along the chronosequence which are usually associated with successional changes in vegetation. Total organic matter increased with community complexity (Fig. 3.12b), and pH decreased (Fig. 3.12a). An increase in the exchangeable bases was also noted, and the substratum became more stable with increasing distance from the sea. Changes in the soil properties noted here can be related to changes (increases) in community complexity (Tables 3.3 & 3.4) and also represent an increase in total biomass of the more complex communities.

Salisbury (1925) was one of the first to show that the organic content of dune soils increased along progressive dune ridges, and that these changes could be correlated with changes in the vegetation. He also noted a progressive leaching of carbonates with increasing age, and a change in pH from alkaline to acid. Mun & Kim (1985) showed that pH decreased and organic content increased on sand bars of increasing age, due to an increase in litter decomposition. Results presented here show a similar trend (Table 3.6; Figs. 3.11 & 3.12). The only other attempt to correlate edaphic changes with dune community succession in South Africa were those of Lubke (1983) and Lubke & Avis (1982a) who noted similar results at Kleinemonde in the Eastern Cape. The above approach was therefore extended at Kleinemonde (see Chapter 4).

Crocker & Major (1955) showed that the establishment of vegetation on bare deglaciated areas initiated gradients in soil properties such as organic matter, pH, bulk density and colour. The pH decreased rapidly with the establishment of vegetation, and then more slowly later. Organic carbon increased along the chronosequence, as did the above surface residue. However, calcium carbonate decreased due to leaching. Olson (1958) showed similar trends at Lake Michigan, and also noted an initial rapid increase in soil nitrogen, moisture equivalence, cation exchange capacity and exchange acidity. This he related to an increase in the organic matter. He also stated that the exchangeable bases should increase for a limited time (1000 years), and then begin to decline after passing a maximum level. Since the oldest community in this study was about 200 years old, it is most likely that the exchangeable bases are still increasing in the dune forests at Mtunzini (Fig. 3.12c).

Kachi & Hirose (1979) and Smith *et al.* (1985) reported increases in organic carbon and a decrease in pH with age of dunes. Smith *et al.* (1985) reported that the most seaward soils had very low total exchangeable bases and related this to their low cation exchange capacity (CEC). The older soils had higher levels of exchangeable bases due to their higher CEC, which was related to higher amounts of organic matter. They also showed that available phosphate remained relatively constant in topsoils, a trend also noted here (Table 3.6).

Results show that as plant succession proceeds, soil development occurs concomitantly, and it was possible to quantitatively correlate, using multivariate techniques, soil development with plant community change (Figs. 3.10 to 3.12). These results support the conclusions drawn by other researchers that soil organic matter increases along the chronosequence, and that furthermore this is the single most important change in the edaphic environment. Other changes, such as an increase in acidity and conductivity are direct consequences of the increase in organic matter. A marked decrease (50%) with increasing depth of all soil properties measured was noted, suggesting that the soils are still very young.

James & Wharfe (1989) found that pH decreased significantly, and organic matter, potassium and magnesium all increased significantly with increasing distance from the sea, which was also used as a surrogate for age. These trends were only significant on the surface (0-1 cm), showing limited depth of soil development.

The accreting shoreline of the Yucatan peninsula in south-east Mexico described by Espejel (1986) appears to be very similar to the situation at Mtunzini. Five vegetation units were isolated, and these followed the topography, with increases in diversity and complexity as one moved inland. An intermediate zone covered by a mixture of pioneer herbs and thicket shrubs was noted, and Espejel (1986) concluded that this vegetation zonation was related to a soil gradient.

QUANTITATIVE STUDIES IN SUPPORT OF CLEMENTSIAN SUCCESSION

The distinct separation of relevés into communities (Table 3.3) along a gradient of increasing age (Figs. 3.5 & 3.6) suggests that these communities do not integrade continuously along the environmental gradients (Whittaker 1975). They appear to form distinct, clearly separated zones more in line with the "community-unit concept" (Clements 1916). The Importance Value curves for diagnostic species (Fig. 3.9) fit rather well with the hypothetical graphical presentations of Whittaker (1975) and Austin (Fig. 1, 1985) for the "community-unit concept". However, this does not prove that this concept applies to the vegetation sequence at Mtunzini, since one cannot prove the one hypothesis by rejecting the other (Shipley & Keddy 1987). The situation is even more confusing when one considers that at the scale of individual species turnover (Fig. 3.8), there is overlap with no sharp boundries between species, suggesting that species turnover follows the individualistic hypothesis of Gleason (1926). However, Shipley & Keddy (1987) have shown that the individualistic concept is unfalsifiable at the level of pattern analysis, allowing one to favour the "community-unit concept". The ordination diagrams (Figs. 3.5; 3.6 & 3.11) suggest an organisational structure of the communities (*vide* Clements 1916), but the figures showing changes at species level (Figs. 3.8 & 3.9) suggest that the communities integrate continuously along this gradient (Whittaker 1975) in an individualistic manner (Gleason 1926). However, ordination methods cannot provide unequivocal evidence for the continuum concept (Austin 1985), but the low level of similarity between communities less than 100 m apart (Table 3.5) suggests that species only integrade over short distances. Possibly, as stated by Shipley & Keddy (1987), one needs to deny this dichotomy and to consider multiple working hypotheses of community structure.

Drury & Nisbet (1973) noted that a common feature of contemporary theories (before 1973) was that they attributed succession to properties of the community. They stated that the Odum-Whittaker hypothesis was unacceptable as a generalization and that succession was the result of certain adaptive strategies being mutually exclusive. For example, species whose seeds travel far and grow rapidly in harsh conditions cannot also grow large and live long. These problems and shortfalls in successional theory led to the Connell & Slatyer (1977) models, and these data support the Facilitation Model. There are also a number of other studies which support these models, and a few of these are briefly reviewed here.

Olson (1958) presented evidence for an autogenic succession on the Lake Michigan sand dunes, and a careful review of his paper shows that two Connell & Slatyer models (mechanisms *vide* Picket *et al.* 1987) play a role in this succession. The foredunes are colonized by pioneer species such as *Ammophila arenaria* which eventually leads to various types of *Quercus velutina* communities (Facilitation Model). There is usually an intervening stage of *Pinus* spp. (see Fig. 12, Olson 1958). The *Populus deltoides* and *Pinus* spp. cast shade too dense for their own seedlings. However, shade-adapted oak seedlings are able to grow underneath them, and this leads to a self-perpetuating climax community of *Q. velutina*. This community does not develop further as the old dunes become acidic due to leaching for all but the acid-tolerant oaks (Tolerance Model or active tolerance of Picket *et al.* 1987). Initially succession is therefore autogenic, and becomes primarily allogenic later.

Succession at Grand Bend, Lake Huron, was divided into three periods based on changes in the heterogeneity of the vegetation (Morrison & Yarranton 1973). The Colonizing Stage was dominated by pioneer grass species established after surface stabilization and other autogenic processes, and heterogeneity increased. In the Transitional Period environmental heterogeneity was established and lead to increased vegetational heterogeneity. This occurred when persistent species invaded and grew at the expense of the colonizing species. During the Persistent Stage these species coalesced to form a more homogeneous community. The most conspicuous feature of this mechanism was the change from the colonizing to the persistent stage. Changes in environmental conditions brought about by *Juniperus virginiana* were crucial to the establishment of persistent species. It behaved like a nucleus for the subsequent growth of patches of persistent species. The term "nucleation" was used to describe this process of facilitation (Yarranton & Morrison 1975). However, once persistent species such as oak dominated their density increased to the extent that the junipers could not survive. At Mtunzini, *Mimusops caffra* acts in the same way as junipers on Lake Huron shores. They are often in the centre of bushclumps which later coalese to form the forest margin and eventually continuous forest (Plate 3.3). These trees do, however, become dominant species in the young forest and are not rapidly replaced as the junipers are.

In a study of coastal sand dunes in Australia, Sacheti & Scott (1986) classified three distinct communities and related the distribution of individual species to organic carbon content. The initial stage of vegetation development was the colonization of bare sand by pioneers such as *Spinifex hirsutus*. Through autogenic processes (Facilitation) shrubs invaded and became dominant at the expense of the herbs and grasses. It was concluded that the pattern corresponded to Connell & Slatyer's (1977) Facilitation Model.

The most recent evidence supporting the Facilitation Model is the succession of a subtropical savanna to woodland described by Archer *et al.* (1988), who suggested that *Prosopis grandulosa* invaded grasslands and served as a recruitment focus for bird-disseminated seeds of other woody species. The woody plant assemblages were organized around the *Prosopis* nucleus, which died in about 25% of the clusters. However, clusters remained healthy and were therefore a persistent feature of the landscape. This is similar to the nucleation process described by Yarranton & Morrison (1975) and can be related to the above observations on *Mimusops caffra*.

There are a number of other studies in the literature which support the Clementsian concept of succession, and its various refinements by Egler (1954), Odum (1969), Horn (1976), and Connell & Slatyer (1977). Olmstead (1937) described a process of facilitation in the succession on Connecticut sand dunes. Williams *et al.* (1969) recognized the importance of autogenic effects in rain forests, and concluded that the process of succession did not support the individualistic hypothesis of Gleason (1926).

Other studies include those of Crocker & Major (1955); Hils & Vankat (1982); Harris *et al.* (1984) and Smith *et al.* (1985). However, there is also support for the individualistic approach to succession, see for example Greig-Smith (1952); Glenn-Lewin (1980); van der Valk (1981) and Belsky & Amundson (1986).

Recently Austin (1985) noted the need for a synthesis of niche and continuum theories and mechanistic models of how plant species behave along environmental gradients. The recent reviews by Connell & Slatyer (1977); Picket *et al.* (1987); Noy-Meir & van der Maarel (1987); Walker & Chapin (1987), and Shipley & Keddy (1987) have addressed these problems. The importance of concepts such as multi-species pattern analysis (Noy-Meir & van der Maarel 1987), multiple working hypotheses of community structure (Shipley & Keddy 1987) and a mechanistic theory approach to contemporary plant ecology (Picket *et al.* 1987) is recognised, but data from this study is insufficient to elucidate the demographic and ecophysiological causes of turnover, and at this stage we know too little about the population biology of these species to apply any of these approaches to this study.

CONCLUSIONS

The data presented here strongly suggest that succession at Mtunzini is predictable, linear, unidirectional and follows a single pathway initially which may become multiple in later stages. The Facilitation Model of Connell & Slatyer (1977) is the main mechanism acting on this sere, but the fact that other mechanisms were not detected does not mean that they do not exist. Application of Major's (1951) functional, factorial approach to the study area led Weisser *et al.* (in prep.) to conclude that the Mtunzini area can be considered an example of primary dune succession. It is felt that the data presented here lends support to the community-unit concept of vegetation change originally proposed by Clements (1916) and refined by various plant ecologists (Egler 1954; Connell & Slatyer 1977). However, it does not provide unequivocal evidence as more work is required on the mechanisms of change before one can generate a model of succession at Mtunzini (Picket *et al.* 1987) and conclude that it follows the Clementsian view of succession, since one cannot rely on negative evidence to support either of the two concepts (Shipley & Keddy 1987).

CHAPTER FOUR

SUCCESSION ON COASTAL DUNES AND DUNE SLACKS AT KLEINEMONDE. II : SUPPORTIVE EVIDENCE FOR THE CONCEPTUAL MODEL.

INTRODUCTION

We have seen that the Eastern Cape coastline is very diverse, with a wide variety of habitats stretching over an area which is transitional between winter and summer rainfall climates (Chapter 1). As a result the vegetation is very diverse (Lubke & Van Wijk 1988), but until recently very little work had been undertaken on the vegetation of this region, particularly studies relating to community dynamics such as those undertaken in Chapter One.

Early studies on the coastal vegetation were made by Dyer (1937) for the Bathurst district and Comins (1962) in the East London region. A more comprehensive study of coastal vegetation was undertaken by Cowling (1983; 1984) who presented a hierarchical syntaxonomic classification of the fynbos vegetation in the Humansdorp region. Tinley (1985) included a broad vegetation classification in a study of the South African coastline, and briefly discussed vegetation dynamics and succession. Burns (1986) undertook a synecological study of dune thicket vegetation from Kei Mouth to East London, and discussed the dynamics of this community. He also investigated the effects of environmental factors such as salt spray on the community, and monitored post-fire successional changes. The vegetation dynamics of the extensive dunefield along the Alexandria coast has been investigated by Young (1987), and McLachlan *et al.* (1987) discussed the energetics and vegetation succession of a dune slack in this region. The increased interest and research in this unique area of the coastline culminated in the publication of a comprehensive field guide of the Eastern Cape coast (Lubke *et al.* 1988b).

Since 1978 a number of more detailed studies have been made on the coastal vegetation in the Kleinemonde region. A survey of the vegetation in the study site was undertaken and a general account of the colonization and succession of the sand dunes, dune slacks and rocky outcrops was given by Lubke (1983), who concluded that the paucity of plants in this dune system is a result of sand movement, salt spray and the inconsistent rainfall. Colonization of dune slacks was investigated in greater detail, and Lubke & Avis (1982a&b) showed that soil moisture and salt spray were major factors affecting the colonization of dune slacks by *Scirpus nodosus*. Furthermore, sand movement and seedling burial were also found to be important controlling factors in dune succession (Avis & Lubke 1985). Annual surveys of a dune slack in this study area have been undertaken since 1981, and this information, combined with previous studies provided a good insight into plant succession on these dunefields (see Fig. 2.9, pg 86).

The initiation of succession may result from the colonization of foredunes with species such as *Scaevola plumieri* and *Sporobolus virginicus,* which create a more favourable environment that can eventually be invaded by shrubs such as *Passerina rigida* and finally tree species, such as *Sideroxylon inerme.* In Chapter Two it was concluded that the colonization of the dune slacks by sedges and rushes such as *Scirpus nodosus* and *Juncus kraussii* during wet periods was the more common pathway in the successional sequence. The greater soil moisture, reduced sand movement and salt spray and colonization by dune slack pioneers created a favourable microenvironment. This facilitated germination and establishment by other species following the autogenic pathway of succession first proposed by Clements (1916) and refined later by other authors (*vide* Egler 1954; Connell & Slatyer 1977). Dune Scrub species such as *Passerina rigida* and *Stoebe plumosa* invaded the slack, and under favourable moisture conditions it was proposed that Dune Thicket species such as *Maytenus procumbens* and *Brachylaena discolor* will become dominant. The controlling environment factors appear to be rainfall and soil moisture, but the strong winds in the area also reduce the growth of the vegetation due to the burial of seedlings and plants and damage from salt spray (Lubke & Avis 1982a&b; Avis & Lubke 1985). Thus, the successional sequence presented in Chapter Two (Fig. 2.9) will only occur under ideal environmental conditions.

The Kleinemonde site was selected to quantitatively investigate dune succession in the Eastern Cape so as to provide further evidence for the conceptual model presented in Chapter Two. It is the ideal study area as the plant communities and vegetation are typical of this region (Chapter 1, Plate 1.2); the area is located only 2km from the Great Fish Point Lighthouse weather station and various studies have been undertaken in the area over the past 10 years on dune succession, vegetation and autecology of *Scirpus nodosus.* The objective of this Chapter is to determine whether the isolated distinct plant communities present in this dunefield corresponded to the suggested successional sequence (Chapter 2), and if so, to determine which species were transitional and which were diagnostic in each stage. Secondly, it was hoped to provide evidence that the suggested sequence of community change was Clementsian and followed Facilitation Model (Connell & Slatyer 1977) of plant succession, as noted at Mtunzini (Chapter 3).

THE STUDY AREA

The study area is located within the Tharfield Private Nature Reserve between the Riet and West Kleinemonde rivers (Fig. 4.1). It is characterized by fairly large unvegetated mobile transverse dunes with their ridges orientated in a north-west/south-east direction, i.e. perpendicular to the shoreline (see Plate 1.2, pg 20). Interdune hollows (slacks or swales) are more common in the eastern part of the region and are usually vegetated (see Plate 2.4, pg 84). Isolated bushclumps, usually associated with aeolionite outcrops, are common among dunes on the western side of the study area, near the Riet River where the dunefield is narrow with buttress barchanoid dunes (Fig. 4.1).

Over half of the shoreline consists of hard ridges, three of which are overlaid by dune rock or aeolionite, thus forming large rocky promontories, the Three Sisters (Fig. 4.1). Above the high water mark incipient foredunes occur along the shoreline. A narrow, vegetated dune cordon is found along the landward side, within which a number of mature and active blowouts occur. These are orientated in a south-westerly or north-easterly direction. A large blowout on the east side has been stabilized with vegetation (Fig. 4.1) (Lubke 1983).

The area is largely subtropical and affected by the warm south-flowing Mocambique-Agulhas current of equatorial waters (Stone 1988). It is located at the western boundary of the south-eastern coastal climatic region (Schultz 1985). Maximum rainfall occurs in spring (October) and autumn (March) and minimum in June (Fig. 4.1). Rain falls mainly as maritime showers, although thunder storms do occur in the summer months. Average annual precipitation is 559mm and only 16.8 days receive more than 10mm of rain. The maximum temperature of 22°C is experienced in December and January, and the minimum of 14°C in July. Average annual temperature is 18°C. In winter the region receives about 70% of its possible sunshine, whereas in summer it is often cloudy to overcast, resulting in only about 50% of the possible sunshine duration. Frost does not occur, and fog is fairly common (Schultz 1985). Winds blow parallel to the coast, and occasionally reach gale force. Winds are predominantly north-easterly and south-westerly in summer and westerly in winter (Fig. 4.1). During late summer northerly or north-westerly warm "berg winds" are experienced. The net result of this wind regime is a 2-3 metre easterly movement of sand per annum (see Fig. 2.1, pg 65; Plate 2.2, pg 75).

The incipient foredunes along the seaward margin of the study area in the eastern sector are colonized by *Scaevola plumieri*, *Arctotheca populifolia* and *Sporobolus virginicus* (see Plate 2.1, pg 71). Along some of these foredunes the introduced grasses *Ammophila arenaria* and *Agropyron distichum* also occur. The most common dune slack species include *Scirpus nodosus*, *Juncus kraussii*, *Vellereophyton vellereum* and *S. virginicus*. The isolated bushclumps have a greater woody element, with species such as *Myrica cordifolia*, *Maytenus procumbens* and *Rhus crenata* being most common. These species usually form a low (less than 3m), fairly dense canopy making them physiognomically similar to the vegetated dune cordon, which is characterized by an unbroken thicket canopy covering the dunes from their seaward to landward bases (Chapter 1). However, the canopy is hedged by salt spray pruning (Tinley 1985). Diagnostic tree species include *Mimusops caffra*, *Sideroxylon inerme* and *Dovyalis rotundifolia*.

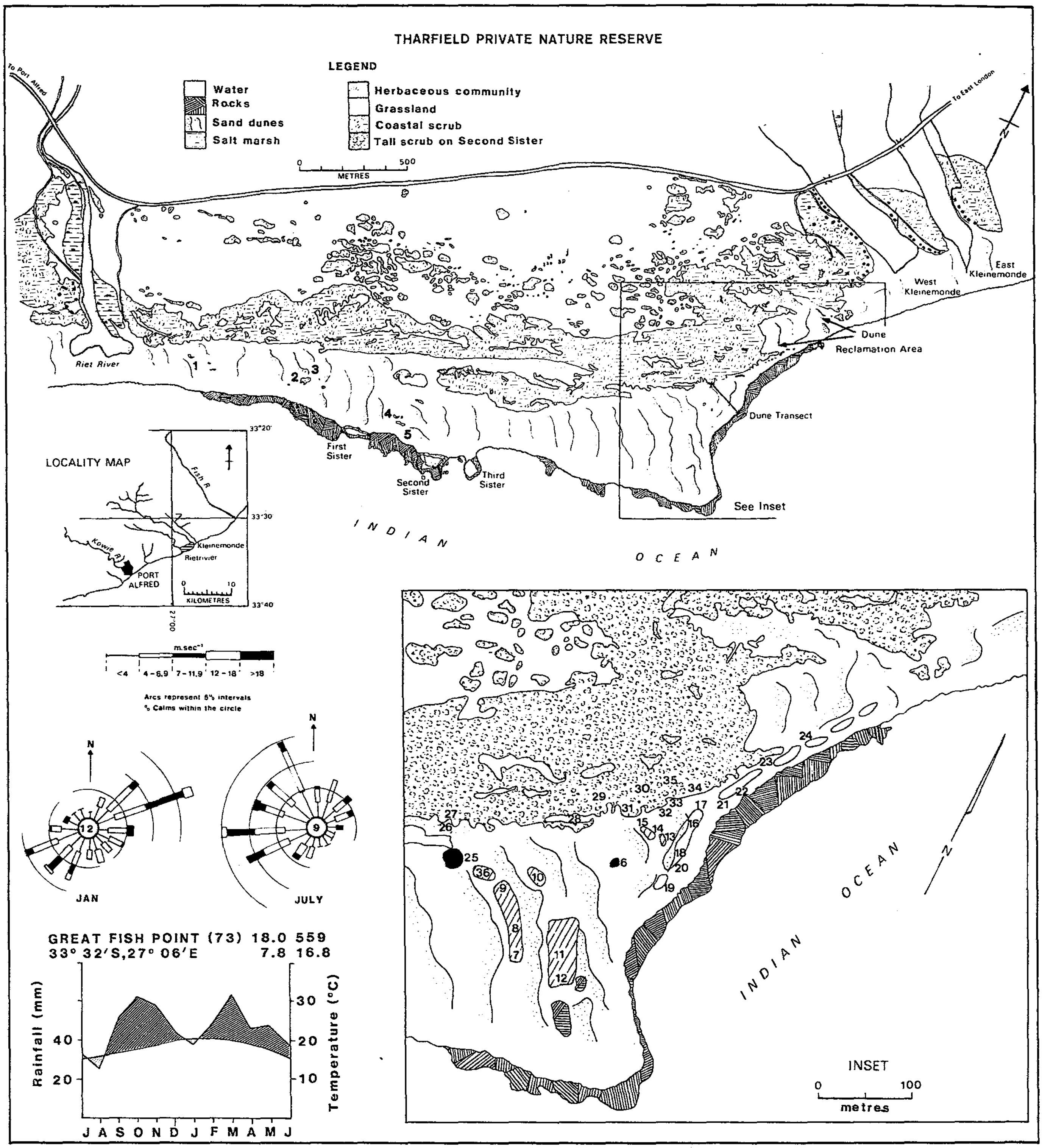


Figure 4.1 Map of the study area, showing the location of the sample sites (numbered), wind roses for January and July, and a Walter-Leith climate diagram for the area. The inset shows the specific location of sample sites on foredunes (shaded); dune slacks (hatching); Bushpockets (black); and thickets. Samples 1 to 5 were taken further west on the bushclumps behind the Three Sisters.

METHODS

VEGETATION SAMPLING

Six plant communities in the study area were identified from aerial photographs and sampled to determine species composition and complexity. These included nine relevés located in communities dominated by foredune species, viz: *Scaevola plumieri, Sporobolus virginicus, Agropyron distichum* and *Ammophilla arenaria*, ten relevés in dune slacks, including three slacks which were known to be more than 10 years old (Lubke 1983); eight relevés in bushclump communities; five relevés located along the fringe of the dune thicket; and four relevés located within the thicket (see inset of Fig. 4.1). Thus, a total of 36 relevés were sampled, using the techniques described in Chapter Three. Because of the paucity of the vegetation in the Kleinemonde area, linear transects could not be laid out as at Mtunzini, and relevés were located where suitable vegetation occurred.

SOIL SAMPLING AND ANALYSIS

Within each relevé three soil samples were taken with a soil auger and sealed in plastic bags for laboratory analysis. Percentage organic matter was determined by combustion, pH and conductivity was measured with a DDS 200 pH/conductivity meter and soil cations (Ca, Mg, K, Na & P) were determined by extraction, using the techniques described in Chapter Three.

DATA ANALYSIS

To enable the direct comparison of results between this and the Mtunzini study, the same techniques for data analysis were employed. The importance values of the species in each relevé were calculated, and the data matrix of 36 relevés and 97 species was analyzed using multivariate methods (TWINSPAN and DECORANA; Hill 1979a&b). Selected species were also plotted on a continuum index to help determine whether the vegetation formed discrete community units or was arranged in a continuum (Cottam 1949; Curtis & McIntosh 1951). The species richness value, alpha diversity (Simpson's diversity, DS), Simpson's dominance (ℓ), mean number of species per relevé, the coefficient of community (Sorenson 1948) and the relative importance value of the life forms in each community were calculated using the techniques described in Chapter Three. A mean value for each soil property was calculated, and these data were also analyzed using DECORANA and TWINSPAN.

RESULTS

PLANT COMMUNITIES - CLASSIFICATION AND DESCRIPTION

Relevé classification using TWINSPAN produced six distinct plant communities, and species classification resulted in eight groups, both at the third level of division. Results are shown as a phytosociological table to reveal species dominance in each community (Table 4.1). These six plant communities are discussed below.

Pioneer Community

A total of nine relevés were sampled on the foredunes, but only six were classified as Pioneers (Table 4.1). This community is characterized by a relatively low mean percentage cover, a low diversity and correspondingly high dominance, a total lack of tree species and very few woody shrubs (Plate 4.1). Herbs are the dominant life form, but grasses are relatively common (Table 4.2). Three subgroups were separated at the fourth level of division, due to distinct differences in dominance. Relevés 17 and 23 are dominated by *Agropyron distichum* ($\ell = 0.470$) (Plate 4.1); relevés 16, 18 and 20 by *Scaevola plumieri* (ℓ - 0.752), with *Sporobolus virginicus* co-dominant in relevé 18; and relevé 24, adjacent to the stabilization area (Fig. 4.1), by *Ammophila arenaria* ($\ell = 0.555$). These communities are relatively young and exposed to harsh environmental conditions. Formation of these incipient foredunes is complex and directly related to biological processes and plant aerodynamic interactions (Hesp 1983; 1984). In Australia it takes between 5 and 10 years for a low (1-2 meter) hummocky terrace to develop into an asymmetric ridge. However, in South Africa aggressive colonizing species such as *Cakile edentula* are absent, and consequently the process is slower. For these reasons it is believed that the age of these foredunes are between 40 and 60 years old, and this is supported by old aerial photographic evidence. However, those adjacent to the stabilization site are only about 5-10 years old (pers. obs.).

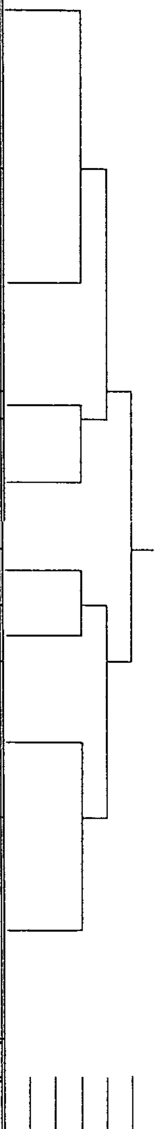
Young Dune Slacks

A total of 7 relevés were sampled in the vegetated interdune hollows between the transverse dune ridges, but the TWINSPAN classification also included three relevés sampled on *Sporobolus virginicus* dominated foredunes (relevés 19, 21 and 22; Table 4.1). This community is characterized by a relatively low percentage cover and a moderately high diversity. Life forms are similar to those found on foredunes, with very few shrubs and no trees (Table 4.2). Although herbs are the dominant life form, the highest number of grasses occur in this community, mainly due to the abundance of the grass, *S. virginicus*, which co-dominates with *Juncus kraussii* and *Vellereophyton vellereum* (Plate 4.2). Relevés 8 and 36 are dominated by *J. kraussii*; 7, 9 and 10 by *S. virginicus* and *J. kraussii*, and 11 and 12 by *Helichrysum praecinctum* and *S. virginicus* (Table 4.1). These slacks are relatively wet (Ranwell 1972), and at the time of sampling the depth of the water table ranged from 0.25 to 1.2m below soil surface. Species composition is very similar to slacks in the Alexandria dunefield where *S. virginicus* is also common (McLachlan *et al.* 1987). In the Alexandria dunefield the average net easterly movement of sand is 7m per annum, and since these slacks are 45m wide, their age is between 6 and 7 years (McLachlan *et al.* 1987). Net sand movement in the study area is 3m per annum (Lubke & Avis 1982a), and slacks are between 30 to 50m wide. Age is therefore estimated to range from 10 to 17 years.

Plate 4.1 View of the foredunes at Kleinemonde, looking east. *Scaevola plumieri* dominates in the foreground, whereas *Sporobolus virginicus* is the main colonizer of the foredunes left of centre. These foredunes have grown considerably since the parabolic blowout (arrowed) was stabilised, altering the beachface. The foredunes in the background are dominated by *Agropyron distichum*.

Plate 4.2 Young Dune Slack community in interdune trough, dominated by *Sporobolus virginicus* and *Scirpus nodosus*.

		T	TM		P	BP		ODS	YDS				P		
			Sh	Exp		Y	O		P	Slacks			A	S	
	SPECIES NAME	2333 9015	222 678	33 24	2 4	--23 1655	2,345	111 345	122 912	-3 86	--1 790	11 12	12 73	112 680	Relevé
Thicket	*Maerua caffra*	-3--	---	-1	-	----	----	---	---	--	---	--	--	---	Thicket
	Cussonia thysiflora	24--	---	3-	-	----	----	---	---	--	---	--	--	---	
	Panicum aequinerve	3455	---	--	-	----	----	---	---	--	---	--	--	---	
	Achyranthes aspera	4344	---	--	-	----	----	---	---	--	---	--	--	---	
	Panicum deustum	5345	---	--	-	----	----	---	---	--	---	--	--	---	
	Kedrostis nana	3-22	---	--	-	----	----	---	---	--	---	--	--	---	
	Cyphostemma cirrhosum	1221	---	--	-	----	----	---	---	--	---	--	--	---	
	Ficinia sp.	5---	---	--	-	----	----	---	---	--	---	--	--	---	
	Solanum sp.	23--	---	--	-	----	----	---	---	--	---	--	--	---	
	Cynanchum ellipticum	14-4	---	--	-	----	----	---	---	--	---	--	--	---	
	Maytenus sp.	4-4-	---	--	-	----	----	---	---	--	---	--	--	---	
	Protasparagus africanus	123-	---	--	-	----	----	---	---	--	---	--	--	---	
	Zanthoxylum capense	-231	---	--	-	----	----	---	---	--	---	--	--	---	
	Grewia robusta	-4-1	---	--	-	----	----	---	---	--	---	--	--	---	
	Dovyalis rotundifolia	-552	---	--	-	----	----	---	---	--	---	--	--	---	
	Cassine bispinosa	5251	---	--	-	----	----	---	---	--	---	--	--	---	
	Allophyllus natalensis	4323	---	--	-	----	----	---	---	--	---	--	--	---	
	Carrisa bispinosa	3-11	---	--	-	----	----	---	---	--	---	--	--	---	
	Acokanthera oppositifolia	12-1	---	--	-	----	----	---	---	--	---	--	--	---	
Thicket and Thicket Margin	*Brachylaena discolor*	42-2	534	45	-	----	---	---	---	--	---	--	--	---	Thicket and Thicket Margin
	Eugenia capensis	---1	---	3-	-	----	---	---	---	--	---	--	--	---	
	Mimusops caffra	2--5	55-	15	-	----	---	---	---	--	---	--	--	---	
	Solanum americanum	----	3-5	3-	-	----	---	---	---	--	---	--	--	---	
	Ipomoea ficoides	----	3-5	--	-	----	---	---	---	--	---	--	--	---	
	Azima tetracantha	-4--	55-	--	-	----	---	---	---	--	---	--	--	---	
	Capparis sepiaria	--3-	42-	--	-	----	---	---	---	--	---	--	--	---	
	Rhus glauca	4---	-35	2-	-	----	---	---	---	--	---	--	--	---	
	Secamone alpinii	---3	-55	-1	-	----	---	---	---	--	---	--	--	---	
	Pterocelastrus tricuspidatus	4--3	--4	-5	-	----	---	---	---	--	---	--	--	---	
	Sideroxylon inerme	4555	553	22	-	----	---	---	---	--	---	--	--	---	
	Cassine tetragonia	2--4	-43	--	-	----	---	---	---	--	---	--	--	---	
	Scutia myrtina	2141	35-	--	-	----	---	---	---	--	---	--	--	---	
	Euclea racemosa	442-	2-1	-4	-	---2	--5	---	---	--	---	--	--	---	
Bushclumps/Exposed Thicket Margin	*Ficinia lateralis*	----	---	1-	-	--11	----	---	---	--	---	--	--	---	Bushclumps/Exposed Thicket Margin
	Chrysanthemoides monilifera	----	4--	15	-	---4	5-45	--5	---	--	---	--	--	---	
	Rhus crenata	---2	525	44	3	-525	-555	5--	---	--	---	--	--	---	
	Pentaschistus heptamera	----	1--	4-	-	-241	----	---	---	--	---	--	--	---	
	Felicia echinata	---1	---	32	-	--51	----	---	---	--	---	--	--	---	
	Maytenus procumbens	---1	21-	55	-	---5	-55-	---	---	--	---	--	--	---	
	Helichrysum sordescens	----	---	34	4	--23	----	---	---	--	---	--	--	---	
Thicket Margin	*Carpobrotus deliciosus*	---1	---	5-	-	--1	----	---	---	--	---	--	-2	---	Thicket Margin
	Rhoicissus digitata	1--4	535	55	-	-35	----	---	---	--	---	--	--	---	
Bush-clumps	*Anthospermum littoreus*	---1	---	12	-	5-55	352-	2--	--3	--	---	--	--	---	Bush-clumps
	Metalasia muricata	----	---	-4	-	--15	----	5--	---	--	---	--	--	---	
	Cynanchum natalitium	----	--1	45	3	5-54	55-5	---	---	--	---	--	--	--2	
Old Slack and Bushclump	*Ipomoea pes-caprae*	----	---	--	-	-5--	----	2--	---	---	---	--	--	---	Old Slack and Bushclump
	Stoebe plumosa	----	1--	--	-	--5-	----	255	---	-4	---	--	--	---	
	Passerina rigida	----	3--	-4	3	3553	5554	455	--3	-2	---	2-	--	---	
	Myrica cordifolia	----	---	--	-	555-	53-5	1--	---	--	---	--	--	---	
	Gazania rigens	----	---	--	-	----	32-2	---	---	--	---	--	--	---	
	Cassine maritima	----	---	--	-	----	5-5-	---	---	--	---	--	--	---	
	Senecio elegans	---2	1--	24	3	354-	----	---	-32	-4	--2	--	--	---	
	Silene primuliflora	----	1--	11	-	-224	----	1--	---	-4	---	--	-2	---	
	Chironia baccifera	---1	---	2-	-	----	---4	5--	---	--	---	-2	--	--1	
Foredune and Young Slacks	*Gladiolus gueinzii*	----	---	--	-	----	2---	---	-3-	--	---	-3	-2	-23	Foredune and Young Slacks
	Scaevola plumieri	----	---	--	-	----	----	---	-3-	--	---	--	45	555	
	Agropyron distichum	----	---	--	-	----	----	-3-	--5	--	---	--	55	---	
	Hebenstretia cordata	----	---	--	5	----	----	2--	4-5	--	---	--	44	-5-	
	Sporobolus virginicus	----	---	--	-	----	----	33-	555	55	5-5	55	--	-5-	
	Helichrysum praecinctum	----	---	1-	-	----	----	1--	--2	--	1--	54	--	---	
	Scirpus nodosus	----	---	--	-	----	----	5--	---	-2	455	44	--	---	
	Vellereophyton vellereum	----	---	--	-	----	----	---	---	--	555	35	--	---	
	Arctotheca populifolia	----	---	--	-	----	----	---	---	54	3-4	--	3-	---	
	Juncus kraussii	----	---	--	-	----	----	535	---	55	555	5-	--	---	
	Helichrysum sp.	----	--1	--	-	--1-	----	3--	---	--	5--	--	--	---	
	Heteroptilis suffructicosa	----	3-3	13	-	-545	2--4	4--	-35	45	1--	52	--	--2	
	Zaluzianskya maritima	----	2--	--	-	--21	----	2--	---	-4	---	--	--	---	
	SPECIES NAME	2333 9015	222 678	33 24	2 4	--23 1655	2345	111 912	122 912	-3 86	--1 790	11 12	12 73	112 680	Relevé
			Sh	Exp		Y	O		P	Slacks			A	S	
		T	TM		P	BP		ODS	YDS				P		



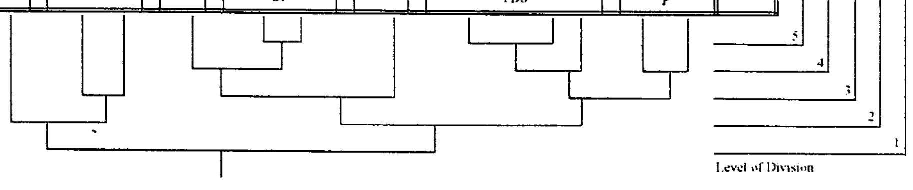


Table 4.1 Phytosociological table and dendrograms generated by TWINSPAN classification from Importance Value data. The dendrogram of stand classification is shown at the bottom of the table, and for species classification on the right. Species and species groups are listed on the left and right of the table, and stand numbers and stand groups at the top and bottom. The position of relevés is shown on Fig. 4.1 (pg 126). Groups correspond to those used for Figures 4.2 (pg 135) and 4.3 (pg 136). The table has had limited re-ordering, and numbers in the table indicate TWINSPAN scores of abundance. T-Thicket; TM-Thicket Margin; Sh-Sheltered; Exp-Exposed; BP-Bushpockets; Y-Young; O-Old; ODS-Old Dune Slacks; YDS-Young Dune Slacks; P-Pioneer; A-Agropyron; S-*Scaevola*.

Old Dune Slacks

Two dune slacks which have been studied previously and are known to be older than 10 years were also sampled (Lubke 1983). These relevés (14 & 15) were grouped together with relevé 13, which was intensively sampled in earlier studies (Lubke & Avis 1982a; Chapter 2). This community is characterized by a greater total mean cover than the previous communities, a greater amount of shrubs (35.5%) and less herbs and grasses. Diversity is similar to young slacks, but the mean number of species per relevé is greater (Table 4.2). Diagnostic species are the shrubs, *Stoebe plumosa* and *Passerina rigida*, and both *Rhus crenata* and *Chrysanthemoides monilifera* commonly found in the Bushclump and Thicket Margin groups occur here for the first time (Table 4.1; Plate 4.3).

Bushclumps

These isolated patches of vegetation vary in size from 400 to 1200m^2, and 7 relevés were sampled in these communities. They are physiognomically more complex than the slack and pioneer communities, and have a greater total mean cover, diversity and species richness (Table 4.2). Woody shrubs are dominant and creepers appear for the first time. Herbs are well represented, but the number of grasses decreases significantly (Fig. 4.2). Of the two subgroups separated at level 5, relevés 1, 6 and 25 are younger bushclumps, and relevé 33 is an exposed thicket margin. Relevés 2 to 5 are older bushclumps associated with aeolionite outcrops (Plate 4.4). Dominant species include the shrubs *Passerina rigida* and *Myrica cordifolia* from the Old Slack and Bushclump species group, *Anthospermum littoreum* and *Cynanchum natalitium* from the Bushclump species group and *Rhus crenata* from the Bushclump/Exposed Thicket Margin group (Table 4.1). Species composition is similar to the bushpockets of the Alexandria dunefield (Talbot & Bate 1991). As was the case at Mtunzini (Chapter 3) this community appears to be transitional between communities dominated by forbs, and those dominated by woody species.

Thicket Margin Community

Six relevés were sampled along the margin of the dune thicket and these separated into two distinct subgroups which appear to be related to their degree of exposure (Table 4.1; Fig. 4.1). This community is physiognomically similar to the bushclump community, particularly the exposed margins, but is floristically more complex. Total mean cover, species richness, mean number of species per relevé, and diversity are all greater than corresponding values recorded for the previous communities (Table 4.2). The significant increase in the number of tree species is accompanied by a decrease in the number of shrubs, herbs and grasses. Of note is the high number of creepers which occur in this community (Fig. 4.7). Relevés 32, 33 and 34 are located on the seaward (exposed) margin of the Dune Thicket, whereas relevés 26 and 28 are on the landward (sheltered) side of inactive blowouts (Plate 4.5). Dominant species include the creeper *Rhoicissus digitata* from the Thicket Margin species group, *Rhus crenata* from the Bushclump/Exposed Thicket Margin group, and *Brachylaena discolor* and *Sideroxylon inerme* from the Thicket species group (Table 4.1). Species in the latter group were not recorded in any of the previous communities.

Table 4.2 Mean values of total mean cover, species richness, mean number of species per relevé, Simpson diversity and dominance, and the relative proportions of six life forms expressed as a percentage, for each of the 6 plant communities.

	Pioneer	Young Slacks	Old Slacks	Bushclumps	Thicket Margin	Thicket
Relevé number	1-18; 20; 23; 24	7-12; 19; 21; 22; 36	13-15	1-6; 25; 33	26-28; 32; 34	29-31; 35
Total mean cover (%)	30. 17 ± 2.38	27.7 ± 3.3	59.52 ± 5.26	83.31 ± 7.24	106.10 ± 10.44	116.32 ± 5.67
Species richness value	17	21	21	30	48	54
Mean number of species per relevé	4.3 ± 0.76	6.2 ± 3.16	10.0 ± 4.51	10.63 ± 1.77	19.80 ± 2.20	25.75 ± 3.52
Simpson diversity (D_s)	0.370 ± 0.12	0.570 ± 0.08	0.660 ± 0.12	0.817 ± 0.023	0.887 ± 0.018	0.901 ± 0.009
Simpson dominance (ℓ)	0.630 ± 0.12	0.430 ± 0.08	0.340 ± 0.12	0.183 ± 0.023	0.113 ± 0.018	0.099 ± 0.009
% Occurrence of:						
Herbs (including succulents)	68	34	14	18	1	6
Grasses	22	34	25	1	21	18
Half-woody and woody shrubs	5	1	68	69	32	14
Vines and creepers	5	0	0	12	24	7
Sedges & Rushes	0	31	16	0	0	0
Trees	0	0	0	0	31	55

Dune Thicket

This, the most physiognomically and floristically complex community sampled, has the highest values of total mean cover, species richness, mean number of species per relevé and diversity (Table 4.2). The greatest number of tree species was recorded, and the number of shrubs recorded was lower than along the Thicket Margin. The number of herbs is less, and the slight increase in grasses is due to the occurrence of shade-loving grass species such as *Panicum aequinerve* and *P. deustum* which, together with the tree, *Sideroxylon inerme*, are dominant (Table 4.1). The trees form a closed upper canopy and smaller trees and shrubs are relatively common (see Plate 1.8, pg 32 & Plate 4.6). The ground cover is sparse, but lianas such as *Capparis sepiaria* and climbers such as *Cynanchum ellipticum* are fairly common. Species are more specialized, with 27 restricted to this community (Table 4.1; Plate 4.6).

Plate 4.3 The study slack at Kleinemonde in 1989, which was classified together with the more mature scrub vegetation to the right, as the Old Dune Slack community. This is the same area shown in Plates 2.2 and 2.3, but note the predominance of *Stoebe plumosa* (arrowed). The bushclump community on the skyline is shown in Plate 4.4.

Plate 4.4 Bushclump shown in Plate 4.3 above, with wet slack behind it after spring rains (November 1989). The bushclump is dominated by wind-pruned woody species, and it is unclear whether this is a remnant patch of thicket, or an old dune slack.

Plate 4.5 Thicket Margin at Kleinemonde, viewed from the end of a blowout colonized by *Passerina rigida*. The thicket is dominated by *Mimusops caffra* and *Sideroxylon inerme*.

Plate 4.6 Sample plot within the Dune Thicket community, showing density of the shrubs and lack of large trees.

FLORISTIC CHANGES ALONG THE SUCCESSIONAL GRADIENT

The ordination by DECORANA shows the arrangement of samples and species in two-dimensional space (Figs. 4.2 & 4.3), with TWINSPAN classification groups (Table 4.1) indicated. Despite eigenvalues 1 and 2 being closer to unity, in both cases axes 1 and 3 expressed the desired information better, due to the emphasis of outliers on axis 2 caused by aberrant samples. A clear gradient from foredunes to climax vegetation was found along axis 1. Groups and subgroups are very distinct and the gradient from left to right is related to an increase in community complexity, and consequently age, with increasing distance from the sea (Fig. 4.2). There is also a change in environmental factors, such as a decrease in salt laden winds and sand movement, and an increase in soil water holding capacity (Avis & Lubke 1985). The group of younger bushclumps (relevés 1, 6, 25 & 33) have a closer affinity with Old Dune Slacks, whereas the other group (relevés 2 to 5) is more closely associated with Thicket Margin vegetation. This suggests that the former are depositional mounds, and the latter remnant knobs (*c.f.* Hesp 1986). Axis 3 shows a gradient of species diversity and dominance. Outlying relevés (for example 16, 17 & 20) have a low alpha diversity and high Simpson's dominance (1.0, 0.526, 0.970 respectively), whereas relevés along the median of the scatter diagram (for example 22, 28 & 35) have low dominance values (0.246, 0.142, 0.088 respectively) and correspondingly high diversity values. The diversity within the pioneer communities, as shown on axis 3, varies greatly, whereas in the more floristically complex communities there is less variability and alpha diversity although higher, is generally constant (Fig. 4.2; Table 4.2).

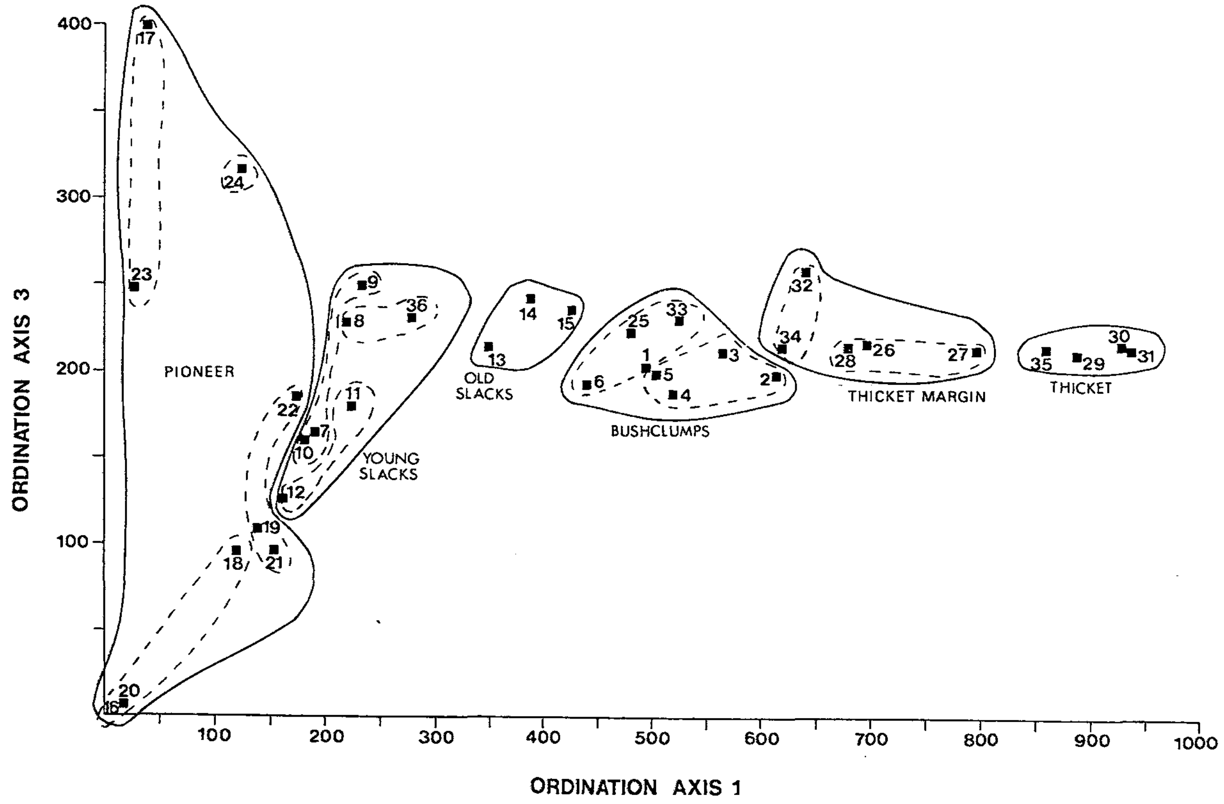


Figure 4.2 Relevé ordination of the data set, showing the distribution of plant communities isolated by TWINSPAN, in relation to axes 1 and 3.

The species ordination shows the same trends, but groups are not as clearly defined due to the large number of species with a widespread distribution (Fig. 4.3). Pioneer and Young Dune Slack species have been grouped together in the TWINSPAN classification since species such as *Sporobolus virginicus* and *Heteroptilis suffructicosa* are common to both communities. Similarly, shared dominant species such as *Passerina rigida* result in the Bushclump and Old Dune Slack species being grouped together. *Rhoicissus digitata* and *Rhus crenata* are common in Bushclumps and Exposed Margins, and *Brachylaena discolor* and *Sideroxylon inerme* are common in both Thicket Margin and Thicket vegetation. Species within the final group are confined to Dune Thicket (Fig. 4.3; Table 4.1). Distribution of species along axis 1 is also related to increasing age, community complexity and decreasing environmental variability from left to right. The variability along axis 3 is related to the specificity of a species to a community. Some species, such as *Sporobolus virginicus* and *Silene primulifolia* are not confined to the community to which they have been assigned, whereas species located along the median of axis 3, such as *Myrica cordifolia* and those within the Thicket group, are usually specific to the community in which they are clustered.

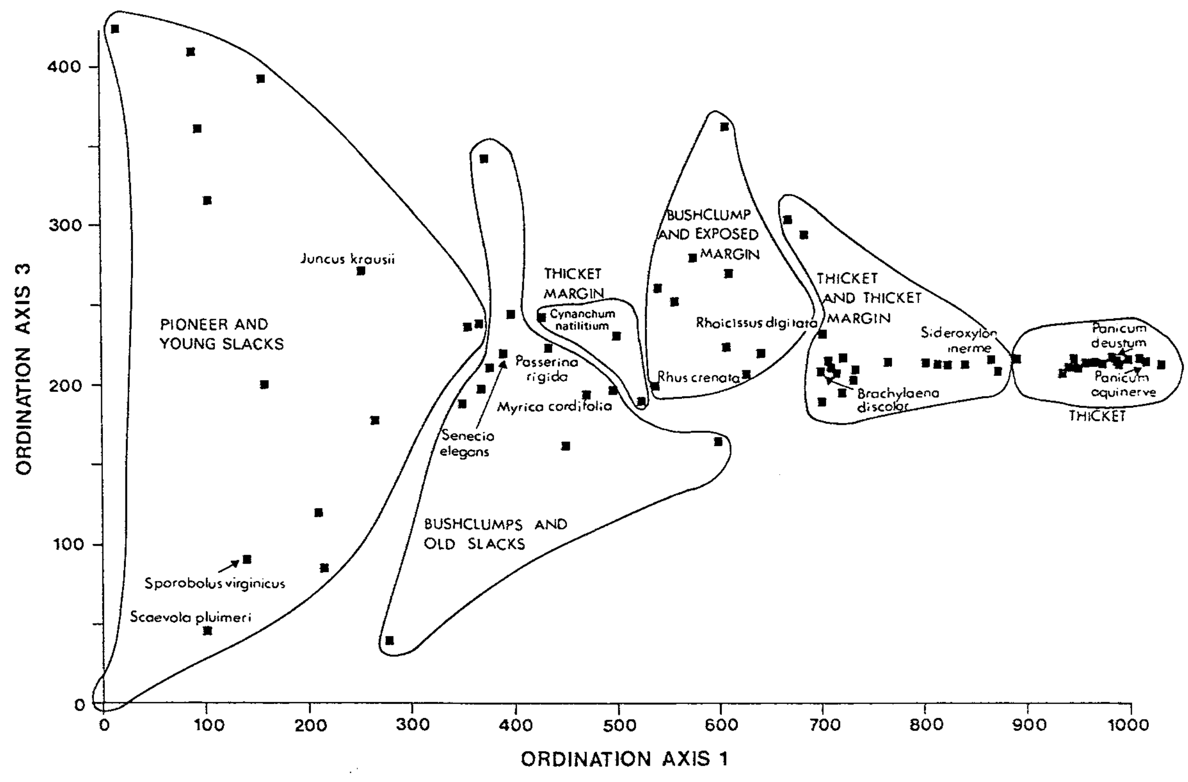


Figure 4.3 Species ordination of the data set, showing the distribution of the species groups isolated by TWINSPAN in relation to axes 1 and 3. The position of diagnostic species is also shown.

The Simpsons' diversity index (D_s) shows a steady increase along the successional sequence, increasing more sharply initially (Fig. 4.4). As expected, the inverse relationship, Simpsons' Dominance (ℓ), mirrors the diversity curve. Diversity is low on the foredunes due to the dominance by pioneer species, but increases as more species are able to colonize and survive in the older communities. High Co-efficient of Community (CC) values are found between Pioneer and Young Dune Slacks, Young and Old Dune Slacks and between Bushclump and Thicket Margin communities, indicative of a high degree of similarity between these communities (Table 4.3). Fairly high values also exist between Old Dune Slacks and Bushclumps, and Thicket Margin and Thicket communities. A low degree of similarity, and therefore a high Beta diversity, is found between the communities of lower successional stages (Pioneers & Dune Slacks) and the Thicket community. This is related to the low number of species common to these communities. Only 3 species found on foredunes occur in the Thicket community, whereas Bushclumps share 22 species with the Thicket Margin community (Table 4.3)

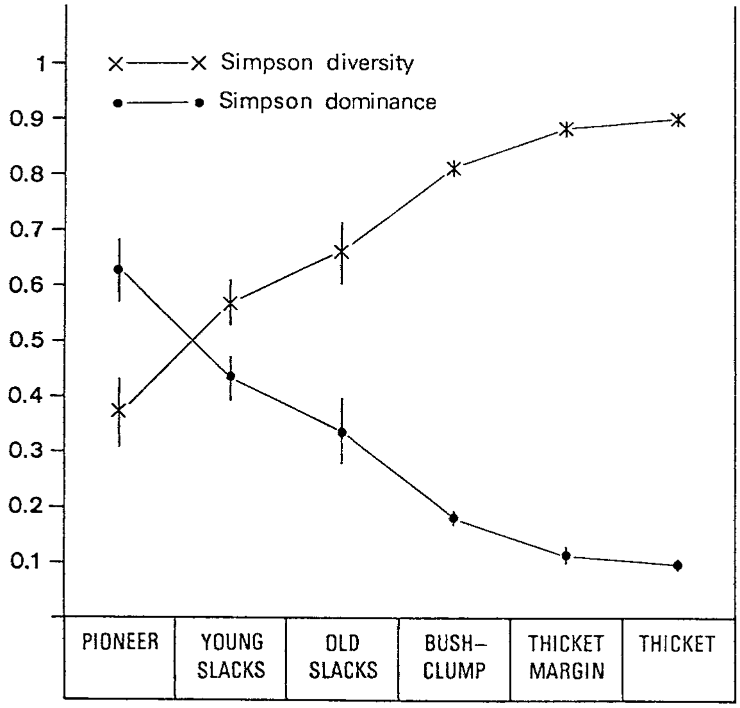


Figure 4.4 Changes in Simpson diversity (D_s) and dominance (ℓ) indices in the six plant communities.

Table 4.3 Matrix showing the number of species shared by the various communities (shaded), the species richness in each community (bold) and the Sorenson's Co-efficient of Community (CC).

	PIONEER	YOUNG DUNE SLACKS	OLD DUNE SLACKS	BUSHCLUMP	THICKET MARGIN	THICKET
PIONEER	**17**	0.631	0.421	0.426	0.184	0.084
YOUNG DUNE SLACKS	12	**21**	0.666	0.431	0.231	0.080
OLD DUNE SLACKS	8	14	**21**	0.470	0.231	0.080
BUSHCLUMP	10	11	14	**30**	0.564	0.297
THICKET MARGIN	6	8	8	22	**48**	0.490
THICKET	3	3	3	9	25	**54**

To reflect these changes in dune communities, histogram plots showing the importance value of 14 species and life form in each community are presented (Figs. 4.5 & 4.7). In addition, importance value curves for 12 diagnostic species have been plotted along a Continuum Index (Fig. 4.6). *Scaevola plumieri* only occurs in the Pioneer community, whereas *Sporobolus virginicus* is found in both pioneer and dune slack communities. It is most common in Young Dune Slacks, and least common in the older slacks. Both these species are therefore restricted to the beginning of the chronosequence. The former has a low Continuum Index (CI) value of 300, and the latter only extends to a CI value of 1400 (Fig. 4.6a). The importance of grasses in the Pioneer communities is in contrast to the situation at Mtunzini, where this life form is more common in the intermediate communities (Fig. 4.7).

The rush, *Juncus kraussii*, is restricted to the dune slacks, being more common in the Young Dune Slack community where it co-dominates with *S. virginicus*. At Mtunzini, due to the lack of wet or dry slacks, no sedges or rushes were observed (Chapter 3) but in the Eastern Cape they are common, although restricted to dune slacks (Chapters 1 & 2; McLachlan *et al.* 1987; Lubke 1988). *J. kraussii* is therefore restricted to the central portion of the chronosequence between CI values 610 and 1510 (Fig. 4.6a).

Senecio elegans, a small hardy herb, is found in all communities except the Old Dune Slacks, but never dominates (Figs. 4.5 & 4.6b). *Passerina rigida*, a hardy shrub, also has a wide distribution but is most common in the Old Dune Slacks and to a lesser extent the Bushclumps (Fig. 4.5). Isolated individuals occur on foredunes in the area, and *P. rigida* was the first woody species to invade the permanently marked study slack (Chapter 2). This is probably due to its tolerance to salt spray. This distribution is reflected in its range along the chronosequence, from CI values of 300 to 2300 (Fig. 4.6b).

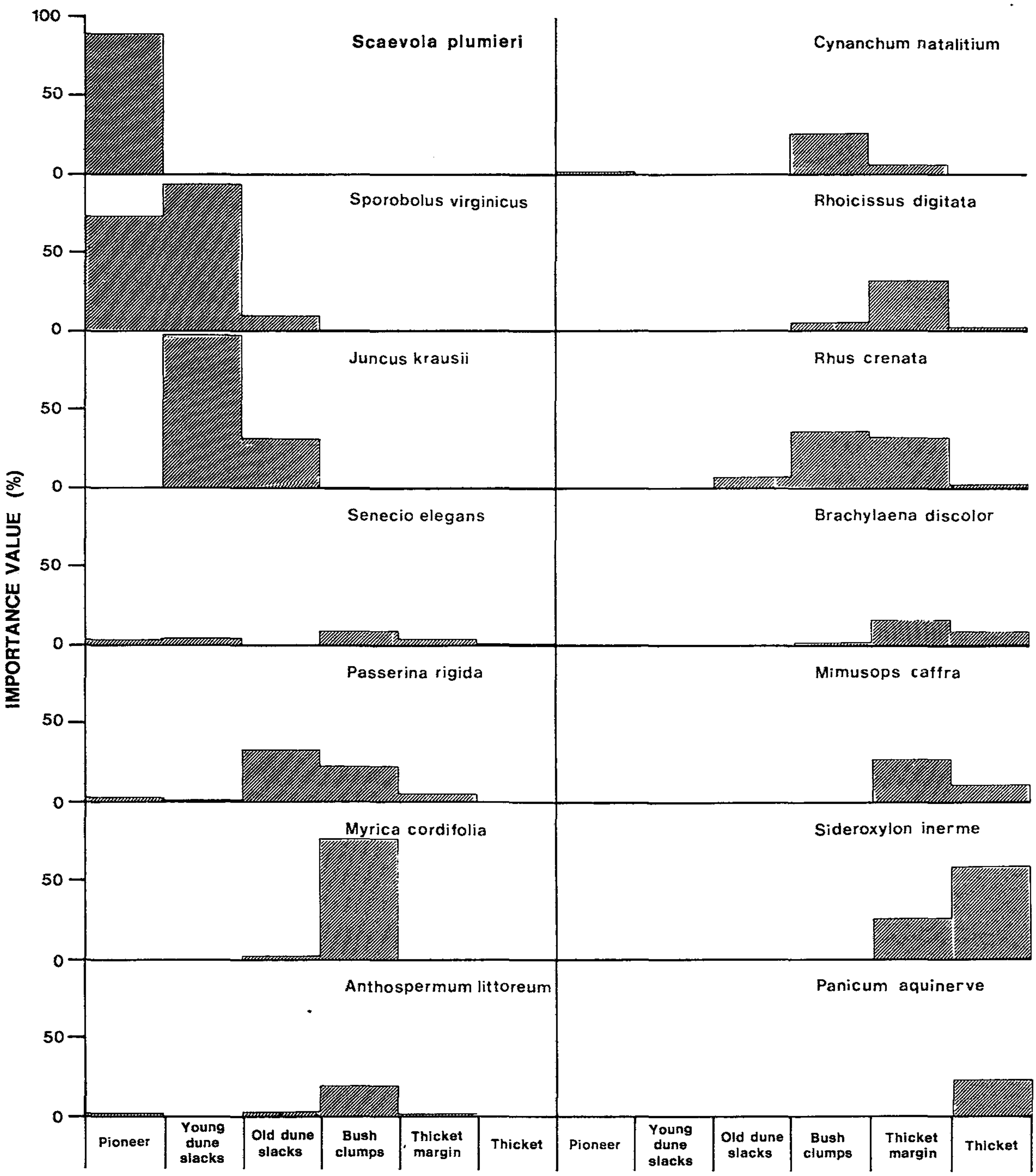


Figure 4.5 The relative importance of 14 diagnostic species in the six communities.

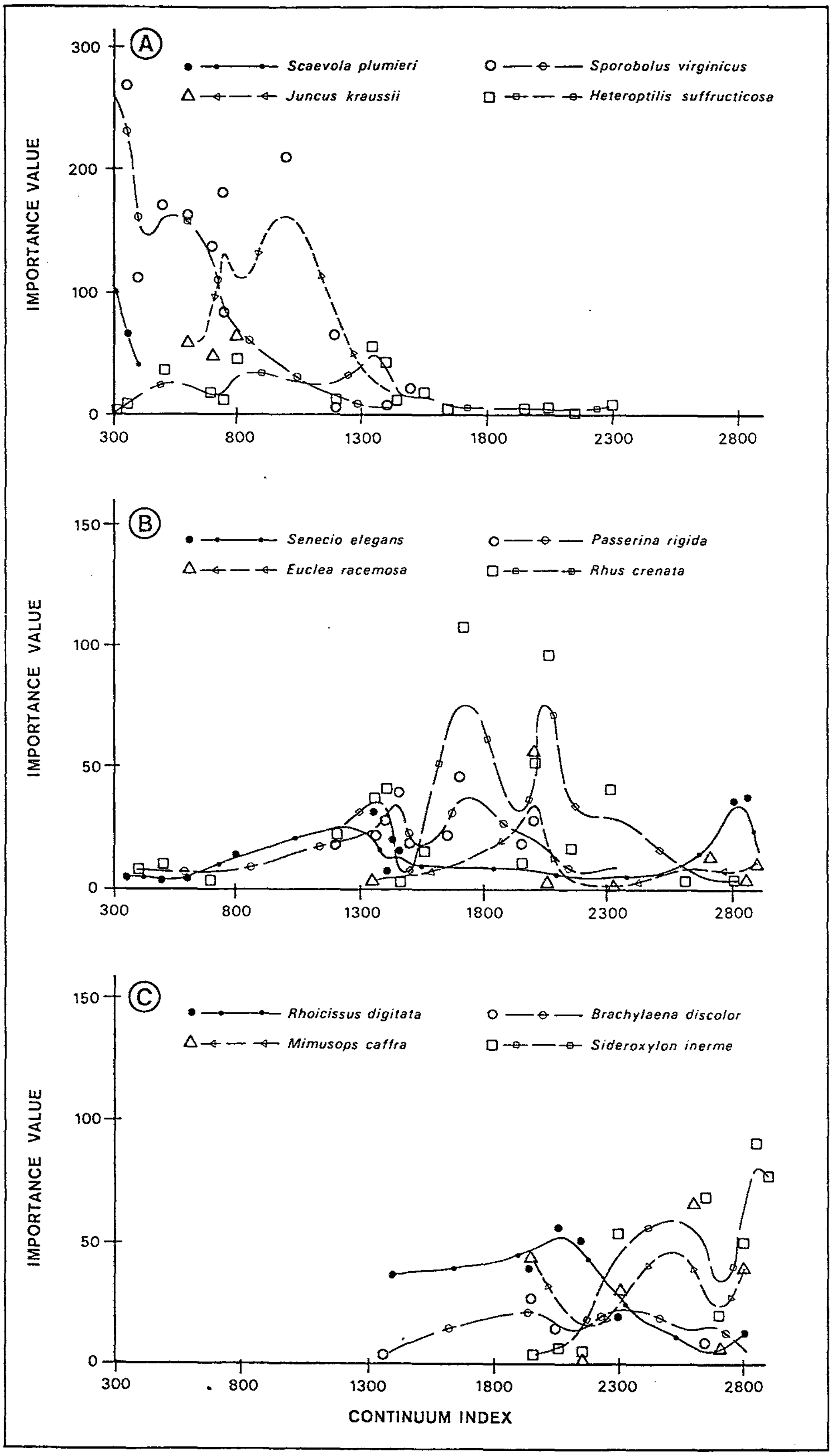


Figure 4.6 Importance value curves for twelve diagnostic species in the dunefield, plotted along a Continuum Index ranging from 300 to 2800. A-sand dune and dune slack colonizers; B-dune scrub species; C-secondary and climax dune thicket species. Note that for A importance value ranges from 0 to 300, and from 0 to 150 for B and C.

Myrica cordifolia, a woody shrub with a sympodial growth form, occurs almost entirely in Bushclumps, except for a few isolated individuals which invaded the study slack (Fig. 4.5; Chapter 2). *M. cordifolia* is one of the most important woody species linking the succession towards a thicket dominated by woody species, and this species was found to characterise bushclumps along the entire coastline (Chapter 1, Plate 1.5). This is also true for *Rhus crenata*, which is common in the Bushclumps, but unlike *M. cordifolia* is not confined to them. It is almost equally common in the Thicket Margin and is also found in the Old Dune Slacks and Thicket (Fig. 4.5). These species contribute to the overall dominance of shrubs in the Old Dune Slacks and Bushclump community (Fig. 4.7). Woody shrubs first appear at a CI value of 1350, which corresponds to the approximate position of the Bushclump community (Fig. 4.6b).

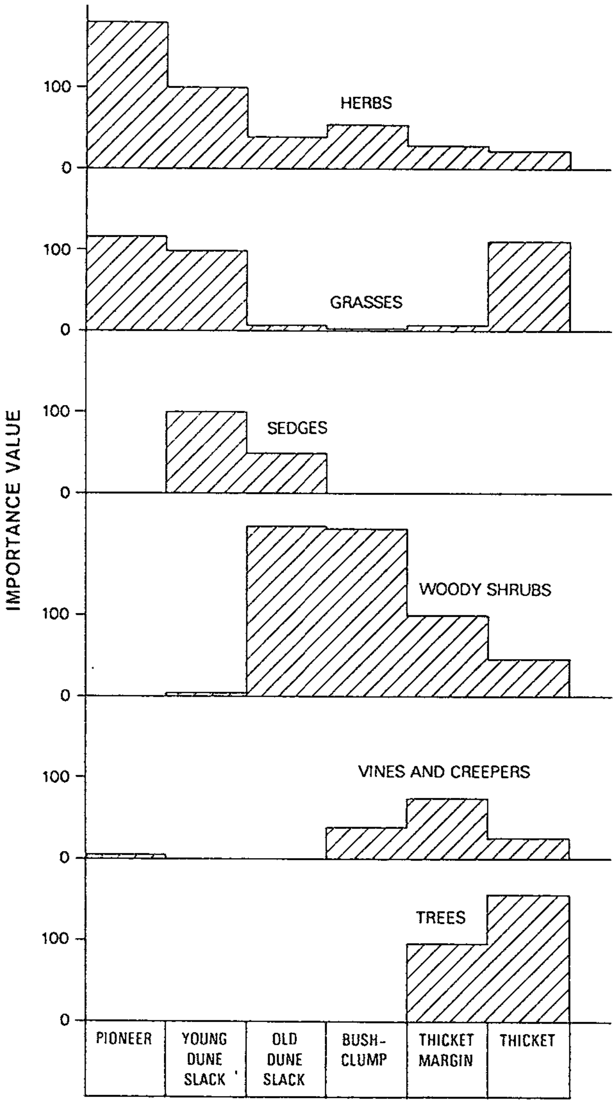


Figure 4.7 The relative importance of the life forms which occur in the six plant communities.

The only creepers found on the foredunes are *Ipomoea pes-caprae* (Table 4.1) and *Cynanchum natilitium*. The former is restricted to the Pioneer community, but the latter is most common in the Bushclump community and is also found in the Thicket Margin (Fig. 4.5). This species, together with *Myrica cordifolia* and *Anthospermum littoreum* are diagnostic species of the Bushclump community. *Rhoicissus digitata*, a woody vine is most common along the Thicket Margin but is also found in the Bushclump community (Fig. 4.5), first appearing at a CI value of 1350 (Fig. 4.6c). Consequently, vines and creepers are more common in the Thicket Margin community, but also occur in the Bushclump and Thicket community (Fig. 4.7).

Bachylaena discolor is a hardy woody shrub or small tree with a wide distribution (Chapter 1), and although it colonizes the Bushclumps, it is most common in the Thicket Margin (Fig. 4.5), first appearing at a CI values of 1350 (Fig. 4.6c). This species has not yet invaded the slack which was studied intensively (Chapter 2). As community complexity increases and soil development occurs, trees become the dominant life form (Fig. 4.7). Typical species include *Mimusops caffra* and *Sideroxylon inerme*. The former is hardy, and *S. inerme* is more typical of the Dune Forests in the region (Chapter 1), and usually becomes established after *M. caffra*. Both appear fairly late in the chronosequence, at a CI value of 1920 (Fig. 4.6c). Shade loving grasses such as *Panicum aquinerve* are also common in the forests (Fig. 4.5) and contribute towards the relatively high number of grasses in the Thicket community (Fig. 4.7). This species is one of 26 others which were only recorded in the Thicket community, in contrast with *Scaevola plumieri* and *Ipomoea pes-caprae* which are restricted to the Pioneer community (Table 4.1).

SOIL CLASSIFICATION AND EDAPHIC CHANGES ALONG THE SUCCESSIONAL GRADIENT

The TWINSPAN classification of samples based on soil characteristics is shown in Figure 4.8. Six groups were produced at the third level of division and although not as distinct as those produced at Mtunzini (Chapter 3), they can be related to floristic groups. The primary division appears to separate soils of plant communities dominated by woody species (Thickets and Bushclumps) from those dominated by forbs (for example Pioneer and slack communities). Soils of Old Bushclumps usually associated with aeolionite outcrops are also found in the latter group. Divisions at level two separated two distinct groups, namely soils of Thicket and Slack relevés. The third level of division separates the samples into a further four groups, of which all except Group 3 are fairly distinct (Fig. 4.8). In all cases vegetation type can be related to these various groups, which have been separated on the basis of their soil properties only.

The soil properties of each group is given in Table 4.4. In groups 1, 2 and 5 (Thicket, Bushclump, Old Bushclumps) concentrations of the exchangeable bases (K, Na, Ca, Mg) and percentage organic matter are greater than for the other three groups. Overall, conductivity, pH and phosphate show less variability. All soil properties except pH, phosphate and calcium are greater in the Thicket group. One would expect pH to be low as it is related to the high organic matter. The high conductivity is related to the high values of exchangeable bases measured. This decrease in pH, and increase in organic matter and other factors supports the conclusion that improved soil properties occur in these older communities.

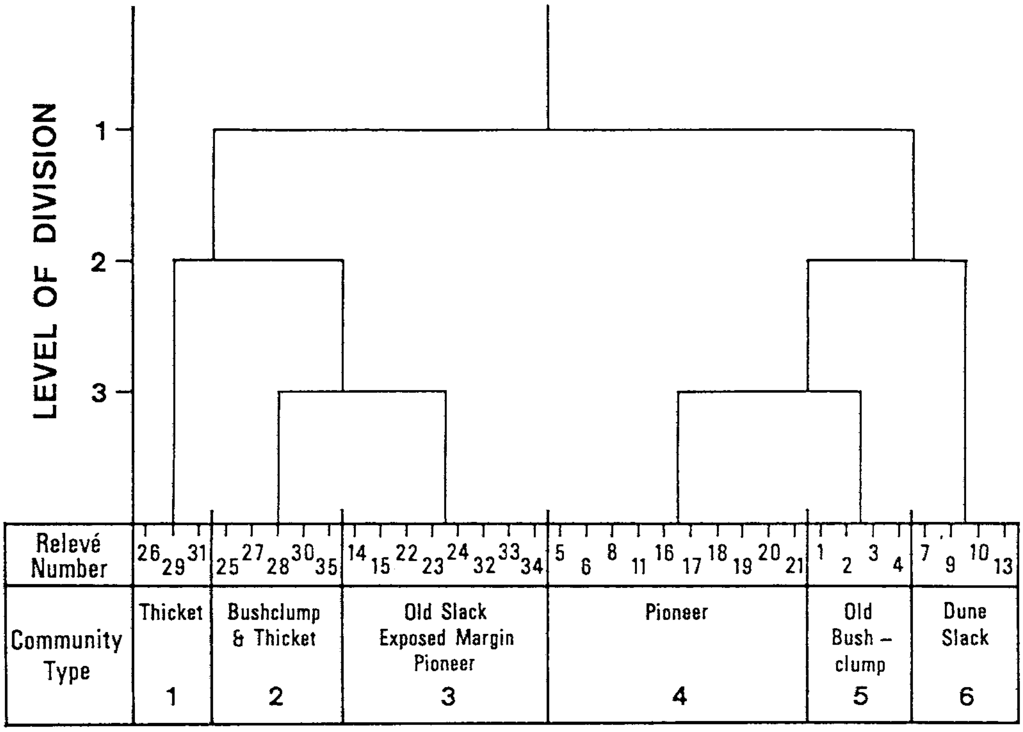


Figure 4.8 Dendrogram produced by TWINSPAN showing sample classification based on soil characteristics. The position of relevés is shown on Fig. 4.1 (pg 126)

The low values of exchangeable bases and organic matter in Group 4 (Pioneers) is related to the age of this community, as is the high pH value. This is also true for Group 6 (Slacks) although values are generally not as low. The higher than expected conductivity in Groups 5 and 6 is not due to the concentration of exchangeable bases, but is related to an accumulation of salt in the sand surface.

The distinct differences in soil properties of the older communities, particularly the Thicket and Thicket Margin, when compared to the younger communities (Pioneers & Young Dune Slacks) indicates that soil development has occurred in these older communities, but in the early stages of succession is relatively slow and unimportant. The mean values of soil factors for each community defined on the basis of species composition rather than soil properties is given in Table 4.4b, and values compare favourably to the groups defined by the TWINSPAN classification on the basis of their edaphic properties (Fig. 4.8).

Table 4.4 Mean value of soil properties in the six groups classified by TWINSPAN. A - On the basis of their soil properties (Fig. 4.8) and B - their species composition (Table 4.1).

A: Communities based on soil properties (Fig. 4.8)

SOIL PROPERTY	THICKET (1)	BUSHCLUMP & THICKET (2)	OLD BUSHCLUMP (5)	OLD SLACKS (3)	SLACKS (6)	PIONEER (4)
pH	8.16 ± 0.26	8.65 ± 0.10	8.75 ± 0.08	9.00 ± 0.06	9.17 ± 0.03	9.14 ± 0.03
Conductivity (µS1cm)	401 ± 6.50	118 ± 6.30	159 ± 6.30	100 ± 6.60	157 ± 63.0	118 ± 13.0
% Organic matter	6.7 ± 2.70	2.07 ± 0.15	1.55 ± 0.15	1.29 ± 0.18	1.1 ± 0.12	1.07 ± 0.09
Phosphate (ppm)	6.05 ± 0.47	6.44 ± 0.42	7.8 ± 0.42	5.5 ± 0.27	5.0 ± 0.22	5.13 ± 0.09
Potassium (ppm)	53 ± 1.90	29.3 ± 1.90	26.2 ± 1.90	22.1 ± 1.90	18.5 ± 1.70	16.5 ± 1.30
Sodium (ppm)	421 ± 24.20	384 ± 3.80	81.2 ± 3.80	393 ± 13.30	101.2 ± 11.70	76.1 ± 4.10
Calcium (ppm)	22869 ± 9968.40	29640 ± 61.90	2618 ± 61.90	32293 ± 208	2565 ± 15.50	2440 ± 30.50
Magnesium (ppm)	468 ± 30.20	423 ± 7.20	103.6 ± 7.20	437 ± 3.40	71.9 ± 2.30	71.3 ± 3.40

B. Communities based on species composition (Table 4.1)

SOIL PROPERTY	THICKET (1)	THICKET MARGIN (2)	BUSHCLUMP (5)	OLD SLACKS (3)	SLACKS (6)	PIONEER (4)
pH	8.24 ± 0.15	8.7 ± 0.60	8.84 ± 0.05	9.11 ± 0.07	9.20 ± 0.06	9.14 ± 0.05
Conductivity (µS1cm)	257 ± 89	171 ± 8.40	149 ± 8.40	102 ± 7.90	184 ± 72.30	112 ± 6.70
% Organic matter	3.9 ± 0.50	2.8 ± 0.70	1.7 ± 0.50	1.1 ± 0.09	0.88 ± 0.20	1.15 ± 0.10
Phosphate (ppm)	7.22 ± 0.51	5.7 ± 0.19	6.81 ± 0.38	4.87 ± 0.07	5.16 ± 0.19	4.98 ± 0.06
Potassium (ppm)	39.9 ± 8.90	36.7 ± 5.60	24.2 ± 2.10	17.8 ± 1.70	18.5 ± 1.30	15.4 ± 1.10
Sodium (ppm)	415.2 ± 11.10	416.5 ± 11.70	165.6 ± 54.10	258 ± 89.30	94.6 ± 11.10	178.9 ± 36.50
Calcium (ppm)	31375 ± 455	32560 ± 335	9903 ± 3280	21990 ± 6159	2568 ± 74.20	12241 ± 3385
Magnesium (ppm)	454.5 ± 20.30	445.8 ± 9.30	315.7 ± 37.30	315.7 ± 76.80	69.9 ± 1.50	193.7 ± 43.3

A scatter diagram was produced by ordinating samples using soil data (Fig. 4.9). Groups are based on the TWINSPAN soil classification (Fig. 4.8). Unlike the ordination diagrams for vegetation (Figs. 4.2 & 4.3), axis 1 does not correspond to increasing age and community complexity directly, but rather to inherent soil properties in each community. The mean values of all properties except pH listed in Table 4.4 for groups 1 to 3 are greater than for groups 4 to 6, particularly the exchangeable bases (Ca, Mg, K, Na) which are all greater by at least a factor of two. However, the overriding factor is the difference in the amount of calcium, which increases from 2565 ppm (Group 6) to 32 293 ppm (Group 3, Table 4.4). It is for this reason that Group 3 has been placed together with the more complex Thicket and Bushclump communities. On axis 2 the most important factor is percentage organic matter, which is highest in Thickets (6.7%) and lower in the Old Slacks (Group 3, 1.29%) and Pioneer communities (Group 4, 1.07% see Table 4.4).

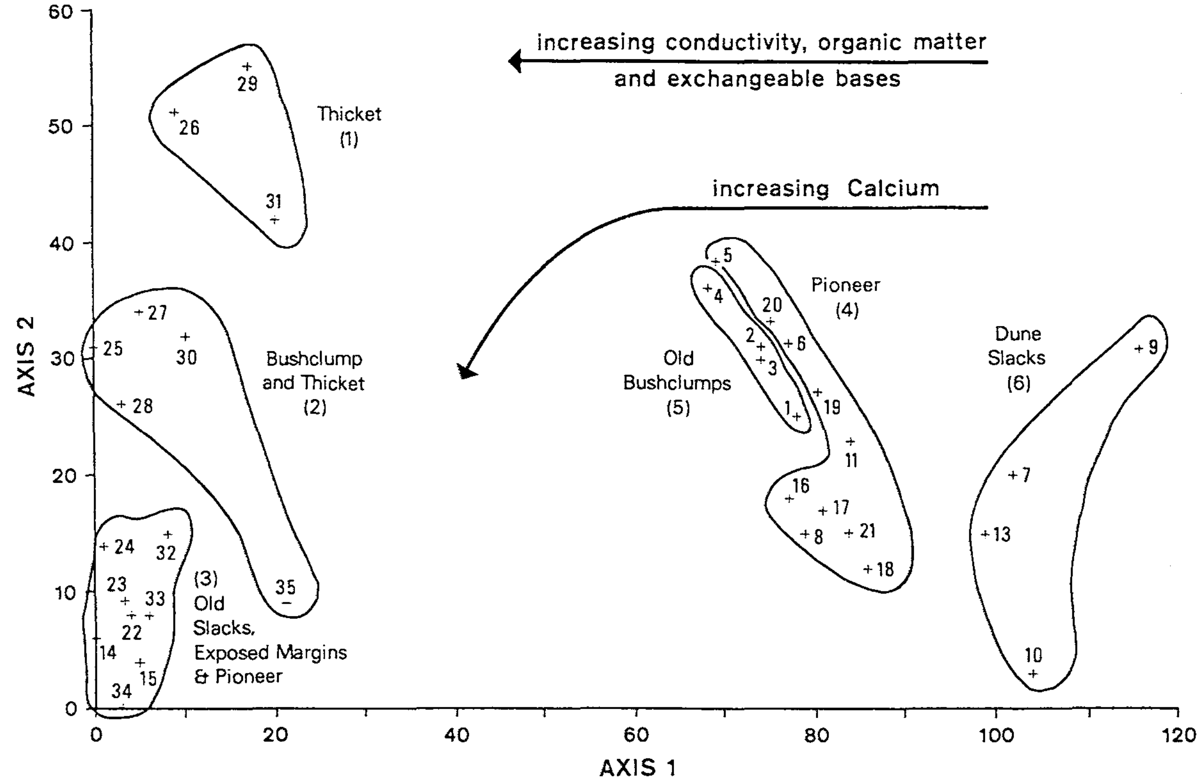


Figure 4.9 Ordination of the 36 samples showing the distribution of groups in relation to axes 1 and 2. Groups were isolated by TWINSPAN (Fig. 4.8), based on their soil properties, and numbers in parentheses correspond to those shown in Table 4.4.

Both the classification and ordination of the soil data resulted in samples with similar properties being clustered (Fig. 4.8) and distributed along a soil gradient (Fig. 4.9). This is not clearly related to the plant communities and in order to show changes in soil properties along the successional gradient, mean values were plotted for each community (Fig. 4.10). There is a steady increase in Mg, Na and Ca from Pioneer to Thicket community, with a slight decrease in Young Slacks. Concentrations in the Old Dune Slacks are greater than for the Bushclumps which, because of their exposed position, may lose these elements

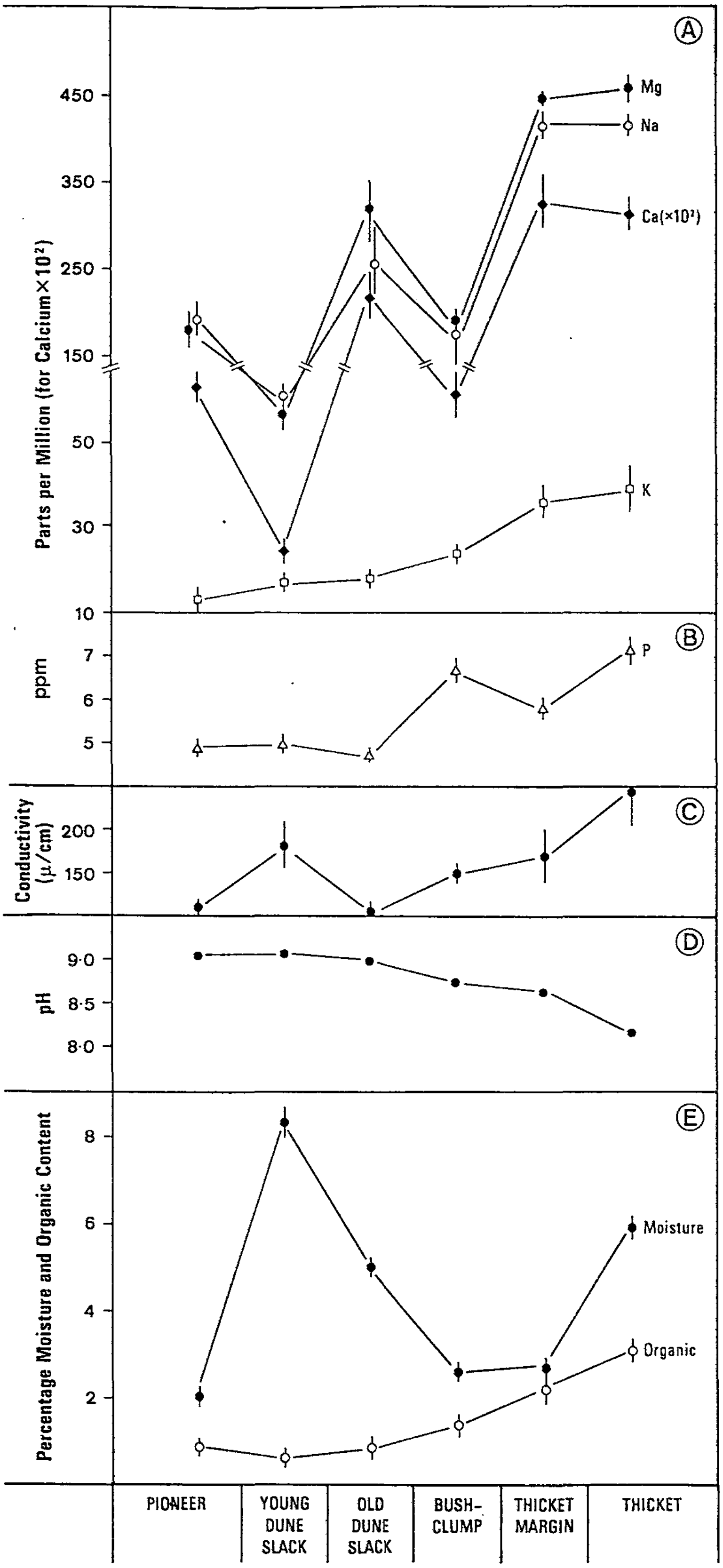


Figure 4.10 Mean and Standard Error of all soil properties measured in the six plant communities (Table 4.4). A - Exchangeable bases (ppm); P - Phosphate (ppm); C - Conductivity [μS/cm]; D - pH; E - % moisture and % organic matter.

more rapidly due to increased leaching. There is only a slight difference in the concentration of these bases between Thicket Margin and Thicket communities. Both K and P (Fig. 4.10b) show a steady increase, although this is more rapid and significant for the former. This increase in exchangeable bases and P is reflected as an increase in conductivity (Fig. 4.10c). The higher conductivity in the Young Dune Slacks, which show a decrease in Mg, Na and Ca is not related to base content, but rather to percentage moisture, as a positive association between moisture and conductivity exists in dune slacks (Chapter 2). The Pioneer, Bushclump and Thicket Margin communities have comparable, but low amounts of moisture (about 3.0%), whereas the Old Dune Slacks and Thicket communities are wetter (6.0 and 7.5% respectively). Soil moisture is significantly higher in Young Dune Slacks (Fig. 4.10e). Percentage organic matter shows a steady increase from Pioneer to Thicket while pH shows a slight decrease (Fig. 4.10d).

DISCUSSION

PLANT COMMUNITIES - CLASSIFICATION AND ORDINATION

At Kleinemonde, six distinct communities based on a TWINSPAN classification of the relative importance of the plant species were isolated (Table 4.1). These communities were arranged by DECORANA along a gradient of increasing community complexity and age, and decreasing environmental variability with increasing distance from the sea (Figs. 4.2 & 4.3). Initially communities were unistratal and dominated by forbs, but shrubs and trees become more common (Fig. 4.7). An increase in organic matter, soil moisture content and exchangeable bases, and decrease in pH was recorded (Fig. 4.10), and it was possible to group samples on the basis of their soil properties (Fig. 4.8). Olson (1958) reported similar trends at Lake Michigan, and also noted that the younger communities were dominated by grasses (*Ammophila arenaria*) and herbs (*Cakile edentula*). It was only once autogenic changes to the micro-environment (shading) and soil (increased organic matter) occurred that woody species were able to invade. Smith *et al.* (1985) reported similar trends in New Zealand, but noted that a woody species, *Metrosideros umbellata* was confined to the seaward margin of the dunefield. This was due to interspecific competition since other woody species, with which *M. umbellata* could not compete, were unable to become established in this harsh environment. At Kleinemonde, a similar situation may occur with *Passerina rigida* which was the first woody species to invade the dune slack (Chapter 2) and is fairly common on foredunes (Chapter 1). This species may be very important in linking the succession, having a similar role to the woody pioneers which link communities of different ages together at Lake Michigan (Olson 1958).

Similar changes in species composition and community complexity with age and distance from the sea have been reported by Kachi & Hirose (1979) in Japan, by Kumler (1969) on the Oregan Coast, by Espejel (1986) in Mexico, Sacheti & Scott (1986) in South-eastern Australia, Chladil & Kirkpatrick (1989) in Tasmania and in South Africa (Chapter 3). However, other workers have noted that this trend is not always so well defined (Kirkpatrick & Hassel 1981) but in this study the difficulty in relating the various communities to a successional sequence was due to past disturbance by man.

Results of the ordinations (Figs. 4.2 & 4.3) suggest that the changes in this successional sequence occur at the community - unit level, rather than along a continuum (Whittaker 1953). However, an analysis of the data using the continuum index formula of Cottam (1949) and Curtis & McIntosh (1951) suggested that at the species level changes may be individualistic (Fig. 4.6). These results infer that further studies are required to determine the mechanisms of turnover, as at this level of pattern analysis the individualistic hypothesis is unfalsifiable (Shipley & Keddy 1987). However, the degree of similarity between lower and higher successional stages is very low (Table 4.3), suggesting rapid species turnover, and similar conclusions were drawn at Mtunzini (Chapter 3).

SUCCESSION AT KLEINEMONDE

The earlier model of succession was based on a relatively short temporal study of a dune slack community which was exposed to a changing local environment. The present investigation of spatial sequences within the dunefield provides further support to this model (Fig. 2.9; Chapter 2). The suggested trend in community change was from either foredune, but usually dune slack, to a dune scrub community dominated by shrubs, and finally a thicket community with shrub and tree species. Ordination of the data in this study showed such a community change from Pioneer to Young and then Old Dune Slacks, Bushclumps, Thicket Margin and finally Thicket (Fig. 4.2), but, unlike the situation at Mtunzini, these communities are not linked spatially. The presence of a distinct Exposed Thicket Margin community (Table 4.1) supports the suggestion in Chapter Two and that of Tinley (1985) that the thicket is retreating. If this is the case it is possible that the climate was more favourable in the past, and therefore a more linked succession may have existed. The long term changes in vegetation dynamics have been investigated in the Alexandria dunefield where Parker-Nance *et al.* (1991) separated four communities and related these to geomorphic age. They showed an apparent successional pathway progressing from dune scrub (Old Dune Slacks/Bushclumps) to dune thicket (Thicket), dune forest and finally Sundays River scrub.

The results of the present study also lend support to the proposed change in species composition (see Fig. 2.9, pg 86). Foredunes are primarily dominated by *Scaevola plumieri*, and to a lesser extent by *Agropyron distichum*. Although *Sporobolus virginicus* dominated three of the foredunes sampled, these communities clustered with the Young Dune Slacks, in which *S. virginicus* is also very abundant (Fig. 4.5; Plate 4.2), suggesting that it is a "linking species", able to invade both dunes and slacks by stoloniferous growth. For this reason it was classified together with *Arctotheca populifolia* as a dune and slack pioneer (see Fig. 2.8, pg 83). The model suggested that the development of more complex communities from the Pioneer communities of foredunes was a less common successional pathway, and these results support this conclusion. For example, Dune Scrub species, such as *Passerina rigida,* were only recorded on one *Sporobolus* foredune, and other woody and herbaceous species more common in slacks and bushclumps were not recorded on the foredunes.

Sand dune colonizers (see Fig. 2.8, pg 83) or dune pioneers have an indirect autogenic effect on the succession; by initiating foredune development these species reduce sand movement and intercept salt spray, thus creating more suitable and protected habitats in the moist slacks which are then invaded by dune slack colonizers such as *Scirpus nodosus.* The importance of foredune development in dune succession was evident at Mtunzini (Chapter 3), but this aspect requires further research, especially on the processes initiating and controlling foredune development at Kleinemonde, where the successional sequence is not as obvious. More detailed studies on micrometeorological and microenvironmental factors as well as autecological studies, such as those undertaken on Lake Huron sand dunes by Baldwin & Maun (1983), are necessary. The pioneer species capable of colonizing foredunes and initiating dune development and growth (sand dune colonizers of Chapter 2) may be so highly specialized that no other groups of species can succeed them, since they are not as specialized. In addition, they may not modify the microenvironment of the foredunes sufficiently to create suitable conditions for other species to invade. Evidence from this study and Chapter Three suggests that it is only along prograding coastlines, such as Mtunzini, that the foredunes will be colonised by secondary species.

As foredune development is responsible for indirectly or directly initiating the successional processes, it is important to understand the role of wind, sand movement, wind-plant interactions and topography in dune development. In a sheltered region at Kenton-On-Sea, about 30 km to the west, foredune formation and growth is rapid due to the accretion of sand and the interaction of communities of the grass pioneer, *Ehrharta villosa.* Studies have been initiated on the autecology of this species, and succession in the area is being monitored. This should provide some answers to the questions posed above, but does not form part of this thesis.

At Kleinemonde it would appear that direct facilitation or "relay floristics" succession only starts from the dune slacks. Under the present environmental conditions this succession is terminated at the Bushclump stage and the true "climax" community of Dune Thicket will not be attained. The foredunes *per se* cannot be invaded by secondary species such as *Stoebe plumosa* and *Rhus crenata* since the coastline is not prograding, and conditions therefore remain too harsh. However, as shown earlier, these species are able to invade older slacks (Chapter 2). The model suggests that slacks will first be invaded by *Scirpus nodosus* and *Juncus kraussii,* which is verified in this study where these two species, together with *Sporobolus virginicus,* dominate young slacks (Fig. 4.5; Table 4.1; Plate 4.2). The abundance of the latter species may be due to prevailing dry conditions, or it may simply be that these slacks are still very young. The slack communities are more complex and diverse than the Pioneer communities due to the invasion of species into these more sheltered habitats (Fig. 4.4; Plate 4.3). However, apart from high percentage moisture, the soil conditions are not more favourable than on the foredunes (Fig. 4.10).

In Chapter Two it was noted that *Passerina rigida* was the first woody species to invade the dune slacks, and it is one of the most common woody species in the Old Dune Slacks (Fig. 4.5). It is also common in bushclumps (Talbot & Bate 1991; Chapter 1), and was found in all communities except the Dune Thicket, suggesting that it may also be a "linking species". As predicted, *Stoebe plumosa* and *Rhus crenata* were also common in Old Dune Slacks and Bushclump communities (Fig. 4.5), which are dominated by shrubs (Fig. 4.7). *Cynanchum natalitium* and *Rhoicissus digitata* are common in both Bushclump and Thicket Margin communities, and together with *Rhus crenata* appear to link these two communities (Fig. 4.5). This evidence linking Old Dune Slacks to Bushclumps, and Bushclumps to Thicket is circumstantial and it is not possible from these studies to determine the origin of bushclumps, i.e. are they climax successional patches developed from dune slacks (depositional moulds) or remnant forest patches (erosion knobs, *cf* Hesp 1986). The latter develop when mobile dunes transgress vegetated portions of the dunefield, killing most of the vegetation but leaving isolated, vegetated mounds and knobs. Depositional mounds are initiated by the germination of *Myrica cordifolia*, usually in slacks (Hesp 1986). More recently Talbot & Bate (1991) noted that bushclumps of the Alexandria dunefields differ in their ability to survive sand burial, and defined two types on this basis. Forest pockets appear to be well enough established and tall enough to survive, but shrubland pockets are buried as the dune advances. However, greater nutrient levels, seed bursts and vegetative reproduction ensures that these bushpockets become re-established once the dune has passed over them (Talbot & Bate 1991). Forest pockets appear to be more permanent features of the dune landscape, with similar species to those of the surrounding thicket. This important aspect which links the successional stage, requires further investigation. If bushclumps at Kleinemonde were shown to be closely related, both edaphically and floristically, to the dune slacks, then this would indicate a "pre-climax" successional patch isolated in the dunefield, and support the original observations (Chapter 2). However, a closer relationship to Dune Thicket may indicate that these Bushclumps are remnant thicket patches that survived when most of the thicket was buried by dunes which became destabilized during a prolonged period of very low or eratic rainfall. This may also have occurred during a period of accretion when mobile dunes were able to invade and smother the vegetated dunes, or a combination of these factors as is thought to have occurred in the Alexandria dunefield (Illenberger 1988).

From this, and earlier studies (Chapter 2; Lubke & Avis 1982a), it is possible to assign specific species to certain stages in the succession. For example, *Scaevola plumieri* is confined to the foredunes, *Juncus kraussii* to dune slacks and *Myrica cordifolia* to the bushclumps (see Chapter 1, Appendix 1.1, pg 56). Furthermore, it is possible to show which species are important in linking together the various stages of succession. These include *Sporobolus virginicus, Passerina rigida, Myrica cordifolia* and *Brachylaena discolor* from foredune to forest. This was shown more clearly at Mtunzini (Chapter 3), and both Olson (1958) and Smith *et al.* (1985) presented similar results at Lake Michigan and in New Zealand, respectively. In Chapter Three it was suggested that a process of nucleation initiated by the tree, *Mimusops caffra*, as originally described by Yarranton & Morrison (1975) at Grand Bend, Ontario, occurred at Mtunzini (Chapter 3), but this does not seem to be the case at Kleinemonde. The dune slacks appear to act as "centres of diversity" which are invaded by a greater number of species due to the more favourable microenvironmental factors and are an important link in the successional sequence. They show the greatest degree of similarity with Pioneer and Old Dune Slack communities, due to the large number of shared species (Table 4.3) Preliminary studies initiated as an adjunct to this study show that while surface and soil temperature at a depth of 1cm are similar for vegetated foredunes and slacks, soil temperature at a depth of 10cm is far more constant in dune slacks, and relative humidity was less variable. Wind speed and light intensity were similar in slacks and vegetated foredunes, but sand movement was more rapid on foredunes (Zwannekin 1989). Thus, although far less common and much smaller than the dune slacks found on European dunes (van Tooren *et al.* 1983), they play a major role in community dynamics and succession within the drier dunefields of South Africa.

A steady increase in species diversity from Pioneer to Thicket communities, increasing more rapidly initially was recorded (Fig. 4.4). This more rapid initial increase was also noted in the previous temporal study at Kleinemonde (see Fig. 2.7, pg 81), as well as at Mtunzini (see Fig. 3.7, pg 108). These results do not seem to support the theory that diversity will decrease in the climax community (Margalef 1968). However, it is possible that samples were too close to the seaward margin of the Dune Thicket and did not include the true climax (Fig. 4.1). Burns (1986) has shown that differences in species composition and physiognomy, which can be related to dune aspect, exist within dune thicket, but the sample size within this community was too small to reveal these differences. The initial low level of species diversity is due to the highly variable and unstable environment on the foredunes. This trend was noted by most of the above researchers, as well as Mun & Kim (1985) in Korea, and at Lake Huron by Baldwin & Maun (1983) and Morrison & Yarranton (1974). They showed an initial rapid increase in species richness and evenness, due to the initial rapid immigration of new species after surface stabilization. The greater species diversity within dune slacks is mainly due to surface stability, since sand movement is a major factor controlling seedling establishment (Avis & Lubke 1985) and distribution of plant communities in coastal dune systems (Lubke 1983; Moreno-Casasola 1986). Although not tested for, it is likely that the more diverse dune slacks show greater vegetational heterogeneity due to increased competition and abundance of vegetation within fairly restricted areas. If this was the case, then the dune slacks would be a transition stage, similar to that reported by Morrison & Yarranton (1974). However, this aspect requires further study.

EDAPHIC CHANGES ALONG SUCCESSIONAL GRADIENTS

Local studies on dune succession have generally neglected investigations on soil properties. Moll (1969) recorded pH along a transect at Mtunzini and van Daarlen *et al.* (1986) noted the depth of the organic layer and value and chroma of the A horizon in this dunefield. Lubke (1983) recorded moisture content, organic content, pH and conductivity along transects at Kleinemonde. In studies on the Alexandria dunefields, McLachlan *et al.* (1987) recorded $CaCO_3$ and Young (1987), N, P, K and $CaCO_3$. Salisbury (1925) first demonstrated changes in soil properties on successive dune ridges at Blackeny Point, United Kingdom. He reported a progressive leaching of carbonates with increasing age, a change from alkaline to acid conditions and a progressive increase in organic content. Generally, the same trends in soil properties with increasing community complexity were noted by all the above researchers on South African dunefields.

At Kleinemonde it has been possible to classify, using TWINSPAN, distinct plant communities based solely on their soil properties (Fig. 4.8; Table 4.4). Progressive development of the soil has occurred contemporaneously with vegetation development (Fig. 4.10). Generally all the exchangeable bases increased from Pioneer to Thicket communities as vegetation changes proceeded. This was related to the increase in organic matter which caused a corresponding decrease in pH due to the production of carbonic acid during decomposition. The high soil moisture content in the slacks is due to the shallow water table (Plate 4.4), and in the Dune Thicket due to the improved water holding capacity of the soil and a reduction in evaporation (Fig. 4.10). These increases in organic matter and exchangeable bases increase the nutrient reserve and modify the moisture and aeration characteristics of the soil (Olson 1958).

Although the soil in dune slacks is stable due to the high moisture content, it is infertile (Fig. 4.10). Species colonizing these areas must be able to grow in a low nutrient medium, and this severely restricts their growth rate. Slack species have been shown to respond favourably to the addition of nutrients (Willis & Yemm 1961) but studies by Hawke & Maun (1988) showed that a beach specialist such as *Cakile edentula* had fairly exacting requirements of N, P and K. In the Alexandria dunefield about 50 km west of this study area, Young (1987) showed that the addition of nitrogen, either by itself or in combination with phosphate, resulted in an increase in phytomass in both field and greenhouse trials. *Arctotheca populifolia* showed the greatest response, but *Juncus kraussii* and *Gazania rigida*, both dune slack species, also showed significant increases in phytomass. She found low levels of nitrogen in this dunefield, but levels of nitrogen were greater on the foredunes than in the dune slacks. This is due to a higher amount of organic matter along the drift line, a result of detritus being washed up by the tides.

Nutrients increase rapidly when trees shade the surface and leaf litter accumulates (Tinley 1985). This increase in the soil-nutrient relationship results in a more favourable soil environment and consequently more species are able to colonize. This was not the case in the Bushclumps, where most of the exchangeable bases decreased despite an increase in woody species and diversity (Figs. 4.4; 4.7 & 4.10). This could be related to their greater exposure, since they are often perched on aeolionite ridges, where leaching is rapid, although nutrient input from salt spray would also be high (Plate 4.4). Levels of nitrogen and organic matter were highest in bushpockets of the Alexandria dunefield, but both potassium and phosphate were lowest (Young 1987). This could be due to a restriction of mineralization and nitrification, and the leaching of nitrate. Generally, however, phosphate and trace elements are present in fairly large quantities and are not limiting.

The steady but significant increase in calcium is difficult to explain as this is contrary to reports in the literature (Crocker & Major 1955; Olson 1958; Baldwin & Maun 1983; Smith *et al.* 1985; Sacheti & Scott 1986). One would expect Ca levels to decrease with age of soil as this cation is valuable in plant nutrition and therefore as soil development proceeds it becomes partially replaced by hydrogen ions (Olson 1958). There appears to be no correlation between Ca and vegetation in this study, and this is in contrast to Parsons & Ware (1982), who reported that Ca showed the closest relationship to vegetation in a coastal swamp in Virginia. Moreover, in the Alexandria area, $CaCO_3$ was shown to decrease steadily with an increase in dune age (Young 1987). It is possible that the high Ca concentration in the older communities is indicative of higher $CaCO_3$ in the sands deposited at this period, since Ca is mainly the result of shell deposits in the young dunes.

Chapter Two suggested that the build up of nutrients as a result of humus decomposition is an important factor in the successful invasion and establishment of other species in the slack. The higher levels of Mg, Na, Ca, K and organic matter recorded in the older slacks (Fig. 4.10) is probably the result of humus decomposition. The low values for most soil properties recorded in young slacks suggests that these factors may not be as important in the early stages of succession; or that since their development is largely autogenic no build up of nutrients has occurred yet in these young communities. Indeed, it is possible that this community may be utilizing more nutrients than it is returning to this rather closed system. At a later stage in the development (Old Dune Slacks) nutrients are returned by decomposition. Foredunes, on the other hand, receive nutrients from detritus deposited on the drift line. The initial rapid growth in slacks is therefore more dependent on the stable sand surface and greater moisture content than on the levels of nutrients, pH and conductivity. In an earlier study (Lubke & Avis 1982a), the distribution of *Scirpus nodosus* within the study slack (Relevé 12) was found to be more closely related to soil moisture than any other edaphic factor, and clearly wetter sand will be more stable. More recently, Dougherty *et al.* (1990) showed that the concentration of soil nutrients (Ca, Mn, K, Na, Fe & Mg) and soil pH were not significantly related to plant growth. Soil nitrogen was the primary growth-limiting nutrient in this dune slack in Louisiana. Additions of phosphorus and potassium did not increase soil levels, possibly due to leaching or uptake by plants. Decreases in the concentration of Ca, Mg and Mn in slacks was attributed to precipitation of soluble salts and plant uptake.

An increase in organic matter and decrease in pH was reported by Crocker & Major (1955) at Glacier Bay, who related these changes to the incidence and age of the colonizing vegetation. Moreover, the type of plant was found to markedly affect the rate of change of pH in the soil. These changes were related to an increase in the phytomass of the community and increased leaf litter, but soils may eventually become less fertile due to illuviation and a greater proportion of the nutrients being bound in the phytomass (Smith *et al.* 1985). A decrease in organic matter or soil fertility was not detected in the Thicket, probably because this community, and therefore the soils, are still too young.

The increase in exchangeable bases and phosphate recorded in this study has also been noted by Olson (1958), Baldwin & Maun (1983), Smith *et al.* (1985) and in Chapter Three. By inference, the Cation Exchange Capacity in the older soils will also increase, and one would therefore expect more leaching, as reflected in the decrease in pH. There is, therefore, a general improvement in soil properties associated with a build up of organic matter. These changes in soil properties are more rapid initially until they eventually approach an upper limit, after which soil conditions may become less favourable. Such changes were noted by Olson (1958), Crocker & Major (1955) and Smith *et al.* (1985), who also recorded improvements in factors such as bulk density, nutrient status and levels of nitrogen and moisture equivalence.

The role harmful soil organisms play in placing sand dune colonizers at a competitive advantage has not been investigated in South Africa. Van der Putten & Troelstra (1990) observed growth reduction in *Ammophila arenaria* in stable sands due to the low number of nematodes, which may become pathogenic when they interact synergistically with other soil organisms, particularly soil fungi. Thus, the high concentration of nematodes in mobile sands reduce the number of harmful soil bacteria, and they concluded that this may influence vegetation succession. The importance of vesicular-arbuscular mycorrhizal fungi (VAM) have also not been considered in this or any other study in South Africa. Rose (1988) showed that the distribution of VAM was related to vegetation and sand dune succession, due to the role played by VAM in aggregating sand particles to produce a more stable substratum. Logan *et al.* (1989) found a very high occurrence of VAM in dune plants in Australia, and these aspects require further study on our dunefields.

COMPARISON OF KLEINEMONDE WITH OTHER SOUTH AFRICAN DUNE SYSTEMS

The model presented in Chapter Two (Fig. 2.9) suggested that the greatest diversity of slack species is likely to occur when *S. nodosus* is the pioneer of wet slacks, and not via dry slacks colonized by *Sporobolus virginicus*. Thus, in slacks colonized by *S. virginicus* plant diversity will not increase substantially and these would probably not be invaded by shrubs. This study proves this hypothesis (Table 4.1; Figs. 4.4 & 4.5) and in three cases samples from *S. virginicus* dominated foredunes were grouped with the Young Dune Slack community, implying a closer affinity of dry slacks with foredunes than with the more diverse Old Dune Slack community, which has a greater number of shrubs (Fig. 4.7). As predicted, shrubs such as *Rhus crenata, Stoebe plumosa* and *Myrica cordifolia* are now common in the dune slack being monitored (Plate 4.3). In the Alexandria dunefield the transverse dune ridges flanking interdune slacks show a nett easterly movement of 7 m y^{-1} and this succession therefore covers a time span of 6 to 7 yrs (McLachlan *et al.* 1987). Thus, the Dune Scrub stage described is never reached. However, vegetation cover increases from east (younger) to west (older) as *Sporobolus virginicus* gives way to *Gazania rigens* and finally *Scirpus nodosus*, which is the normal climax species in these slacks. Further west the dunes have been artificially stabilized and these slacks are invaded by *Myrica cordifolia* (Chapter 8). Water and nutrients such as nitrogen and phosphorus, unlike sand movement and salt spray, are not limiting factors in these slacks (McLachlan *et al.* 1987).

Young (1987) sampled a number of dune habitats at Alexandria, using a similar stratified random sampling technique. TWINSPAN was only able to identify three communities, namely, forebeach, seaward dunefield (dune slacks) and landward dunefield communities, and she concluded that although the communities displayed progressive habitat stability, they were not distributed along a successional sequence, as one community did not replace the other with time. However, studies at Kleinemonde (Chapter 2) and elsewhere (Chapter 1) suggest that temporal replacement of species within the dune slacks occurs in a directional manner. The various spatially disjunct and distinct communities isolated in this study (Table 4.1; Fig. 4.1) appear to be distributed along a gradient of time and community complexity (Fig. 4.2), with a number of species diagnostic to certain communities but also found in others (Figs. 4.5 & 4.6).

Parker-Nance *et al.* (1991) reported two successional pathways operating on older dunes at Alexandria (6500, 120 000 and 220 000 yrs). The first occurred on sandy habitats, where succession progressed from an open dune scrub to a climax dune forest vegetation. The second took place over a longer geological time-scale from sandy habitats to shallow but more developed soils. Climatic conditions along the Natal coast of South Africa are more favourable for plant growth, with warm, humid days and a high rainfall (see Fig. 3.1, pg 92). Succession is therefore more rapid and easily discernable. Ward (1980), in his studies on the plant communities at Isipingo Beach in Natal reported that succession after the foredunes were invaded by pioneer species formed a continuum of closed wooded communities from dune scrub to dune forest. Intermediate communities included open and closed dune scrub, and a *Mimusops caffra* dominated woodland. Salt spray and edaphic factors were the most important environmental factors influencing this succession, and his results support the conclusions drawn in Chapter Three.

A number of researchers have highlighted and described the fine example of primary succession occurring at Mtunzini (Weisser & Backer 1983; van Daarlen *et al.* 1986). The clear and continuous chronosequence from pioneer species to climax forest is attributed to the favourable climate and rapid accretion of sand (Chapter 3). Although the dunefield at Kleinemonde is not accreting and the climate less favourable for plant growth, many similarities between this area and Mtunzini can be drawn. At Mtunzini, it was possible to accurately age the dune ridges and the eight communities found on them. Ordination of the data showed a clear trend of increasing community complexity with age and increasing distance from the sea (see Figs. 3.5 & 3.6, pgs 106 & 107). A similar trend was noted in this study (Figs. 4.2 & 4.3), but a number of differences are apparent. Relative to the climax Thicket community, the Pioneer communities were more diverse with a greater range on axis 3 (Fig. 4.2). This greater euqitability or uniform distribution of abundances within the Thicket is opposite to the trend observed at Mtunzini, where the Forest Communities showed greater variability (see Fig. 3.5, pg 106). This may have been due to insufficient samples in the Mtunzini forests, or may be related to an increase in canopy cover, accumulation of humus, increase in the moisture regime and other age related factors. However, if these reasons are correct, one would expect the same trend at Kleinemonde. It appears that at Kleinemonde species composition within the thicket is relatively constant when compared to the species composition within the Pioneer communities, which differs markedly. This is reflected in the dominance of foredunes by a range of different species at Kleinemonde, whereas at Mtunzini foredunes are only dominated by *Scaevola plumieri.*

Furthermore, at Mtunzini, although the various stages of succession were linked spatially they could still be divided into discrete and recognizable units, thus lending support to the community unit concept of vegetation science and classical Clementsian succession (Clements 1916; Egler 1954). At Kleinemonde the vegetation is not linked spatially, but occurs as islands within the dunefield, and the object was to determine whether these could be linked in a succession similar to that described earlier (Fig. 2.9), or whether the vegetation formed a continuum despite being spatially disjunct. This is possible as a spatial relationship between sites with similar values on a gradient is not necessary (Austin 1985). In both these studies, the data suggest that the vegetation forms discrete communities which can be linked to a pathway(s) of succession. Similar results were found by Weisser *et al.* (1982), Weisser & Baker (1983) and Weisser & Muller (1983) at Mtunzini, and the data presented here supports the model of succession for Eastern Cape dunefields (Chapter 2).

It is possible that a greater number of successional pathways exist at Kleinemonde than at Mtunzini, since the less favourable climate may result in a wider range of specialization and adaptation in species. In these cases rigid convergence to a single climax may not occur, but rather divergence as the condition of equilibrium is never reached since the variable of community change is approaching another variable rather than a constant. This was also noted by Olson (1958) but at Mtunzini it appears that convergence occurs due to the more favourable climatic and environmental conditions prevalent in that system.

CONCLUSION

The results of this study support the model of community change given in Chapter Two. Although not spatially linked in the dunefield, the various communities sampled were positioned along a gradient of increasing community complexity (higher species diversity; larger plants; structural development). There was a corresponding change in edaphic properties, the most notable being an increase in organic matter and exchangeable bases, and decrease in pH. These directional changes appear to support the community unit concept of vegetation science. They are autogenic, with the dune slacks acting as centres of diversity and the foredunes providing indirect facilitation by protecting these more mesic habitats from factors such as salt spray and sand movement. Multiple pathways of succession probably act on these systems in response to the harsh environmental conditions which prevail, but at this descriptive level they are not possible to elucidate. Further work is planned on the autecology of the "linking species" identified in this study.

PART TWO : MANAGEMENT STUDIES

An ecological approach to coastal dune management has been discussed in the introduction, and recent perspectives presented by van der Meulen *et al.* (1989) support the need for more applied ecological research. However, the marrying of ecology and management is problematical, because models are usually of little practical use, and secondly because of inherent limitations of ecology as a means of analyzing management problems (Tivy 1974). Liddle (1975a) very clearly enlarges upon this as follows "... ecology is the scientific study of living organisms in relation to the environment. Ecology is not and should not try to be a means of determining visitor requirements, nor is it a means of telling a manager what criteria of maintenance or management he should adopt - these are management decisions which the ecologist may wish to influence, especially in relation to the conservation of rare species or habitats, but they are not scientific study. What the ecologist can and should do is to produce information by investigation and experimentation so that he may tell the manager what can be done and how he can manipulate the environmental process to achieve certain management criteria". Human need, the state of tension between what mankind has and what mankind wishes to have, will almost always lead to an environmental disturbance. This will set off a series of ecological effects, and if these effects degrade the ecosystem, they will cause an environmental impact which detracts from human needs (Clark 1974). Thus, to prevent an ecological effect becoming an environmental impact, one needs to assess the reaction of an ecosystem to a disturbance. This is particularly so in South Africa, where there is an urgent need for more applied ecological studies on aspects such as the tolerance of dune systems to recreational pressure, and the desirability and success of manipulative processes such as dune stabilization.

The second part of this thesis therefore investigates levels of beach utilization at a specific site, and assess the ecological impacts of recreation on dune vegetation. The application of successional concepts discussed in Part One, to manipulate ecological processes are evaluated with respect to current techniques in dune stabilization and the resilience of ecological systems to small scale environmental perturbations.

CHAPTER 5

RECREATIONAL USE OF THREE URBAN BEACHES AT EAST LONDON AND EFFECTS ON COASTAL DUNE VEGETATION

INTRODUCTION

Recreation refers to the activities pursued by people outside their production or wage earning time (Nelson 1976 in Sutcliffe 1981), and factors contributing to higher levels of recreation include increase in population, improved economic circumstances, paid leisure time and increased mobility (Malan 1983). South Africa is one of the world's fastest growing nations, and coupled with the recent diffusion of income into the non-white segment of society, significant increases in the demand for recreational opportunities can be expected. Much of this increased demand will be concentrated in coastal areas, which offer diverse landscapes and the potential for a wide range of recreational opportunities (Sowman 1984). Furthermore, 44% of outdoor recreation participants favour water-based activities (Tanacredi 1983). The decision-making authorities, well aware of this potential threat to the coastal zone, have produced guidelines outlining both the principles and objectives of coastal zone management (CZM) and coastal land use (Council for the Environment 1989 & 1991). However, legislation protecting the environment is ineffectual (White 1991), and the protection and wise use of these areas therefore relies heavily on the altruism of the landowner. An urgent need for applied research on aspects of CZM therefore exists, so that the carrying capacity of these areas are not exceeded. This is particularly germane to coastal dune systems and beaches in an urban setting, for the following reasons:

* They are exposed to higher levels of recreational pressure than elsewhere (Carter 1980a; Eastwood & Carter 1981; Tanacredi 1983; Sothern *et al.* 1985).
* These systems are sensitive to recreational pressures, such as trampling (Trew 1973; McAtee & Drawe 1980; McDonnell 1981; Sothern *et al.* 1985) vehicle use (Carter 1980a; Godfrey & Godfrey 1980) and other indirect effects (Vogt 1979).
* No information is available on the ecological effects of human trampling in South Africa (Heath 1987), and no estimate of the carrying capacity of dune systems can therefore be made.
* Dunes and beaches are listed as sensitive and dynamic systems which should be subject to strict control (Council for the Environment 1991), but support for this control is difficult to achieve if no quantitative information on tolerance and utilization levels is available.

Vogt (1979) notes that data on the condition of the environment and on current recreational uses should give the manager an idea of the recreation preferences of the public as well as the amount of use taking place. This information, together with the natural features and their sensitivity, should at least give an indication of whether protection or increased access is in order. This is most useful in view of the contradictory nature of the primary goals of CZM; namely to increase public access to the shoreline for recreation, and at the same time to preserve this valuable and unique resource (Vogt 1979). Despite the increasing demand for recreational facilities within the coastal zone, little data are available on the number of people visiting urban beaches in South Africa. In the city of Durban, on the Natal Coast, the 1987 Christmas season holiday rush of 126 000 people overwhelmed the coastal facilities, leading to unpleasant confrontations (Little 1989). In Port Elizabeth Glassom & McLachlan (1989) investigated the level of use at three beaches over the December/January period at the request of the local authority. Abroad, studies on beach utilization have been undertaken by Williams & Randerson (1989) in South Wales, Carter (1980a) in Northern Ireland and Trew (1973) in the United Kingdom, in an attempt to relate current utilization with potential ecological effects. Burden & Randerson (1972) showed the importance of assessing the intensity of recreational pressure an area is exposed to by considering the number of people, their distribution and activities, as well as the season of the year and length of time for which the pressure is applied. One way of assessing this is by means of a questionnaire survey (Usher 1978), as undertaken by Eastwood & Carter (1981), although their survey was aimed at assessing visitor's perceptions and motivations which underlie behaviour patterns such as entering dunes. Trew (1973) undertook a questionnaire survey to assess the opinion of the beach user to various aspects such as capacity and adequacy of facilities, as did Glassom & McLachlan (1989) in Port Elizabeth.

This study was undertaken on three beaches at East London, a coastal city in the Eastern Cape (see Fig. 1.1, pg 17). Beaches are defined here in the vernacular sense as simply the shore of the sea, which is generally the area above the low tide mark. This definition therefore includes small foredunes and the leading edge of vegetation (*cf* Barbour 1992), as most people think of this entire area as the beach. East London was chosen for this study, rather than the other larger centres of Port Alfred and Port Elizabeth, as no similar studies have been previously undertaken in this area, and the municipality required information on levels of beach utilization and carrying capacities, due to a growing demand for facilities. Furthermore, three distinctly different types of beaches are found in close proximity to each other, and valuable indigenous vegetation occurs adjacent to these important recreational facilities (Lubke & Strong 1988).

An important aspect of the present study was therefore to determine carrying capacity, which is defined here as "the level of recreational use an area can sustain without an unacceptable degree of deterioration of the character and quality of the resource, or of the recreation experience" (Pigram 1983). Three types of carrying capacity, as defined by Brotherton (1973), were considered. Physical capacity is simply a measure of the number of "use units" (people, cars) that a given area can accommodate. Ecological carrying capacity is the maximum level of a particular type of recreation use that a particular ecosystem is able to support without undergoing unacceptable change. The latter is considered here as change which may threaten ecosystem integrity (for example erosion leading to blowouts) and not, as stated by Brotherton, change that would affect the enjoyment of visitors. This anthropogenic aspect is covered by the definition of perceptual carrying capacity, which relates to the visitors perception of others present at the same time, and the effect of crowding on their enjoyment and appreciation of the site. Significant deterioration of the recreational experience will indicate that the perceptual carrying capacity of the area has been exceeded (Vogt 1979).

The determination of ecological carrying capacity has as its main limitation the ability to accurately predict what constitutes unacceptable change to an ecosystem. Other problems are discussed in more detail by Brotherton (1973), Vogt (1979), Pigram (1983) and Sowman (1987), but essentially assessment of ecological capacity must include three aspects;

(1) the nature of the recreation activity, and its frequency, intensity and distribution;
(2) the nature of the plant and animal communities that will be affected, and the likely effect; and
(3) the amount of change to the resource base that is unacceptable or irreversible (Brotherton 1973).

Similarly, the determination of perceptual carrying capacity may also be subjective, mainly because people's perceptions are dependant on so many factors. These and other aspects relating to perceptual carrying capacity are discussed by Brotherton (1973), Trew (1973), Greist (1976), Vogt (1979), Pigram (1983) and Glassom & McLachlan (1989), and are not dealt with further here.

To achieve the primary objective of assessing the carrying capacity of the beaches investigated, a three part study was initiated, with the following main aims:

(1) To determine the current utilization of the beaches under study, and to predict any trends in beach utilization.
(2) To assess, by means of a questionnaire survey, the popularity of beaches amongst recreators of various ages, the adequacy of existing facilities and whether perceptual carrying capacity had been reached.
(3) To determine the tolerance of adjoining natural vegetation types to human trampling.

THE STUDY AREA

East London is one of the largest cities in the Eastern Cape, with a population of around 175 000. It is spread over a series of undulating hills on both banks of the Buffalo River. The city's coastal resources are unique, as no other major urban area in South Africa has such an extensive natural coastline in close proximity to the city centre. Conditions for coastal water sports are of the best available in South Africa (Revel Fox & Partners 1986), and the Nahoon Reef area is internationally known for its excellent surfing waves. The climate is mild and well suited to year round outdoor recreation, the only limitation being winds which, although only occassionally strong, are frequent (see Fig. 1.2, pg 18).

Plate 5.1 Aerial view of the Eastern Beach and Esplanade area looking east towards Nahoon Beach. The large building is the cafe and restaurant, and behind this is the Marina Glen. The road sited in the dynamic zone of the beach is clearly visible.

Plate 5.2 Aerial view of the Nahoon Beach, looking north, showing the distinctive half-heart shape of the embayment. The parking area is towards the left, and Hlaza River on the right. To the right of this is the Lifesavers Clubhouse (arrowed). Note the steep dune with patchy vegetation cover backing the beach.

Despite the extensive coastline, sandy beaches and safe swimming areas are limited to the Nahoon, Eastern and Orient Beaches (Fig. 5.1). The Nahoon Beach is a highly rated watersport venue with excellent conditions for boating, sailing, surfing and swimming (Fig. 5.2). The Orient Beach is more protected and like the Eastern Beach, offers safe conditions for swimming and surfing.

Average daily use of the beach is of a low intensity as 70% of the region's population live away from the coast. Over weekends or public holidays, however, the coast is within commuting distance of over half a million people, with the Eastern and Orient Beaches being most accessible. Current socio-political changes, the direction of urban growth, improved public transport facilities and greater mobility associated with economic upliftment means that the level of occasional use of East London's beaches will increase.

This study concentrated on three beaches which have a definite shortage of facilities (Revel Fox & Partners 1986). The Eastern Beach is a narrow dynamic feature lying on either side of the Blind River (Fig. 5.1). The coastline further north-west is rocky, and the esplanade which runs parallel to the beachfront carries through traffic not destined for the beach (Plate 5.1). The Eastern Beach forms an urban contact with the beachfront (Dennis Moss Partnership 1988a). The bathing beach is backed by a road sited within the sensitive dynamic zone and is therefore subjected to storm wave attack. However, the beach environment appears to be in equilibrium, with no long term loss of sand occurring (Revel Fox & Partners 1986). This road separates the Marina Glen behind it from the beach, and reduces the amount of sandy beach available for recreation to 6.5 ha. Although there is 800 m of waterfrontage, only a 50 m length is safe for swimming. The area is highly accessible, with 357 formal and 120 informal parking bays. According to Pigram's (1983) scale of "modern to primative", the Eastern Beach is semi-modern, and the Orient Beach, which is a small stable pocket-beach trapped between the eastern breakwater of the harbour and the rocky coastline to the south-east, is a modern facility (Fig. 5.1). It has 1.5 ha of sandy beach, a 200 m^2 lawned area and 250 m water frontage, all of which is safe for swimming (Revel Fox & Partners 1986). It is also highly accessible, with 330 formal and 110 informal parking bays. No detailed studies, other than census counts were undertaken at the Orient Beach.

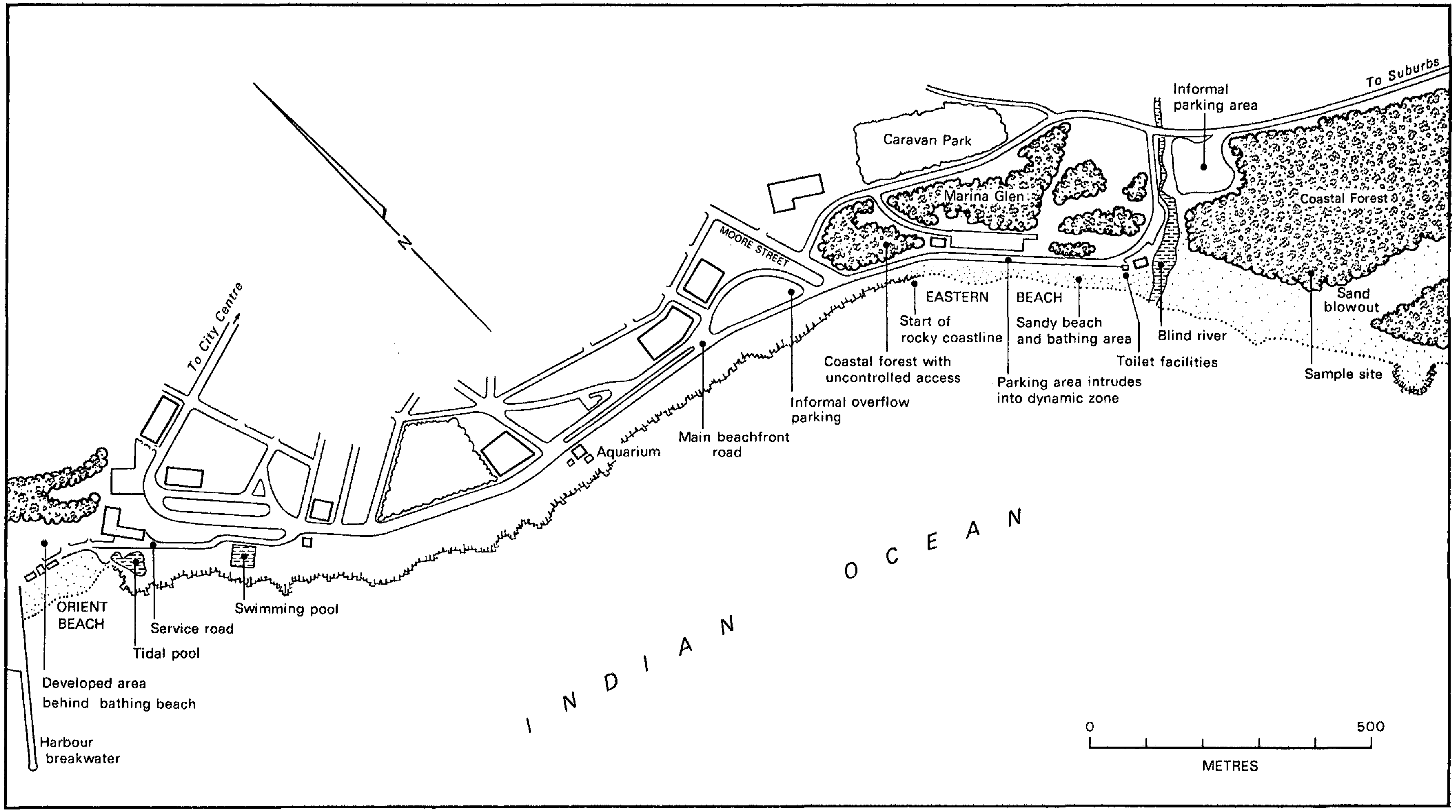


Figure 5.1 Orient Beach, central beachfront and Eastern Beach, showing ecological aspects, access and facilities (modified from Revel Fox & Partners 1986).

The Nahoon Beach has about 6.2 ha of sandy beach between a parking area sited in the dynamic beach zone, and the Nahoon River (Fig. 5.2). There are 110 formal parking bays, and 200 bays in the informal parking area. Of the 900 m of water frontage, only about 50 m is safe for swimming at any one time (Revel Fox & Partners 1986). It is intermediate between semi-modern and semi-primitive and the beach is backed by a steep dune, the seaward face of which has been largely devegetated due to damage to vegetation from recreational pressure, and subsequent surface mass slides of the steep dune (Tinley 1985) (Plate 5.2). The foot of the dune is prone to erosion through direct storm wave attacks, as is the carpark, and this dune probably acts as a source of sediment during periods of erosion. The small Hlaza River opens out over the central part of the beach, and to the east is a Lifesavers Clubhouse and parking area situated within the dynamic beach/dune zone, which becomes wider towards the mouth of the Nahoon River (Fig. 5.2). This sand spit is colonized by pioneer species such as *Ipomoea pes-caprae*, which form embryonic dunes, and *Scaevola plumierii* which forms hummock dunes. Although fairly wide and extensive, this dune area interacts intimately with the river and is subject to erosion during storm and flood conditions, when more than 60 m of the dunefields width can be removed (Avis 1986).

The Nahoon River area surveyed in this study stretches from the launching site to the mouth of the river (Fig. 5.2). It is located on an inner bend of the river and during low rainfall periods sand accumulates on its western bank. It has a dynamic sand spit on its western side and is fixed by a flat rocky shelf, composed of shale, to the east. This semi-modern to semi-primative "beach" has 400 m of river frontage which falls within a dynamic zone subject to storm erosion, and is backed by a narrow band of sensitive dune forest subject to trampling and erosion from water running off the road surface above. The dune forest is wider towards the mouth, but has been damaged through uncontrolled vehicular access. Only 30 informal parking bays exist, with no formal parking. A large caravan park nestles within the inland portion of the dune forest (Fig. 5.2). There is about 4000 m^2 of sandy beach, and 300 m of safe swimming area (Revel Fox & Partners 1986). Small ablution facilities have been constructed within the dune forest, causing damage to this environment (Plate 5.5).

METHODS

AERIAL CENSUS

To determine the number of people at the four main urban beaches, viz. the Orient, Eastern and Nahoon Beaches and Nahoon River, aerial census counts were undertaken during peak periods. The beaches were photographed obliquely from a fixed wing aeroplane at an altitude of 200 m. The number of people in the following zones were counted directly from the colour plates with the aid of a disecting microscope: parking areas; dunes or grassed areas; beach or shorezone; bathers. The number of cars at each of the parking areas was also determined. The first census was on 30 December 1984, and was repeated on 1 January 1986 and 1989 to determine long term trends in peak beach usage. Weather data for the days of the census were obtained from Weather Bureau reports and synoptic charts. Photographs were taken close to midday, when the beaches would be at maximum capacity and the effect of shadows minimal.

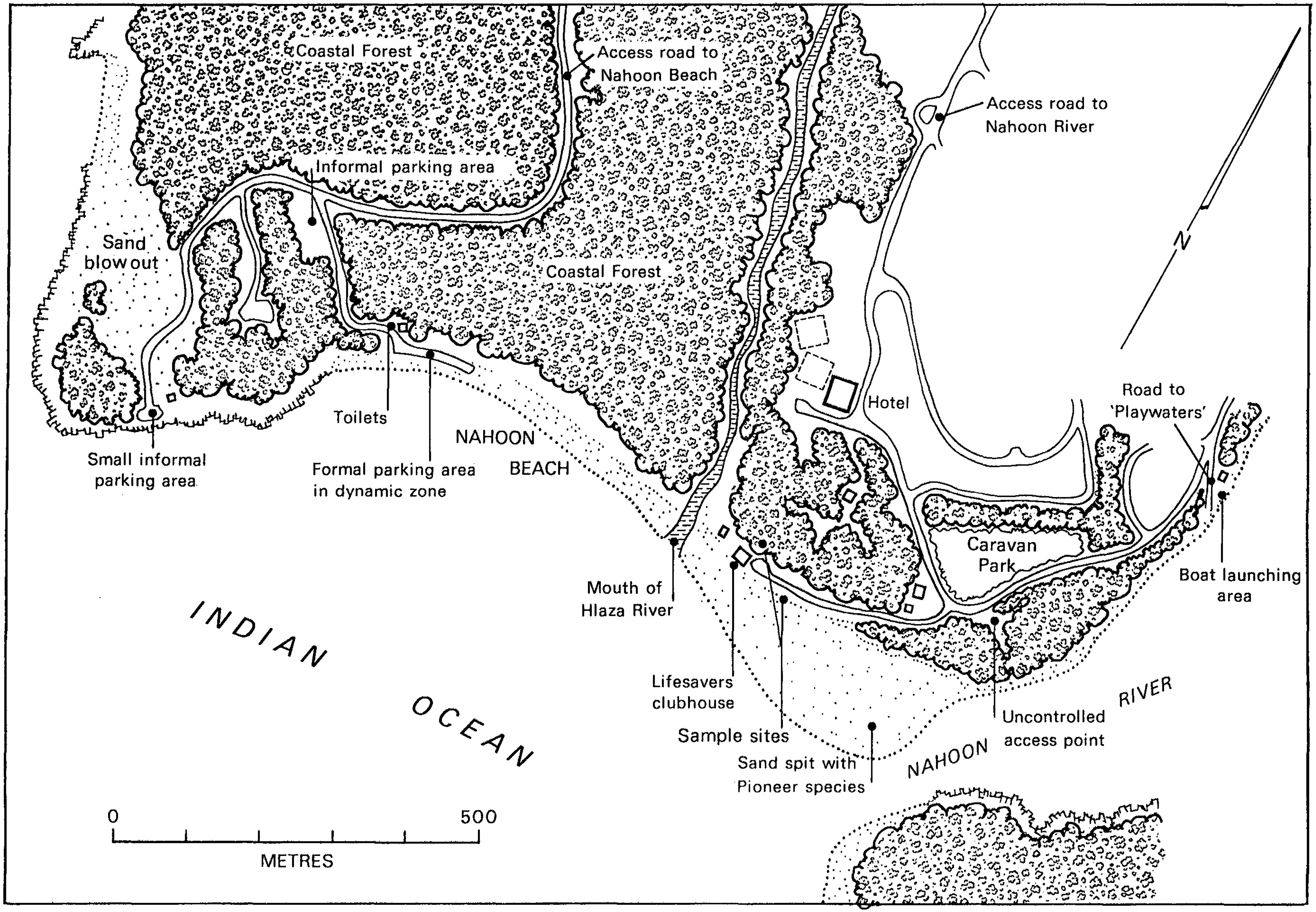


Figure 5.2 Nahoon Beach and Nahoon River recreation areas, showing ecological aspects, access and facilities (modified from Revel Fox & Partners 1986).

QUESTIONNAIRE SURVEY

On Sunday, 30 December 1984, questionnaires were distributed to beach users at the Eastern, Nahoon Beach and Nahoon River. The Orient Beach was not included in this survey as the area is very developed with few natural features and no shortage of basic facilities. The other beaches lack certain facilities and their popularity was not known. The main aims of the questionnaire (Appendix 5.1) were to determine:

a) Visitor's place of residence and popularity of beaches;
b) Age distribution of recreators (*cf* Sutcliffe 1981), and general activities of visitors;
c) Adequacy of parking facilities;
d) Perceptual carrying capacity of beaches;
e) Whether any activites were undertaken by the visitors that could be detrimental to the surrounding vegetation.
f) What additional facilities beach visitors felt were required.

Most of the questionnaires were completed by interviewing the respondent on the beach, and others were handed out together with stamped, self addressed envelopes for return by post. Between 14 and 32% were returned, with the Nahoon Beach having the best response rate (Table 5.1).

Table 5.1 Number of questionnaires completed on the beach and number returned by post.

BEACH	No. Completed on the beach	No. handed out	No. Returned	% returned	Total completed
EASTERN	53	100	14	14	67
NAHOON BEACH	33	75	24	32	57
NAHOON RIVER	47	50	12	24	59

The 183 questionnaires and 18 questions were analysed using the Statistical Package for the Social Sciences (Nie *et al.* 1975, SPSS). Cross-tabulations between the various questions (variables) were generated and statistically compared using chi-squared values. Results are presented as a series of tables comparing the most important variables.

TRAMPLING STUDIES

The herbaceous forest layer at the Eastern and Nahoon Beach (behind the Lifesavers Clubhouse), as well as Dune Scrub dominated by *Chrysanthemoides monilifera*; and the embryonic dunes covered with *Ipomoea pes-caprae* were experimentally treated with measured amounts of trampling. Plots of 10 m by 0.5 m were sampled using a Point Frame to measure the plant height of all species between successive passages (Lindquist 1931 in Hylgaard 1980). The number of passages varied according to the tolerance of the vegetation (Table 5.2), which was exposed to a maximum number of passages by a barefoot person of 75 kg weight that resulted in approximately 50% reduction in plant height on a single occassion (Liddle 1975a). Ten transects of 0.5 m wide were sampled at 1 m intervals perpendicular to the pathway, to give a total sample size of 50 points, as at each 1 m, height was recorded for 5 points at 10 cm intervals (Fig. 5.3). Sample plots were not replicated as this was a pilot survey to determine the best experimental approach for further studies (see Chapter 6). The species, transect number, point number and plant height to the nearest centimetre were recorded, and from these data it was possible to calculate species diversity and mean cover.

The total mean height and standard error of the 10 samples for points 1 to 5 was calculated after each trampling treatment. Data are presented as a plot of mean height of vegetation against number of passages, for points 1 to 5 (Figs. 5.4 - 5.7). A two way analysis of variance was performed to determine if differences in height between treatments and between the 5 points were significant. Shannon diversity indices were calculated for the sample plot after each treatment using the techniques described earlier (Chapter 3; Brower & Zar 1984). A students t-test was used to determine if differences in species diversity were significant.

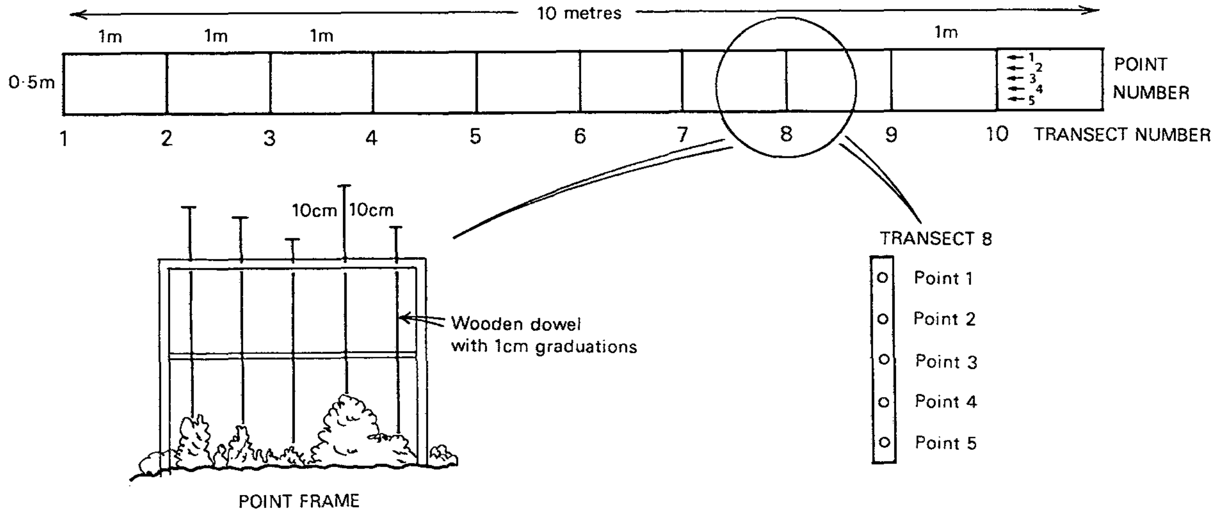


Figure 5.3 Example of layout of sample plots for recording change in plant height exposed to trampling.

Table 5.2 Number of passages to which various dune communities were exposed, showing sampling interval.

COMMUNITY	SAMPLING INTERVAL
Eastern Beach Forest Layer	0; 10; 20; 35; 50; 70; 100; 130
Nahoon Beach Forest Layer	0; 1; 3; 5
Nahoon Beach Dune Scrub	0; 1; 2; 3
Nahoon Beach Dune Pioneers	0; 15; 30; 45; 70; 100

RESULTS

AERIAL CENSUS

Counts of people in the various zones of the beaches, for the three years of the study, are recorded in Table 5.3. The most notable trend was the significant decrease in the number of people at the Orient and Nahoon Beaches in 1989, and the significant increase in people at the Eastern Beach. The decrease was due to the weather, which was not favourable for beach users on 1 January 1989. The ten fold increase in numbers at the Eastern Beach was the result of mass action by the black population in protest against the racially based "Separate Ammenities Act", which only allowed whites to use the Eastern Beach. Use of all facilities by all races has been legalized with the relinquishment of this Act, and this has had important consequences for beach usage in East London. Large numbers of people still frequent the Eastern Beach, particularly on New Years Day, as this is traditional amongst the Xhosa people. Studies were therefore commissioned by the East London Municipality to investigate ways of increasing the carrying capacity of the Eastern Beach (for example Revel Fox & Partners 1986); or encouraging people to use the under-utilized beaches and other facilities on the coastline to the west of the Buffalo River - the West Bank area (Dennis Moss Partnership 1988a&b). In 1984 this area was not well patronised, but in 1989 a total of 5251 people were counted at the West Bank (pers. obs). This was in addition to the 2294 people at the Eastern Beach, and despite the fact that the poor weather resulted in the under utilization of the Nahoon and Orient Beaches. A trend of increasing utilization of the beaches in East London is therefore apparent.

Table 5.3 Number of cars and people at different areas of four urban beaches on 30 December 1984; 1 January 1986 and 1 January 1989. On 30 December a north north-easterly wind of 13.5 km/hr^{-1} was blowing. The day was sunny, with a 23.6°C max temperature. On 1 January 1986 a north-easterly wind of only 5.4 km/hr^{-1} was blowing, but cloud cover was 50%. The midday high was still 24.3°C. On 1 January 1989 a strong north north-easterly wind of 16 km/hr^{-1} was blowing, peaking at midday. Maximum temperature was 27.3°C, but a cold front was moving in. (Source : various Weather Bureau reports). Note that NE and NNE winds are onshore at all three beaches.

	BEACH AND YEAR OF CENSUS									
	ORIENT			EASTERN			NAHOON			NR
YEAR	1984	1986	1989	1984	1986	1989	1984	1986	1989	1984
NO. OF VEHICLES	N/A	N/A	N/A	210	271	411	197	118	44	21
NO. OF PEOPLE IN SEA/SWIMMING	219	114	24	23	437	264	217	148	4	13
NO. OF PEOPLE ON GRASS/DUNES	725	408	81	0	380	140	55	6	17	N/A
NO. OF PEOPLE ON BEACH	363	573	51	88	1183	860	863	512	27	93
NO. PEOPLE IN PARKING AREA	N/A	N/A	N/A	96	358	1030	67	47	13	N/A
TOTAL NO. OF PEOPLE	1307	1095	156	207	2358	2294	1202	713	61	106

N/A Not applicable to that particular beach. NR Nahoon River, census taken in 1984 only.

The Orient Beach was the next most popular beach, with a large proportion of people spending their time on the 200 m^2 grassed area backing the beach and tidal pool. The beach or shorezone is also popular, but less densely utilized than the lawned areas. The lower number of people at the Eastern Beach in 1984 was due to it being more exposed, with people favouring the Orient Beach. In 1984 it was also not utilized by blacks. Nahoon Beach was relatively full in 1984, but less full in 1986. Most people spent their time on the beach, and fortunately only a few frequented the steep dunes (Table 5.3). The lower number of people at the Orient and Nahoon Beaches in 1989 may be as a result of local whites going to beaches outside the East London area, or not frequenting the beaches due to fears that these areas may be overcrowded. Beaches outside East London were surveyed in 1986 as well, and a larger number of people were recorded on beaches at resort areas along the east coast than at Nahoon Beach, lending support to the former explanation. The low number of people at Nahoon River in 1984 was largely due to the strong wind, but may also be an underestimate as people under trees are not visible in the photographs. The relatively large number of people noted in the dunes at the Eastern Beach may result in damage to this vegetation, and this aspect was investigated further. It is also important that improved facilities are provided, as discussed below.

QUESTIONNAIRE SURVEY

The results of the questionnaire survey are presented as a series of tables for the most important findings. These tables show whether responses differed significantly, and questions have been grouped under separate headings. The question numbers refer to those of the questionnaire, given in Appendix 5.1.

Visitors place of residence and their preference for different beaches (Question 1, 2 & 6)

The object of the first two questions was to determine the place of residence of people using the three beaches (Table 5.4), and how often they visited East London's beaches. Forty three percent of the people interviewed were locals, and of the tourists, 30.8% had visited East London for the first time. The largest proportion of visitors (49.4%) came to East London annually and 19.8% visited the city more than once a year. Most people spent between 1 to 2 weeks in the city (43.8%), but many also spent longer periods (29.2%).

Local residents showed no preference for any of the three beaches, and neither did visitors from other coastal cities. The latter group was small (19), and most visitors were from inland cities (75, Table 5.4). They appeared to prefer the Eastern Beach, followed by the Nahoon Beach, and the largest group of people at the Eastern Beach were tourists from inland (34 or 50.7%). This is mainly due to the close proximity of a caravan park (Fig. 5.1) where these visitors were staying. The Nahoon Beach had a fairly even distribution of people, with no significant difference noted. However, the Nahoon River was definitely favoured by the local population.

Table 5.4 Cross tabulation to compare the beach at which the questionnaires were completed with the visitors place of residence (Question 1). Comparisons within columns (vertical) show the number of respondents from a particular city at each of the three beaches. Comparisons within rows (horizontal) show the place of residence of respondents at each beach. Note: In all tables actual counts appear in the first line: row percentages in the second; and column percentages in the third line. Row totals and row χ^2 are given at the right, and column totals and column χ^2 are given at the bottom. When χ^2 values are significant, the probability is also given.

ORIGIN OF RESPONDENTS	EASTERN BEACH	NAHOON BEACH	NAHOON RIVER	ROW TOTAL	ROW χ^2
1. EAST LONDON	29	30	30	89	0.040
Row%	32.5	35.7	33.7	43.6	NS
Column%	43.3	51.7	51.7		
2. OTHER COASTAL CITIES	4	5	10	19	3.26 NS
Row %	21.2	26.3	52.5	10.4	
Column %	6.0	8.6	17.2		
3. INLAND CITIES	34	23	18	75	5.36
Row %	45.3	30.7	24.0	41.0	$P<0.01$
Column %	50.7	39.7	31.7		
COLUMN TOTAL	67 36.5	58 31.7	58 31.7	183 100.00	
COLUMN χ^2 (ignoring 2)	0.396 NS	0.924 NS	3.00 $P<0.10$		

Table 5.5 Cross tabulation to compare the beach at which the questionnaires were completed with the respondents preference for a particular beach (Question 6). Rows compare the beach the respondent was at, with a particular preference. Columns compare the preferences of respondents at particular beaches.

RESPONDENT'S PREFERENCE	EASTERN BEACH	NAHOON BEACH	NAHOON RIVER	ROW TOTAL	ROW χ^2
1. EASTERN BEACH	29	0	0	29	57.99
Row %	100.0	0	0	15.9	$P<0.001$
Column %	43.9	0	0		
2. NAHOON BEACH	23	56	19	98	22.46
Row %	23.5	57.10	19.4	53.8	$P<0.001$
Column %	34.8	96.60	32.8		
3. NAHOON RIVER	3	2	32	37	39.15
Row %	8.1	5.40	86.5	20.3	$P<0.001$
Column %	4.5	3.40	55.2		
4. ORIENT BEACH	11	0	7	18	10.3
Row %	61.1	0	38.9	9.9	$P<0.01$
Column %	16.7	0	12.1		
COLUMN TOTAL	66 36.3	58 31.9	58 31.9	182 100.0	
COLUMN χ^2	24.92 $P<0.001$	157.25 $P<0.001$	35.52 $P<0.001$		

Although questionnaires were completed at specific beaches, it is possible that the beach respondents were at was not their first choice. An analysis of question 6 (Table 5.5) revealed that of the 66 subjects interviewed at the Eastern Beach, only 29 (43.9%) said they preferred the Eastern Beach, whereas 37 (56.1%) preferred other beaches. Of these 23 said they preferred the Nahoon Beach (Table 5.5). Of the 58 subjects interviewed at Nahoon Beach, 56 (96.6%) said they preferred this beach. At Nahoon River, 55.2% of the 58 subjects preferred this area, but 32.8% showed a preference for the Nahoon Beach. Only 12.1% of subjects at the Nahoon River said they preferred the Orient Beach, and none preferred the Eastern Beach.

A total of 53.8% of all subjects interviewed preferred the Nahoon Beach, even though 23 and 19 of them were at the Eastern Beach and Nahoon River at the time of the interview (Table 5.5). It is clear that Nahoon Beach was the most popular area, with all differences highly significant. It is also apparent that people who used the Nahoon Beach are very specific about their preference for it, as no subjects showed a preference for either the Orient Beach or Eastern Beach. The latter appears to be the least popular, with most of the people using it preferring one of the other beaches.

Age distribution, frequency of visits and general activities (Questions 7,8,9 and 11)

At the Eastern Beach, the distribution of people within the four age groups was even, with no significant differences (Table 5.6). At Nahoon Beach there were significantly more people in the 21 to 40 year age group (41.7%), and less people older than 40 years (13.8% $P<0.001$). The same trend was observed at the Nahoon River, except that fewer people of age 15 to 21 years were present (Table 5.6). A comparison of the age groups at the three beaches shows that no significant difference existed for the less than 21 year old age groups. This may indicate that children and young adults had no real preferences, but may also be due to their reliance on adults for transport to the beach. There were significantly less people between 21 to 40 years at the Eastern Beach, when compared to the Nahoon Beach and Nahoon River and both these areas were more popular among the 21 - 40 year age group (Table 5.6).

Question 8 revealed that 55.5% and 54.4% of people at the Eastern and Nahoon Beach respectively, spent either less than 10, or between 11 and 20 days at the beach per annum, with significantly less spending more time ($P<0.001$). At the Nahoon River 56.6% of people spent between 11 to 50 days, with fewer spending less than 10 days when compared with the other two beaches. This is mainly because the area is popular amongst the local population who are able to spend more time there, and do so because they actively participate in water sports. Generally, people spent less than 20 days a year at the beach, and these are usually concentrated over the approximately 30 summer weekends available.

Table 5.6 Cross tabulations to compare the beach at which questionnaires were completed at, with the age groups of respondents (Question 7). Rows compare the number of people in each age group with the three beaches, and columns compare whether a particular age group is more common at any of the three beaches.

AGE GROUPS	EASTERN BEACH	NAHOON BEACH	NAHOON RIVER	ROW TOTAL	ROW χ^2
< 15 YEARS Row % Column %	69 34.9 26.5	59 29.8 23.2	70 35.3 24.8	198	1.1 N.S.
15 - 21 YEARS Row % Column %	53 36 20.4	54 36.7 21.3	40 27.3 14.2	47	2.55 N.S.
21 - 40 YEARS Row % Column %	68 23.0 26.2	106 35.8 41.7	122 41.2 43.3	296	15.66 P<0.001
> 40 YEARS Row % Column %	70 45.2 26.9	35 22.6 13.8	50 32.2 17.7	155	11.9 P<0.005
COLUMN TOTAL	260 32.6	254 31.9	282 35.4	796 100	
COLUMN χ^2	2.94 N.S.	42.97 P<0.001	56.78 P<0.001		

An analysis of the number of hours spent at each of the three beaches showed that at the Eastern Beach no single time period was more popular. However, at the Nahoon Beach and Nahoon River a significantly greater number of people spent either 2 to 4 hours, or 4 to 6 hours at these beaches with few spending less than 2 hours. This may be due to the slightly greater distance that must be travelled to get there, as well as the fact that these areas are less exposed than the Eastern Beach, which may be why a significantly larger number of people spend less than 2 hours there.

Activities did not vary significantly at the three beaches, except that at the Eastern Beach paddleskiing and windsurfing were not popular mainly because this beach is favoured by older people (Table 5.6). The latter activity was most popular at Nahoon River. Generally, sunbathing and swimming were the most popular activities (39.4 and 35.8% respectively), and surfing the most popular of the more strenuous activites, viz. surfing, paddleskiing and windsurfing.

Parking facilities (Questions 3, 4 & 5)

One of the main objectives of the questionnaire was to determine whether parking facilities were adequate. Significantly more people at the Eastern Beach (76.9% P<0.001) stated that parking was adequate, whereas at Nahoon Beach and Nahoon River, no significant differences were noted, with about half the respondents stating that parking was inadequate. Significantly more people at the Nahoon Beach and Nahoon River (41.3% and 38.7% resp. P<0.05) stated that parking was inadequate when compared to the Eastern Beach, whereas significantly more respondents (47.2% $P<0.05$) at the Eastern Beach stated that parking was adequate when compared to the other two beaches. Thus, it appeared that parking facilities were perceived to be inadequate at the Nahoon Beach and to a lesser extent at the Nahoon River.

Solving the parking problem would require the construction of additional parking areas, and question 5 was designed to determine whether beach users would be prepared to walk from a more distant parking lot. No significant differences existed between distance categories of less than 50 m to 150 m; and greater than 150 m. These values have therefore been combined, and the differences between these two main groups presented in Table 5.7. The largest proportion of respondents (70.5%) were prepared to walk distances in excess of 150 m along established pathways to the beach. This is in sharp contrast to the situation in Ireland, where the majority of people walk less than 100 m from their parked vehicle, and very few walk more than 500 m (Eastwood & Carter 1981). At the Eastern and Nahoon Beaches, this number was significantly greater, whereas at the Nahoon River it was not (Table 5.7). This is probably because most people using the Nahoon River are involved in water sports such as power boating and windsurfing, and are not prepared to carry their equipment long distances. It is interesting that even at the Eastern Beach, where parking facilities are adequate, people were prepared to walk from more distant parking lots. This is fortunate as parking areas can be situated well back and outside the dynamic zone, and is important as 92% of respondents travelled to the beach by motor vehicle.

Table 5.7 Cross tabulations to compare the beach at which questionnaires were completed with the distance respondents were prepared to walk to the beach from a more distant parking lot, along an established pathway (Question 5). Rows compare the beach the respondent was at with the two distances, and columns compare whether the respondents attitude to walking these distances differed between the three beaches.

DISTANCE PREPARED TO WALK	EASTERN BEACH	NAHOON BEACH	NAHOON RIVER	ROW TOTAL	ROW χ^2
<50 - 150 M Row % Column %	10 21.7 17.5	17 37.0 32.1	19 41.3 41.3	46 29.5	2.93 N.S.
> 150 M Row % Column %	47 42.7 82.5	36 32.7 67.9	27 24.6 38.7	110 70.5	5.467 P<0.1
COLUMN TOTAL	57 36.5	53 34.0	46 29.5	156 100	
COLUMN χ^2	24.0 P<0.001	6.8 P<0.01	2.12 N.S.		

Perceptual carrying capacity (Questions 10 & 12)

All respondents stated that they would return to the beach at which they were interviewed (Question 10 - Appendix 5.1), suggesting a certain degree of satisfaction. However, it is important to determine whether the perceptual carrying capacity of these beaches has been reached, and Question 12 was aimed to achieve this (Table 5.8). The opinions given at the three beaches did not differ significantly, suggesting similar perceptions at all beaches, namely that there was still room for more people (Table 5.8). In other words, the perceptual carrying capacity of these beaches had not been reached, as few people (31.1%) considered the beaches fully used, and almost none (6.1%) considered them overcrowded. These differences are significant for all three beaches (P<0.001, Table 5.8), and so is the difference between the fully used and room for more people categories (P<0.05). The largest number of people who felt the beach was fully used were at Nahoon Beach, as people at this beach are attracted by its natural appeal.

Table 5.8 Cross tabulations to compare the beach at which questionnaires were completed with the respondent's perception of capacity (Question 12). Rows compare respondents' perceptions according to three predefined categories, and columns compare differences in perception for the three beaches.

RESPONDENTS PERCEPTION OF CAPACITY	EASTERN BEACH	NAHOON BEACH	NAHOON RIVER	ROW TOTAL	ROW X^2
OVERCROWDED Row % Column %	4 36.4 6.2	4 36.4 6.9	3 27.3 5.3	11 6.1	0.182 N.S.
FULLY USED Row % Column %	18 32.1 27.7	21 37.5 36.2	17 30.4 29.8	56 31.1	0.464 N.S.
ROOM FOR MORE PEOPLE Row % Column %	43 38.1 66.2	33 29.2 56.9	37 32.7 64.9	113 62.8	1.36 N.S.
COLUMN TOTAL	65 36.1	58 37.2	57 31.7	180 100	
COLUMN χ^2	20.77 P<0.001	21.96 P<0.001	37.70 P<0.001		

Activities and perceptions affecting natural dune areas (Question 14, 15 & 16)

Very few people at any of the three beaches entered the coastal forest or walked over the vegetated dunes (7.1% & 19.2% respectively), with the latter actively being more common. No significant differences were noted between the three beaches, but slightly more people climbed up dunes at the Eastern Beach (22.7% as opposed to 17.2%). It is possible that these numbers are an underestimate, as people answering positively were asked to give reasons, and to avoid doing so, may have simply answered no. These percentages equate to about 450 people walking over vegetated dunes, and 170 entering the coastal forest, based on peak numbers at the Eastern Beach (Table 5.3). The ecological effects of this activity were therefore investigated in more detail.

Respondents perceptions of the forested areas did not differ significantly between the three beaches, and most people felt the forested areas were either attractive or exceedingly attractive. Only 2 people found it an eyesore, and 13 thought it was unattractive. Clearly the forested dunes have an aesthetic value that makes them well worth protecting, and further development in these areas should not be considered without first determining whether the necessity for the facility outweighs the need for an aesthetically pleasing environment. It would therefore be important to determine whether these dunes are more valuable as natural areas, or as potential sites for development. The opinion of natural areas, when weighed against other alternatives such as a hotel or housing development, may differ from that recorded here.

Facilities required (Questions 13, 17 & 18)

A preliminary investigation of the 3 beaches revealed the lack of certain facilities, and questions 17 and 18 attempted to determine what facilities people thought should be provided. Positive responses to the four categories of question 17 are given in Table 5.9, and similar results were obtained when question 17 was compared to question 6, preferred beach, except that the positive response to picnic spots at Nahoon Beach was significant. All respondents felt that picnic spots should be provided at the three beaches, whereas most people at the Nahoon Beach (75.9%) and Nahoon River (74.1%) did not think a restaurant should be provided. At the Eastern Beach more people felt one should be provided (46.3%), and the difference between positive and negative responses is therefore not significant. The presence of a restaurant close to the Eastern Beach at Marina Glen appears to be adequate, but when the three beaches were compared significantly more people at the Eastern Beach thought that restaurants should be provided. It was only at Nahoon Beach that a significant number of people thought a beach café should be provided (Table 5.9). Such a facility is provided at the Eastern Beach in the form of a tea room and the restaurant, but 56.7% of respondents felt that a beach cafe should also be provided. At Nahoon River 58.6% responded positively, and generally most people at the three beaches think that beach cafés should be provided (χ^2= 49.31 P<0.01). On the other hand most people think that restaurants are not a good idea (χ^2=49.32 P<0.001)

The above three questions all relate to the provision of facilities for eating on the beach, and to see whether there is a need for such facilities, the number of people having lunch on the beach or elsewhere was assessed. Just less than half the people interviewed (46.4%) ate lunch on the beach, and only 2.7% said they ate lunch in the dunes. At the Eastern Beach a significant number of people ate lunch elsewhere (64.2% P<0,01), whereas at the Nahoon Beach an equal number ate lunch on the beach and elsewhere (48.3%). At the Nahoon River most people ate lunch on the beach (60.3%). Due to the large number of people that eat lunch on the beach, and the fact that many people at Nahoon River felt that picnic spots should be provided (Table 5.9), one can conclude that there is a real and perceived need for these facilities. At Nahoon Beach a large number of people felt that picnic spots should be provided, and a significant number stated that a beach café was needed (Table 5.9). Since 51.7% of respondents lunched at the beach, additional facilities are required. At the Eastern Beach there was a definite need for picnic spots, despite the fact that most people did not lunch on the beach (35.8%). However, the reason for this could be due to the lack of facilities, as no formal picnic spots exist.

Table 5.9 Cross tabulations to compare the beach at which questionnaires were completed with positive responses to the provision of : picnic spots; restaurants; beach café and improved access (Question 17). Rows show whether responses differed between the three beaches. The column χ^2 shows whether the differences between positive and negative responses was significant for each of the four facilities tested.

FACILITIES	EASTERN BEACH	NAHOON BEACH	NAHOON RIVER	ROW TOTAL	ROW χ^2
PICNIC SPOTS Row % Column %	44 38.3 65.7	33 28.7 56.9	38 33.0 65.5	115 62.8	1.58 N.S.
COLUMN χ^2	6.58 $P<0.025$	1.10 N.S.	5.59 $P<0.025$		
RESTAURANTS Row % Column %	31 51.7 46.3	14 23.3 24.1	15 25.0 25.9	60 32.8	9.10 $P<0.025$
COLUMN χ^2	0.37 N.S.	15.52 $P<0.001$	13.52 $P<0.001$		
BEACH CAFÉ Row % Column %	38 34.5 56.7	38 34.5 65.5	34 30.9 58.6	110 68.1	0.291 N.S.
COLUMN χ^2	1.21 N.S.	5.58 $P<0.025$	1.72 N.S.		
IMPROVED ACCESS Row % Column %	27 27.8 40.9	43 44.3 74.1	27 27.8 46.6	97 53.3	5.27 $P<0.1$
COLUMN χ^2	2.18 N.S.	13.52 $P<0.001$	0.27 N.S.		

A significant number of respondents felt that access to the Nahoon Beach, and access from the parking area onto the beach should be improved (Table 5.9). At the other two beaches, the differences were not significant, and most people did not perceive access as being a problem. The significance at Nahoon Beach is because most people want the gravel road surfaced, and the provision of this facility will improve access.

In question 18, people were asked to make any additional comments, and from the 85 comments made (46.6%), five main points emerged (Table 5.10). At the Eastern Beach a significant number of people wanted improved toilet and shower facilities; and similar comments were also made by people at the other two beaches, making this the most popular of all additional comments. At Nahoon Beach a significant number of people wanted the main access road upgraded from gravel to asphalt, and this was the most common comment at this beach. Eleven people felt that more litter bins should be provided and that the beaches be kept cleaner, and most of these were at the Nahoon Beach.

Table 5.10 Cross tabulation to compare the beach at which questionnaires were completed with additional comments (Question 18) categorized as follows : better toilet facilities; resurface gravel road, i.e. improve road; reduce pollution/litter; develop commercially; do not develop commercially. Rows show differences in responses between the beaches; columns show the number of people making specific comments.

SPECIFIC COMMENTS	EASTERN BEACH	NAHOON BEACH	NAHOON RIVER	ROW TOTAL	ROW χ^2
BETTER TOILET FAC.	16	5	7	28	7.36
Row%	57.1	17.9	25.0	15.3	$P<0.05$
Column %	23.9	8.6	12.1		
IMPROVE ROADS	1	9	2	12	9.50
Row %	8.3	75.0	16.7	6.6	$P<0.01$
Column %	1.5	15.5	3.4		
LESS POLLUTION	2	6	3	11	2.36
Row %	18.2	34.5	27.3	6.0	N.S.
Column %	3.0	10.3	5.2		
MORE COMMERCIAL DEV.	10	1	1	12	13.50
Row %	83.3	8.3	8.3	6.6	$P<0.001$
Column %	14.9	1.7	1.7		
LESS COMMERCIAL DEV.	3	6	11	20	4.90
Row %	15.0	30.0	55.0	10.9	$P<0.05$
Column %	4.5	10.3	19.0		
NO COMMENTS	35	30	33	98	0.357
Row %	35.7	30.6	33.7	53.6	N.S.
Column %	52.2	51.7	56.9		
COLUMN TOTAL	67	57	57	183	
	36.6	31.7	31.7	100	
COLUMN χ^2	37.40	10.58	19.38		
	$P<0.001$	$P<0.10$	$P<0.005$		

Conflicting comments were made concerning more commercial developments, such as restaurants, hiring equipment, changerooms, etc. At the Eastern Beach 14.9% of respondents wanted the area developed more commercially, and this ties in with the large number of people who felt that picnic spots, restaurants and beach cafés should be provided at the Eastern Beach (Table 5.9). This suggests the Eastern Beach could be developed along similar lines to the Orient Beach. However, beach users at the Nahoon Beach and Nahoon River have the opposite opinion, as 10.3% and 19% of all respondents stated emphatically that they did not want the area developed more commercially. This was the most popular additional comment at the Nahoon River, and second most popular comment at the Nahoon Beach. This attitude of limiting development in these areas is supported by the low number of people who wanted restaurants at these beaches (Table 5.9), together with the large number of people who regarded the forested areas as attractive (91.5%).

TRAMPLING STUDIES

The herbaceous layer of the forests on the high dunes backing the Eastern Beach (see sample site, Fig. 5.1) is dominated by grasses typical of this region, such as *Panicum aequinerve, P. deustum* and *Dactyloctenium australe*. Herbs are less abundant, but the most common species encountered in the sample plot were *Pupalia atropurpurea,* and the creepers, *Commelina africana, Clematis brachiata* and *Solanum americanum*. The forests are fairly species rich, and Lubke & Strong (1988) recorded 39 species per 10 by 10m relevé in the coastal forest in this area. It is therefore important to consider changes in species diversity which may result from increased recreational pressure.

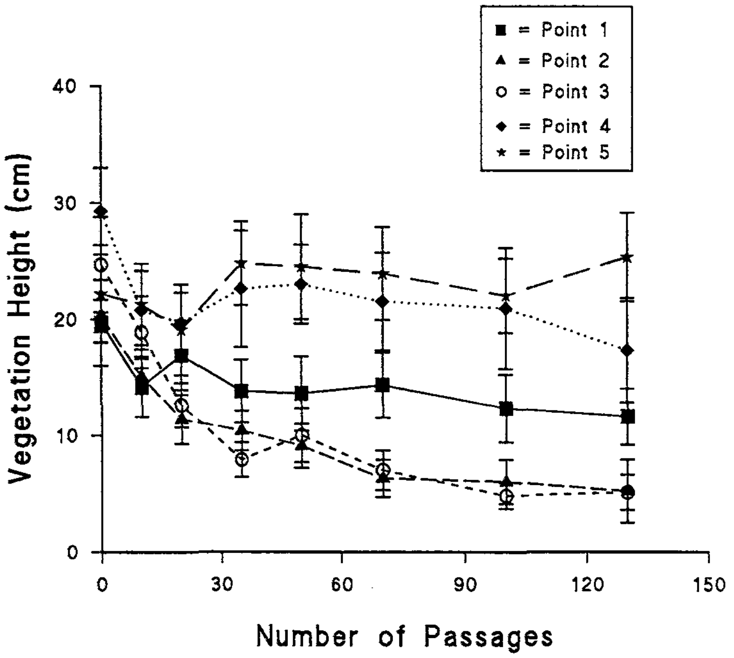


Figure 5.4 Reduction in plant height with increasing passages for points 1 to 5 in the Forest layer at the Eastern Beach.

This vegetation is relatively tolerant to trampling, and average height of plants decreased by only 3.2 cm (14.9%) after 10 passages. After this initial rapid decrease in height, differences were less marked, with an average decrease of 25% after 35 passages. Height continued to decrease with successive treatments, and after 130 passages average height in the sample plot was 12.9cm, a decrease of 39.2% (Fig. 5.4). The first 10 passages therefore resulted in almost the same percentage decrease in height as the subsequent 120 passages, indicating that the first few passes are the most destructive, as noted by Liddle (1975a) and others. These changes in plant height are significant (Table 5.11), as are the differences between the five points. Plant height in the first three points decreased more significantly than for points 4 and 5, as this is where the footpath developed (Fig. 5.4). This shows that most of the damage was restricted to an area of about 30 cm wide, as points are 10cm apart (Fig. 5.3). Initial plant cover was 66%, and increased to 74%, due to the more resistant grasses being flattened and therefore covering a larger area. After a month, cover was 66%, as some of the damaged plants had died (Plate 5.3). It therefore appears that cover is not as reliable as plant height to measure the immediate effects of trampling (see also Sothern *et al.* 1985). No real significant decrease in species diversity was noted, except after 35 passages ($p<0.05$; Table 5.12). This decrease is not very real, but it is likely that a more significant decrease would be detected after about a month, as the more sensitive damaged species would begin to die. This was tested at this site by resampling one month later, and the Simpson's diversity of 0.665 was significantly less ($t=2.15$; $p<0.05$). It is therefore important to look at the recovery rate, and to resample after at least one month, to detect changes in species diversity.

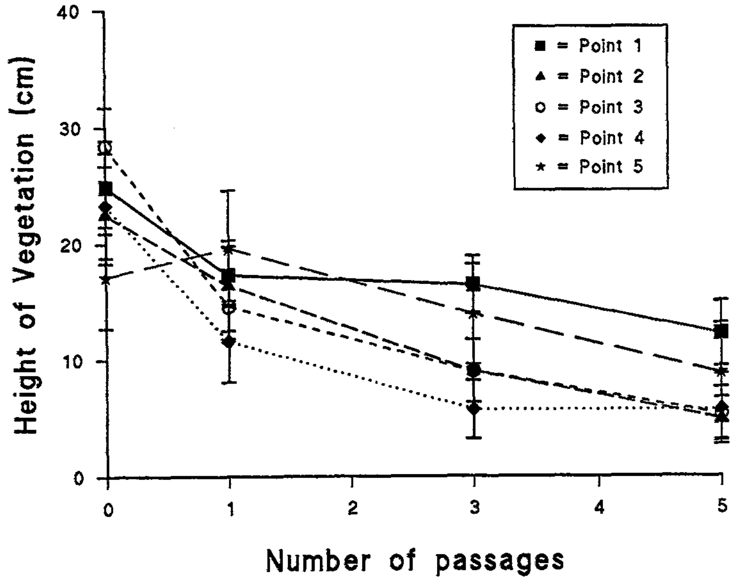


Figure 5.5 Reduction in plant height with increasing passages for points 1 to 5 in the Forest layer at Nahoon Beach.

The herbaceous layer of the forest behind the Lifesavers Clubhouse at Nahoon Beach (see sample sites, Fig. 5.2) was found to be much more susceptable, with a 30.9% reduction in plant height occurring in the sample plot after a single passage. A total of five passages reduced height by 67.9%, from the original height of 23.7 cm to 7.4 cm (Fig. 5.5; Plate 5.4). These differences in height are highly significant, but there is no significant difference in height between the points (Table 5.11), indicating that damage was spread more evenly over the sample plot. However, plant height at the edges of the plot (points 1 & 5; Fig. 5.5) was greater than towards the centre, but these differences were not as marked as with the previous sample (Fig. 5.4). Plant cover also decreased from a total of 88% for the sample plot to 54%. This sample had a similar diversity to the vegetation at the Eastern Beach, but no significant reduction in Simpson's diversity was noted (Table 5.12). The far greater susceptability of this community relates directly to species composition. It is dominated by soft herbaceous creepers such as *Solanum americanum* (24% cover) and *Cynanchum obtusifolium* (14%), and herbs such as *Hypoestes aristata* (10%), with no grasses present (Plate 5.4). The latter have flat leaves and are more conduplicate, and therefore more tolerant (Bates 1935; Liddle 1975b).

Table 5.11 Results of a 2-way Analysis of Variance for sample plots in 4 vegetation types at the Eastern and Nahoon Beaches. Treatments show if significant differences in plant height occurred after trampling (Table 5.2), and blocks show whether plant height differed significantly between points 1 to 5 (Fig. 5.3).

LOCALITY	HABITAT	SOURCE	D.F.	F.CAL	F.TAB	SIGNIF
Eastern Beach	Herbaceous layer of Dune Forest	Treatments Blocks	7 4	5.66 25.92	3.47 4.62	0.001 0.001
Nahoon Beach	Herbaceous layer of Dune Forest	Treatments Blocks	3 4	21.69 1.73	5.42 27.1	0.001 N.S.
	Chrysanthemoides monilifera dominated Dune scrub	Treatments Blocks	3 4	35.44 4.68	5.42 3.72	0.001 0.005
	Ipomoea pes-caprae Dune Pioneer community	Treatments Blocks	5 4	1.07 12.74	12.1 4.62	N.S. 0.001

The road to the Clubhouse at Nahoon Beach passes along the edge of the Dune Forest (Fig. 5.2) and the seaward dunes are colonized by Dune Scrub dominated by *Chrysanthemoides monilifera* (Simpson's dominance = 0.742). Access from the road through this vegetation could therefore threaten the stability of the dunes, and the sensitivity of this community to trampling was also investigated (see sample sites, Fig. 5.2). The first passage reduced height by 25%, from 70.8 cm to 53 cm. A further two passages reduced height by 52% to 33.9 cm (Fig. 5.6), and these changes are highly significant (Table 5.11). However, change in cover was not significant (98% to 80%) as, due to the height of the vegetation, lower branches become exposed as the upper ones are damaged. The changes in height between points is also significant (Table 5.11), as point one was affected less than the other four points (Fig. 5.6). A significant increase in diversity was noted with increased trampling (Table 5.12), and this was the result of creepers such as *Cynanchum natalitium* being exposed as the cover of the *C. monilifera* was reduced. The intolerance of this community to trampling is due to the soft stemmed, woody *C.monilifera*, which is brittle and therefore breaks easily when damaged.

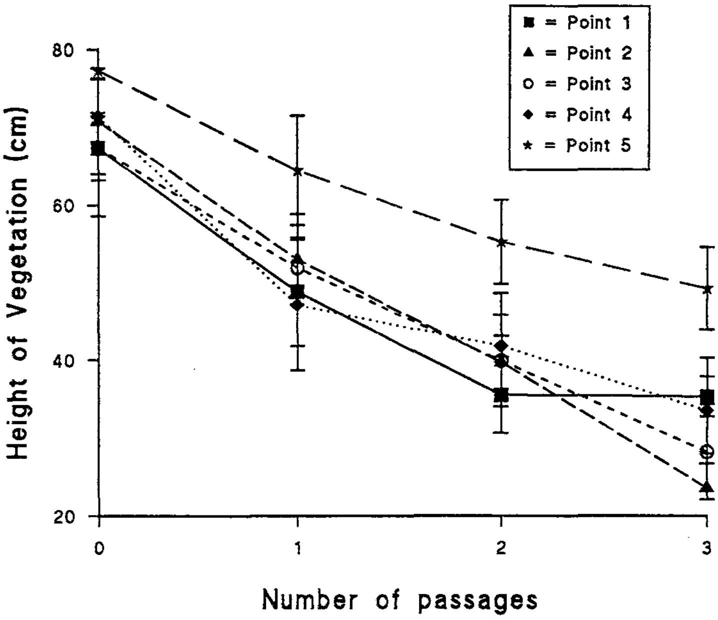


Figure 5.6 Reduction in plant height with increasing passages for points 1 to 5 in the *Chrysanthemoides monilifera* dominated Dune Scrub at Nahoon Beach.

The sand spit which stretches from the Hlaza River to the Nahoon River (see sample sites, Fig. 5.2) is sparsely vegetated with *Ipomoea pes-caprae*, which forms embryonic dunes that are often found close to river mouths (Chapter 1). This vegetation is very low, with a mean height of 1.84 cm that was reduced to 0.42 cm after 100 passages (Fig. 5.7). The first 15 passages caused a 27.2% reduction in height, and after 70 passages height was reduced by 74% to 0.48 cm. However, these differences were not statistically significant (Table 5.11), and this is probably because the sample size of 50 points was not large enough, hence the large standard errors. Total cover before trampling was 24%, which meant the sample size was only 12 points, as the other 38 points struck bare sand. A larger sample size should therefore be taken in sparsely vegetated foredune communities to ensure that reliable results are obtained. Despite *I. pes-caprae* being dominant (Simpson's dominance = 0.618), significant changes in diversity were noted (Table 5.12). This is mainly due to the loss of individual plants which would affect this small sample size, as total cover was reduced from 24% to 10%.

Table 5.12 Changes in Simpson's diversity index after trampling and corresponding values of Students t and levels of significance.

EASTERN BEACH FOREST LAYER

No. of Passages	0	10	20	35	50	70	100	130
Simpson's diversity	0.772	0.744	0.709	0.635	0.707	0.722	0.733	0.702
Students t	-	0.425	0.372	0.879	0.803	0.227	0.185	1.106
Significance	-	N.S.	0.40	0.05	0.40	N.S.	N.S.	0.40

NAHOON BEACH FOREST LAYER

No. of Passages	0	1	3	5
Simpson's diversity	0.722	0.692	0.691	0.663
Student t	-	0.430	0.0163	0.987
Significance	-	N.S.	N.S.	N.S.

NAHOON BEACH DUNE SCRUB COMMUNITY

No. of Passages	0	1	2	3
Simpson's diversity	0.258	0.257	0.438	0.463
Student t	-	0.0087	1.623	1.928
Significance	-	N.S.	0.20	0.1

NAHOON BEACH DUNE PIONEER COMMUNITY

No. of Passages	0	15	30	45	70	100
Simpson's diversity	0.381	0.358	0.358	0.280	0.215	0.184
Student t	-	0.231	0.001	0.759	1.28	1.689
Significance	-	N.S.	N.S.	N.S.	0.2	0.1

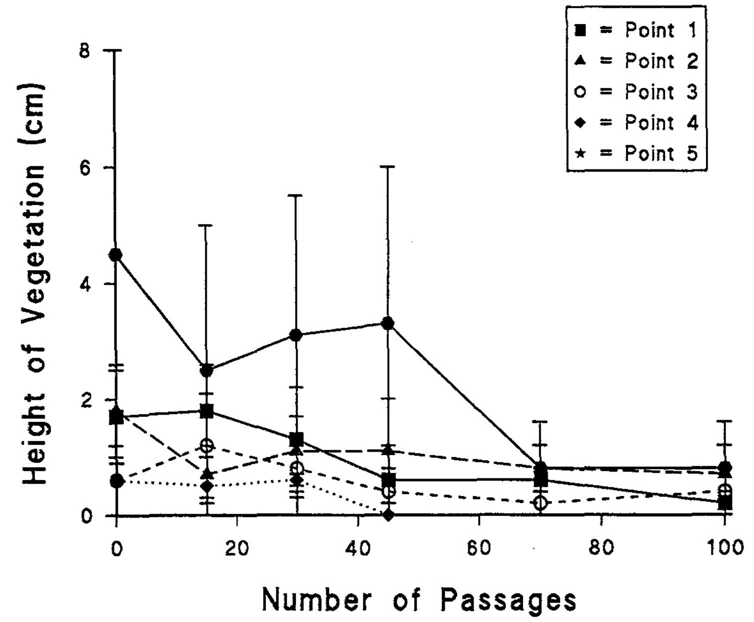


Figure 5.7 Reduction in plant height with increasing passages for points 1 to 5 in the *Ipomoea pes-caprae* dominated foredunes at Nahoon Beach.

Plate 5.3 Forest layer at Eastern Beach 28 days after exposure to 130 passages, indicating the position of the sample points. Control plot is to the right, and the path on the left is due to trampling during sampling.

Plate 5.4 Forest layer at Nahoon Beach immediately after 5 passages, showing extensive damage to the herbaceous vegetation on the left. Note Point Frame in the background, and control area to the right.

Plate 5.5 Damage to the same community shown in Plate 5.4 above, due to extensive long term trampling caused by the incorrect siting of ablution facilities.

DISCUSSION

AERIAL CENSUS

The beaches at East London do not appear to be heavily utilized when compared with other coastal areas in Natal (Little 1989) and Northern Ireland, where 8000 people/km of shoreline is not unusual (Carter 1980a). Levels of use during the peak season at the Orient beach are comparable with values of 1200 to 2300 reported by Glassom & McLachlan (1989) for a similar beach in Port Elizabeth. However, the utilization of the more natural Nahoon Beach was far greater than a similar undeveloped beach at Sardinia Bay in Port Elizabeth (1202 compared with 300), and this is probably because Nahoon Beach is much closer to the city centre than Sardinia Bay. The lower number in 1989 is simply due to poor weather conditions, but it is postulated that the decrease in 1986 (Table 5.3) is due to fears of overcrowding, which was prompted by a pre-planned influx of the non-white sector of the population onto local beaches. This resulted in a ten fold increase in numbers on the Eastern Beach, and numbers were still high in 1989, despite the poor weather conditions (Table 5.3). These values are comparable to the New Year's day peak of 3500 reported in 1988 at Joorst Park, a predominantly non-white beach in Port Elizabeth (Glassom & McLachlan 1988). Thus, although a trend of increasing utilization of the Eastern Beach is apparent, levels are comparable to similar beaches in the Eastern Cape, but much less than the more developed beaches of Natal (Little 1989). Capacities are also far less than those reported by Carter (1980a) in Ireland, Williams & Randerson (1989) in Wales, and many American beaches (Vogt 1979).

QUESTIONNAIRE SURVEY

At the Eastern Beach only 210 of the 357 formal parking bays were occupied in 1984, but this number increased to 411 in 1989, with additional vehicles spilling over into the informal parking area (Fig. 5.1). The low number of vehicles relative to the number of people is because lower income blacks utilizing these beaches cannot afford their own vehicle. Consequently, a large number travel to the beach by bus and taxi. At Nahoon Beach and Nahoon River, parking bays were never fully occupied (Table 5.3), yet significantly more people stated that parking was inadequate when compared to the Eastern Beach, and about half felt that more parking was required. This is difficult to explain, since people are prepared to walk from more distant overflow parking areas (Table 5.7), which would not have been fully occupied. Thus, although there is a perceived need for additional parking facilities, data on the capacity of existing parking areas suggest that they are adequate. However, this was not the case with other essential services, such as toilet and shower facilities. At all beaches, but particularly the Eastern Beach, a significant number of people felt these facilities were inadequate and should be improved (Table 5.10). Similarly, picnic facilities and a beach café could be provided at all three beaches, but particularly at Nahoon Beach where such facilities do not exist. A restaurant could also be provided at the Eastern Beach, but not at the other two areas (Table 5.9). At Joorste Park in Port Elizabeth, Glassom & McLachlan (1989) also found that parking and café facilities were inadequate.

Results of this study suggest that the physical carrying capacity of these beaches has been reached, but the predicted rate of demand and average turnover time per user would need to be determined to gain more information on the numbers and sizes of the various facilities required (Brotherton 1973). Nevertheless, the development of formal picnic areas would reduce the number of people wandering into the forests to find suitable sites to lunch. The provision of other facilities, such as a beach café and more ablutions, will increase the physical carrying capacity of the beaches.

A balance between this resultant increase and the maintenance of a quality recreation experience means that the perceptual and ecological carrying capacities of the beaches must be determined. Recognition of the conflict between access and preservation is the first step towards solving this resource allocation problem. With sound management and sensible planning it is possible to "have your cake and eat it too, as long as you don't eat all of it" (Vogt 1979). To decide how much of the resource cake to save, a decision has to be made as to whether increasing access to the coastline is more, or less, important than protecting the resource, or equally important. This decision should be shaped by legal constraints, natural features, amount of shoreline available, current uses, public attitudes (Vogt 1979), ecological sensitivity (Brotherton 1973; Tanacredi 1983), physical carrying capacity (Burden & Randerson 1972; Brotherton 1973; Sowman & Fuggle 1987) and geomorphic sensitivity (Carter 1980a).

A number of questions were aimed at determining public attitude towards the various beaches and their natural features, with a view to determining beach preference and the reasons therefore, so that the perceptual carrying capacity of these beaches could be assessed. This survey showed that the Nahoon Beach was the most popular of the three beaches studied, and this preference was very specific (Table 5.5). Most people at the Nahoon Beach and Nahoon River were between 21-40 years, whereas there was no age preference at the Eastern Beach (Table 5.6). The number of days spent at the Nahoon and Eastern Beaches per year, and the activities undertaken by beach users, did not differ significantly. However, these two factors differed for the Nahoon River, mainly because the area is frequented by the local population who participate in activities such as windsurfing. These aspects therefore cannot explain why the Nahoon Beach is preferred over the other beaches. The only question that may have shed some light on the reason for this, namely to determine what respondents thought of the forested dunes, showed no significant differences between the three beaches. Glassom & McLachlan (1989) found that preference for particular beaches at Port Elizabeth centred around factors such as facilities, greatest number of people, locality and scenic aspects such as absence of rocks, cleanliness and good surf. However, at the undeveloped, natural Sardinia Bay beach they found that factors such as few people, peacefulness and lack of development were most important. At Nahoon Beach and Nahoon River a significant number of people specifically stated that these areas should not be developed more commercially (Table 5.10), and this is supported by the low number of people wanting restaurants (Table 5.9). In Port Elizabeth, Glassom & McLachlan (1989) found that despite the fact that very few facilities were available at Sardinia Bay, the majority of respondents were against the introduction of shops and other facilities. Results from the present study suggest that the main reason for people preferring the Nahoon Beach and Nahoon River are their attractive, natural and aesthetic settings, and the Nahoon Beach is preferred to the Nahoon River because it offers more opportunities for popular leisure activities such as swimming, body surfing and surfing. This aspect of scenic beauty should factor into the decision of whether to develop more facilities to increase the physical carrying capacity of these two beaches.

According to Brotherton (1973), perceptual carrying capacity can be assessed by determining whether people feel the area is overcrowded, fully used or has room for more people. The limitation of this technique is that individuals who are crowd intolerant may stay at home, but solutions to this problem are impractical and require surveys to be undertaken at peak and off-peak seasons. In this survey all respondents stated that they would return, and the majority (62.8%, Table 5.8) felt that there was still room for more people. Only a small percentage (6.1) considered the beaches to be over-crowded, but a relatively large number considered the Nahoon Beach to be fully used, supporting the contention that the natural appeal of this beach is important. It is not surprising that the perceptual carrying capacity of these beaches had not been reached. In 1984, based on the census counts (Table 5.3), there was 314 m^2 per person at the Eastern Beach, $50m^2$/ person at Nahoon Beach and $38m^2$/person at Nahoon River. Baud-Bovy and Lawson (1977, in Glassom & McLachlan 1989) consider $3m^2$/person to be the critical level at which crowding starts. However, it is unlikely that South Africans would tolerate such capacities, and Glassom & McLachlan (1989) found that at Joorst Park significant dissatisfaction was registered by respondents on New Years day, when there was $9m^2$/person. It is suggested here that people will consider a beach crowded at densities of between 6 to $9m^2$/person, but for people seeking more natural areas this density would probably be unacceptable. At a density of $50m^2$/person, 36.2% considered the beach at Nahoon to be fully used (Table 5.8). The tenfold increase in the utilization of the Eastern Beach in 1986 only increased densities to $28m^2$/person, and the area will be able to support a larger number of people before the perceptual carrying capacity is reached.

Vogt (1979) argues that population pressure can be used to support both increased access and preservation. If the population is increasing and participating more in leisure activities, which is the situation in South Africa, access to the seashore must be increased to meet the demand. Conversely, if a quality recreation experience is to be had at the beach, steps must be taken to protect the resource from degradation. This can be achieved by placing restrictions on use, which are part of the costs that must be borne in order to provide a satisfying recreation experience (Vogt 1979). However, Glassom & McLachlan (1989) found that the majority of respondents were against numbers of people being limited. Pigram (1983) has found that any form of rationing discriminates to a certain extent against some participants, and criticises the use of fees or eligibility standards to apportion recreational opportunities. Vogt (1979) suggests that one solution to the preservation versus access dispute is to partition resources into a series of "use zones" that can accommodate different types of recreation, as has been successfully achieved at Gateway National Recreation Area, New York (Tanacredi 1983). From this study, it would seem advisable to develop the Eastern Beach into a modern facility, similar to the Orient Beach. The Nahoon Beach should be developed so that more coastal-dependent uses, such as windsurfing, surfing and paddleskiing are not overwhelmed by a large influx of people.

The above conclusion is based on the perceptual carrying capacity of these beaches, but the adoption of an ecological approach to dune management means one should also consider the ecological carrying capacity, and the value of the natural features. At all three beaches the forested dunes were considered attractive or very attractive, so any plans to develop these beaches must ensure that these natural features are not damaged or destroyed. Fortunately, only 7.1% of beach users enter the coastal forest, and 19.2% walk over vegetated dunes. This is in sharp contrast to the situation in Ireland, where over 25% of beach users spend their time in the dunes (Wilcock & Carter 1975). Eastwood & Carter (1981) found that people who did manual or unskilled labour, and/or who visited the beach for the first time and/or were in small groups, tended to spend their time on the vegetated dunes, and were classified as dune consumers. For socio-political reasons, most non-whites in South Africa are employed as manual or unskilled labourers, and it is therefore likely that proportionally more people will enter the forests or spend more time on the vegetated dunes. Personal observations lend support to this statement, and Glassom & McLachlan (1989) noted that the greatest activity on dunes was at Jooste Park, which was frequented at that time by non-whites. This factor should therefore be considered when determining the recreational capacity of beaches in South Africa.

TRAMPLING STUDIES

To make resource management decisions, perceptual and ecological carrying capacities should be considered together (Vogt 1979). As noted earlier, to achieve the latter one needs to determine the nature and frequency of the recreational activity, which has been determined here through aerial census counts and questionnaire surveys. From these results and the current literature, it became apparent that human trampling was one of the most likely affects, and the amount of change to some of the vegetation was therefore assessed experimentally. The general response to vegetation exposed to trampling as reported in the literature (Liddle 1975a) and noted here, included a persistent reduction in height, a reduction in total cover and an increase in bare areas. Changes in diversity did not show any expected trends, but this is mainly because a measurable response cannot be achieved unless longer term data is collected (Burden & Randerson 1972; Liddle 1975a; Hylgaard 1980). Nevertheless, one would expect that diversity would decrease with longer term wear, as only the most tolerant species survive (Trew 1973; Liddle 1975a; McDonnell 1981). Long term vehicle use on the West Bank area of East London has resulted in a marked decrease in the diversity of coastal grasslands in that area (Avis *et al.* in prep.)

All the communities tested showed an initial rapid decline in plant height, with the greatest response occurring after the first few passages (Figs. 5.4 - 5.7). Similar results were noted by Bowles & Maun (1982), who showed that the number of shoots in open dune communities decreased by 60% after only three tramples. However, the response of the four plant communities to trampling differed significantly. The forest layer at the Eastern Beach was the least sensitive, owing to the more level topography and the greater abundance of grasses and other conduplicate species, which are more tolerant to trampling (Bates 1935; Liddle 1975b). Monocotyledonous species have also been shown to be more tolerant, and to become abundant in areas exposed to long term trampling at the expense of dicotyledonous species (Liddle 1975a&b). At the Nahoon Beach, the forest layer is more herbaceous and has a steeper gradient, and these factors lead to increased sensitivity (Sothern *et al.* 1985). It therefore appears that the vegetation at the Eastern Beach has a greater ecological carrying capacity, so that the development of this area into a more modern facility should not lead to an unacceptable change to the resource base.

At the Nahoon Beach, the forest layer is very sensitive to trampling (Fig. 5.5) and long term exposure has resulted in extensive damage to this community (Plate 5.5). The Dune Scrub communities which protect part of the access road to the Lifesavers Clubhouse are also very sensitive to trampling (Fig. 5.6), and fixed access points clearly defined by boardwalks will need to be constructed to improve the ecological carrying capacity. Construction should be such that these boardwalks blend in well with the natural environment, as has been done in other sensitive habitats (Anon 1987a). These areas should also be well signposted, with boards explaining why it is preferable not to walk indiscriminately in these habitats, as has been done in the United Kingdom (Ranwell & Boar 1986) and United States (Carlson & Godfrey 1989).

Results from this study suggest that the *Ipomoea pes-caprae* dominated foredunes at Nahoon Beach are as tolerant to trampling as reported for heath-grasslands at Lake Huron (Bowles & Maun 1982) and *Ammophila breviligulata* dominated dunes at Cape Hatteras, USA (Nickerson & Thibodeau 1983). The latter authors suggested that at rates of 200 passages per 5m^2 during a summer season, visitors should be discouraged from following established paths. The same may also hold for the foredunes at the Nahoon Beach, but results of this pilot survey are considered unreliable. As a result of this, as well as the importance of foredunes and their widespread distribution along the coast (Chapter 1), more detailed studies were initiated to investigate the tolerance of a number of important pioneer species to human trampling and off-road vehicle effects. These results are discussed in more detail in Chapter Six, but for the purposes of this study it is possible to conclude that this area is less sensitive than the forest layer, and since few people walk over these vegetated dunes (19.2% - 100 people on peak days), current levels of use pose no threat to the ecological integrity of the system.

CONCLUSIONS

Recreational use of the beaches in East London have not reached levels that exceed the physical, perceptual and ecological carrying capacity of these areas. Nevertheless, current trends suggest that utilization levels are increasing, and will continue to increase, due to socio-political changes and increases in population numbers. There was a significant preference for the Nahoon Beach and results of the questionnaire survey suggest that this area, and the Nahoon River, should not be commercially developed as people are attracted to its natural and undeveloped character. The forested dunes backing the beach also have a lower ecological carrying capacity. At the Eastern Beach, more facilities should be developed to increase the physical carrying capacity of this area, which is ecologically less sensitive. This is in line with Vogt's (1979) suggestion of partitioning the resource base into a number of use zones. More emphasis should be put on resource protection at the more sensitive and natural Nahoon Beach, whereas more emphasis should be put on increasing the capacity of the Eastern Beach and developing it into a more intensive use zone.

Appendix 5.1 Copy of Questionnaire used in the survey of East London's beaches.

QUESTIONNAIRE ON EAST LONDON BEACHES

The objective of this questionnaire is to ascertain how often the beaches of East London are used in order to determine whether there is a need for the provision of more facilities. Your help and co-operation in this respect will be greatly appreciated. Simply tick the relevant block.

1. Where are you from?

			Specify which
East London	Yes	No	
Another coastal town	Yes	No	________
Inland	Yes	No	________

2. How often do you visit East London ______________ and how long do you usually stay for? ______________________

3. How did you travel to the beach?

Motor vehicle		Motor cycle		Public transport		Walk	

4. Do you think that the parking facilities are adequate | Yes | No |

5. Would you be prepared to walk from a more distant parking lot, along an established pathway?

| Yes | No | From how far?

50m	Yes	No
100m	Yes	No
150m	Yes	No
200m	Yes	No
More than 200m	Yes	No

6. Which beach do you prefer? [PLEASE TICK]

Eastern	☐
Nahoon	☐
Nahoon river	☐
Orient	☐

7. Number of people in your group of the following ages:

Less than 15 years	☐
15-21 years	☐
21-40 years	☐
More than 40 years	☐

8. How many days a year do you visit the beach? ______________________

9. How long do you usually stay (hours)? ______________________

10. Will you come again? | Yes | No |

PTO

11. What do you usually do on the beach?

Sunbathe [Yes | No] Swim [Yes | No] Surf [Yes | No]

Paddleski [Yes | No] Windsurf [Yes | No] Other (specify) ....

12. Do you think that the beach is:

Overcrowded [Yes | No] Fully used [Yes | No]

Still room for more people [Yes | No]

13. Do you have lunch:

On the beach [Yes | No] In the dunes [Yes | No]

Somewhere else [Yes | No]

14. Do you climb or walk over the vegetated dunes?

[Yes | No]. If yes, why? ....

....

15. Do you enter the coastal forest in areas with no pathways?

[Yes | No] If yes, why? ....

....

16. Do you consider the forested areas along the beach:

Exceedingly Attractive [Yes | No]
Attractive [Yes | No]
Not attractive [Yes | No]
An eyesore [Yes | No]

17. Do you think that the following should be provided:

Picnic spots [Yes | No] Restaurants [Yes | No] Beach Cafe [Yes | No]

Improved access to the beach [Yes | No]

18. Any other comments ....

....

THANK YOU

CHAPTER 6

THE EFFECTS OF HUMAN TRAMPLING AND OFF-ROAD VEHICLES ON DUNE VEGETATION AT GREAT FISH POINT, EASTERN CAPE

INTRODUCTION

It was evident from the studies carried out at East London (Chapter 5) that more information is needed on the ecological effects of human trampling on foredune vegetation to assess ecological carrying capacity. Furthermore, no information on the effects of off-road vehicles (ORV's) on the coast is available in South Africa, and consequently government and local authorities are forced to base their legislation on overseas data (van der Merwe 1988). As a result, there is no national policy concerning the use of ORV's (Schneier 1986).

Research abroad has shown that the general effects of trampling are a reduction in total cover of vegetation, which is most rapid following the initial application of trampling (McDonnell 1981; Bowles & Maun 1982); and a persistent reduction in height of the vegetation (Liddle 1975a). There is also a general decline in species diversity (McDonnell 1981), but this effect is not always clear due to the introduction of new species (Burden & Randerson 1972). However, with increased use and before complete denudation, diversity decreases as only the most tolerant species survive (Trew 1973; Liddle 1975a). For example, McDonnell (1981) showed that long term trampling pressure favoured *Ammophila breviligulata* over other more sensitive species, and Liddle & Greig-Smith (1975b) have suggested that controlled trampling could be used as a management tool to artificially manipulate the species composition of coastal grasslands. This is possible as light wear can stimulate the growth of some species of grasses, and dicotyledonous species initially increase at the expense of monocotyledons at moderate levels. At higher levels only the more resistant monocotyledonous species are able to survive (Liddle 1975a). Certain more tolerant species become common in trampled areas, but in untrampled sites these species are at a competitive disadvantage and become overgrown by trampling sensitive species (Burden & Randerson 1972). This is because many morphological characteristics of plants, such as size, erectness and strength of leaves, strength of petioles and nodes, woodiness and erectness of stems and growth form affect susceptibility (Liddle & Greig-Smith 1975b). Bates (1935) noted that resistant species were usually conduplicate, and species having leaves and stems resistant to injury and a protected growing point are less vulnerable (Hylgaard & Liddle 1981). Liddle (1975b) has suggested a relationship between the vulnerability of vegetation and primary production, according to which highly productive vegetation should be most tolerant to trampling.

Changes in soil resulting from trampling include an increase in bulk density due to compaction, which is directly related to the number of passages (Liddle & Greig-Smith 1975a; McAtee & Drawe 1981). This relationship is linear until the maximum value of bulk density is reached, after which further compression does not take place (Liddle & Greig-Smith 1975a). This compaction reduces the amount of water available to the soil, but by increasing the capillary strength, the field capacity of the soil may be increased. Under dry conditions, compaction will therefore increase the water content of dry sand dunes (Liddle & Greig-Smith 1975a), but these inter-relationships are complex (Liddle 1975a). The primary effect of track formation on the thermal microclimate is to make temperatures more extreme, resulting in an increase in the soil temperature range of pathways (Liddle & Moore 1974; McAtee & Drawe 1981). Essentially the vegetation must be able to cope with conditions very different to those found in untrampled areas.

It is evident from the literature that the ecological effects of ORVs in the coastal zone is far greater than the effects of human trampling. Based on an extensive research project undertaken at Cape Cod National Seashore in Massachusetts, Brodhead & Godfrey (1979a) concluded that dune vegetation had no carrying capacity for ORVs. They showed that vehicle damage leads to an increased loss of soil moisture, and that the first few passes over *Ammophila breviligulata* were most damaging, with a significant effect after only 70 passes. Continued impacts prevented growth, and further studies have shown that the seaward edge of *Ammophila* foredunes may retreat by as much as 6 metres when exposed to only 1 pass per week for 2 years (Anders & Leatherman 1987a). However, regrowth is fairly rapid, and foredunes showed a complete recovery after four years. Nevertheless, wheel ruts and scars remain for much longer periods (Brodhead & Godfrey 1979a). The angle at which a vehicle passes over a dune is also important, with the greatest impact resulting from a perpendicular approach. In this case no further damage occurred after 100 passes, indicating that maximum damage had already occurred. Greater sand movement was also noted, and this damage can lead to blowouts developing (Brodhead & Godfrey 1979a). Stabilized dunes were found to be more sensitive, with 50 passes completely destroying heather (*Hudsonia*); and tracks still clearly visible after 3 years. The upright portions of bearberry (*Arctostaphylos uva-ursi*) were completely killed after 50 passes, but the hard, woody creeping stems of this species were not broken. Recovery was therefore rapid, and after 3 years, the track was barely visible (Godfrey *et al.* 1978; Brodhead & Godfrey 1979a). The general conclusion drawn from these observations were that areas least tolerant of changing environmental conditions or physical stress were damaged the most by ORVs.

The drift line, usually found above the high spring tide mark, is also very sensitive. Only a few passages are necessary to break up the organic deposit and destroy regenerating plants, which play an important role in new dune formation (Godfrey *et al.* 1978; Zaremba *et al.* 1979). Despite the difficulties experienced in studying these changing habitats, ORVs were found to reduce diatom populations by 90%, and bacterial populations by 50% (Godfrey & Godfrey 1980). On the other hand, algal and invertebrate populations were highly variable and seemed to exhibit no apparent effects from vehicle impact (Zaremba *et al.* 1979). Similarly, van der Merwe & van der Merwe (1991) found that intertidal species showed a high tolerance to vehicular traffic, but the supralittoral species *Tylos capensis* was highly susceptible due to the deep tracks ploughed into the less compact sand around the drift line. However, the most sensitive of all coastal habitats are salt marshes and intertidal flats, with some plants being destroyed by 1 to 5 passes (Brodhead & Godfrey 1979b).

ORVs also effect the geomorphology of beaches and Leatherman & Long (1977) showed that beach profiles were more variable along impacted areas of the barrier island at Cape Cod. The tentative conclusion that smaller scale modifications of beach profiles by ORVs could be significant on an incremental basis was investigated further by Anders & Leatherman (1987a&b). They showed that slope, sand compaction and number of vehicle passes in the same track were principle factors controlling the measured net seaward displacement of sand, and that ORV use could contribute to the overall erosion rate of beaches.

In 1982, Brokensha recommended that a research project on the impact of vehicles on beaches in South Africa be funded and initiated as a matter of urgency. The lack of information on the ecological impacts of ORVs in South Africa lead the Divisional Council of Dias, which is responsible for controlling utilization of the coastline between the Gamtoos to Great Fish River (see Fig. 1.1, pg 17), to recommend a total ban on ORVs (Anon 1983). This was to be phased in over a 5 year period, and was largely based on the research undertaken at Cape Cod by Leatherman, Godfrey and others (Godfrey *et al.* 1978; Leatherman & Godfrey 1979). This lack of local information (van der Merwe 1988) lead to a research project being initiated to determine the extent of ORV use in the Eastern Cape (Els & McLachlan 1990), and their effects on the macrofauna of beaches (van der Merwe & van der Merwe 1991).

Vegetated foredunes are very common features along the South African coastline (Tinley 1985). In the Eastern Cape they are often colonized by pioneer species such as *Scaevola plumieri* and *Sporobolus virginicus*, and one of the only shrubs common on foredunes is *Passerina rigida*, although it occurs more commonly on rear dunes (Chapter 1). These ecotone communities are widespread, forming the leading edge of vegetation in coastal systems (Barbour 1992), and play a very important role in contributing towards the dynamic equilibrium which usually exists along coastlines. Although only superficially stable, they absorb wave energy, protect developments against corrosive sea spray, sand-blasting and inundation by sand blown inland, are important for recreational purposes and function as barriers and storm energy absorbers (Vogt 1979; Ranwell & Boar 1986; van der Merwe 1988).

Since no data is available on the susceptibility of dune vegetation to trampling and ORVs in South Africa, this study was initiated to:

* determine how susceptible typical pioneer communities of coastal foredunes, and shrub species of rear dunes, are to both human trampling and ORV effects.

- * monitor the recovery rates of these communities, and
- * assess whether these communities could tolerate low levels of impact for extended periods of time without irreversible damage occurring.

It was hoped that the human and ORV carrying capacities of coastal dunes could be determined, with a view to making recommendations concerning vehicle use along the South African coastline.

STUDY AREA

Following the initial extensive survey of the coastline (Chapter 1), a suitable area was found for this study less than 1 km west of the mouth of the Great Fish River (see Fig. 1.1, pg 17). It was selected because of the large number of foredunes found in a relatively small area, this being the result of westerly transported sand accumulating upwind of a low rocky shelf protruding into the sea (Plate 6.1). Small hummock foredunes dominated by the grass *Sporobolus virginicus* are found just above the high water mark on the gently sloping beach face. Higher incipient foredunes dominated by the fine leaved thymeleaceous shrub *Passerina rigida*, occur behind the *S. virginicus* community. The slightly more level area behind the *Passerina* is dominated by a common foredune species, the succulent, rhizomatous, woody shrub *Scaevola plumieri* (Plate 6.1; Fig. 6.1). All three communities are very homogenous, with only a few other pioneer species found in the area.

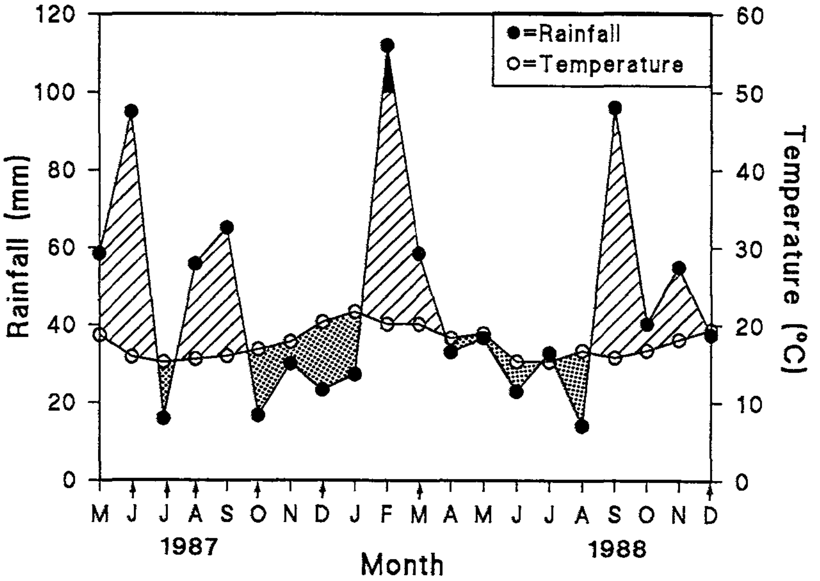


Figure 6.1 Monthly temperature and rainfall data for the duration of the study, presented in the form of a Walter-Leith climate diagram. Arrows show the dates of sampling.

Weather data are recorded at the Great Fish Point Lighthouse, a few kilometres west of the study area. A climate diagram and wind rose are presented in Chapter 1 (see Figs. 1.1 & 1.2). Rainfall is bimodal and peaks in the growing season (September to December) and in autumn (March to May). Mean annual precipitation is 559 mm and mean annual temperature 18°C. Winds are predominantly westerlies and south-westerlies in winter, and easterlies in summer. The area is windy with only 38 calm days a year. The relatively harsh climate makes these foredune communities susceptible to environmental perturbations. More detailed information on rainfall and temperature were extracted from the Weather Bureau's monthly weather records for the period of the study. Although rainfall was 11% less than the long term average, only two distinct dry periods occurred. These were from October to January 1987, and April to August 1988 (Fig. 6.1). The former was in the growing season, and the latter fell during the winter months. Rainfall peaked in the winter months of May and June 1987, and the summer (February and March) and spring (September to November) of 1988. This corresponds to the bimodal pattern of rainfall for this area. Temperatures do not fluctuate widely, and were lowest in July (15.2°C) and highest in January (21.7°C; Fig. 6.1).

METHODS

TREATMENTS

The study area was fenced and signposted to avoid disturbance from local residents and visitors to the sample plots, and all three communities were subject to both human trampling and off-road vehicle effects. The former was achieved by a barefoot individual of 75 kg weight walking through sample plots, and the latter by driving a Land Rover (approximate weight 1.5 tons) at constant speed (<20km/hr) over sample sites. In some cases, due to slope and topography variation, it was not possible to drive at a constant speed, and the implications of this are discussed later.

All communities were exposed to five different treatments, except for the *Passerina rigida* community, which was only exposed to four vehicle treatments, as summarised in Table 6.1. The "50% damage on one day" treatment involved measuring the immediate effect of trampling or vehicle passes after successive treatments on a single occurrence, and was undertaken to assess the *resistance* of the three species to the immediate impact of trampling by foot and wheel (*vide* Liddle & Thyer 1986). The "50% recovery" treatment involved measuring the recovery rate of the vegetation in the sample plot over a period of 19 months to assess the tolerance of the damaged plants to the impact, and their *resilience*, which is the potential to regenerate after damage (Liddle & Thyer 1986). From this initial treatment it was possible to determine how many passages were required to cause a particular reduction in plant height. Selected sample plots were then exposed to repeated damage at levels which resulted in a 10, 20 and 35% reduction in height, but the *P. rigida* community could only be exposed to ORV treatments at levels of 35 and 50%, as these corresponded to 1 and 2 passes respectively (Table 6.1).

Plate 6.1 Aerial view of the study site near the Great Fish River, looking north. The *Sporobolus virginicus* community is in the foreground, and the more densely vegetated dunes are covered with *Passerina rigida*. The *Scaevola plumieri* community is behind the *P. rigida*. Note the bushclump behind and to the left of the fenced area, which is covered by woody species as discussed in Chapter One. The transverse dunes move accross the dunefield from left to right, under the influence of strong westerly winds.

Plate 6.2 Point Frame used to sample height of vegetation. Note the damage to *Passerina rigida* after one passage a month for 5 months.

Table 6.1 Summary of treatments, showing number of passages and actual level of damage, and sample plot codes used in Figure 6.2.

TRAMPLING					
Community	**Treatment**	**Homogeneity of Sample plot**	**Code**	**No. of passages**	**Actual level of damage**
Sporobolus virginicus	50% damage & recovery	No	T1a	N/A	N/A
	10% damage repeated	Yes	T1b	3	9%
	20% damage repeated	Yes	T2a	10	20%
	35% damage repeated	No	T2b	24	35%
Scaevola plumieri	50% damage & recovery	Yes	T3a	N/A	N/A
	10% damage repeated	Yes	T3b	2	15.2%
	20% damage repeated	Yes	T4a	3	21%
	35% damage repeated	Yes	T4b	7	35.4%
Passerina rigida	50% damage & recovery	No	T5a	N/A	N/A
	10% damage repeated	No	T5b	1	12.3%
	20% damage repeated	No	T6a	2	23.8%
	35% damage repeated	No	T6b	4	38%
OFF-ROAD VEHICLE					
Sporobolus virginicus	50% damage & recovery	Yes	V1	N/A	N/A
	10% damage repeated	No	V2	2	14%
	20% damage repeated	Yes	V3	5	19.6%
	35% damage repeated	Yes	V4	10	34.7%
	Control for ORV & trampling	Yes	C1	N/A	N/A
Scaevola plumieri	50% damage & recovery	Yes	V5	N/A	N/A
	10% damage repeated	Yes	V6	2	9.1%
	20% damage repeated	Yes	V7	7	20.6%
	35% damage repeated	Yes	V8	17	34.5%
	Control for ORV & trampling	No	C2	N/A	N/A
Passerina rigida	50% damage & recovery	No	V9	N/A	N/A
	35% damage repeated	No	V10	1	37%
	50% damage repeated	No	V11	2	54%
	Control for ORV & trampling	No	C3	N/A	N/A

EXPERIMENTAL LAYOUT AND SAMPLING PROCEDURE

The position of sample plots within the study site was dictated by vehicle access and homogeneity of the three communities sampled. The older *Passerina rigida* community on larger foredunes was only accessible from the north, and the *Scaevola plumieri* sample V7 was located on a steep foredune, whereas V8 was on a level area (Fig. 6.2). The *Sporobolus virginicus* sample plots were situated just above the high tide mark, and in most cases trampling plots were located in less accessible areas. The *Passerina rigida* trampling plots were on the highest incipient foredunes found in the centre of the study area (Fig. 6.2; Plate 6.1).

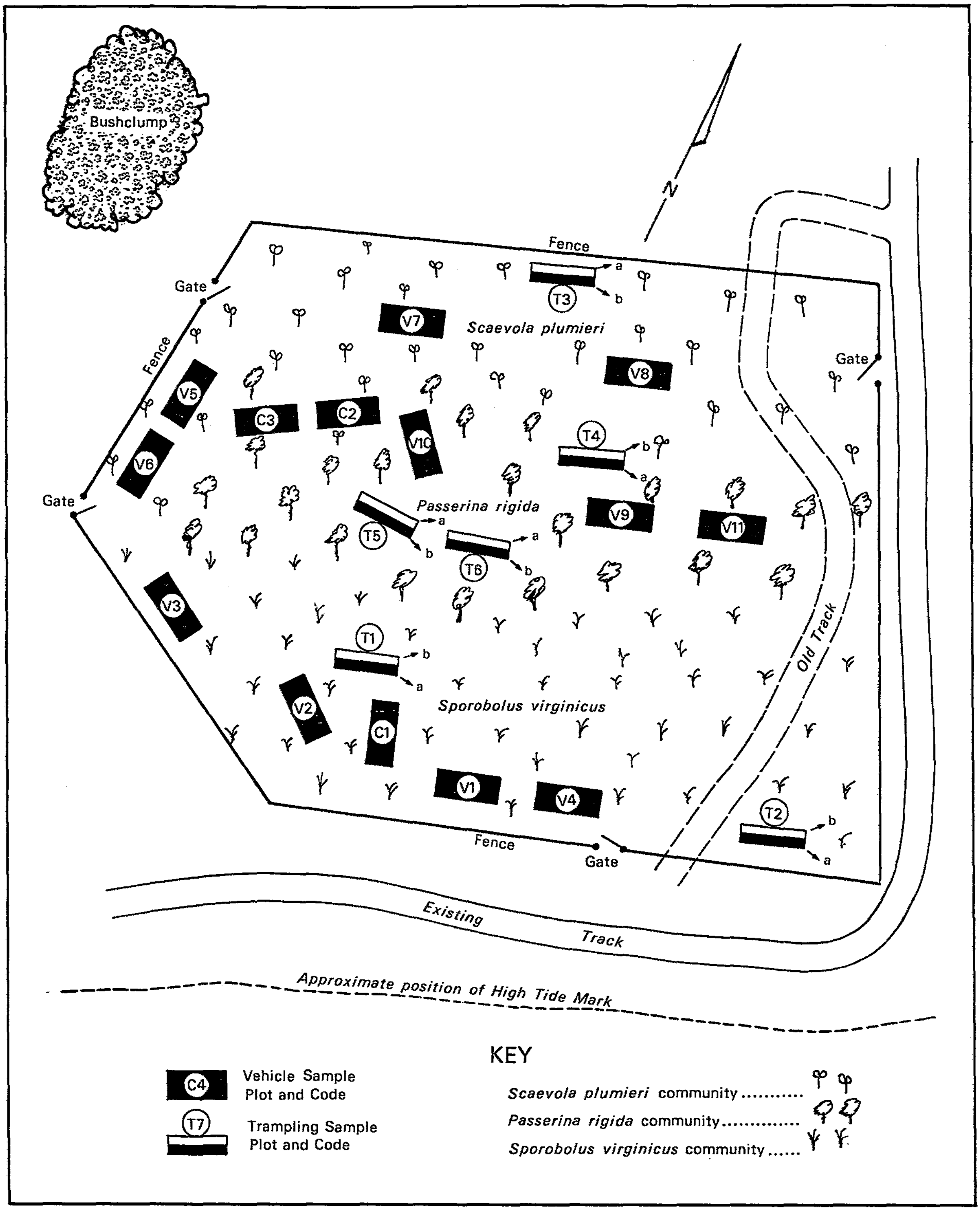


Figure 6.2 Map of the study area, showing approximate position of the sample plots in relation to the three dominant communities and position of the high tide mark (for locality see Fig. 1.1, pg 17).

Sample plots for the off-road vehicle treatments measured 10 m by 3 m wide, and were divided into 15 transects at intervals of 0.75 metres. Each 3 m wide transect was sampled with a Point Frame, as described earlier (Chapter 5; Plate 6.2). In a separate study, this technique proved to be the most suitable and reliable of the three techniques investigated (Avis 1990). Samples were taken at 10 cm intervals, making a total of 30 points per transect (Fig. 6.3). Total sample size for ORV treatments was therefore 450 points. Sample plots for trampling treatments measured 10m by 0.5 m wide. Two plots separated by a 1 m wide buffer strip were situated next to each other and were divided at 0.25 m intervals into 40 transects. As each transect was sampled at 5 cm intervals, total number of points for each transect was 10, and for the sample plot a total of 400 points were taken (Fig. 6.3). However, owing to the greater density of the *Passerina rigida* community, transect intervals were increased to 0.5 m, making a total sample size for this community of 200 points. The four corners of each plot were permanently marked with wooden poles with nails in the centre to mark the exact distance between poles.

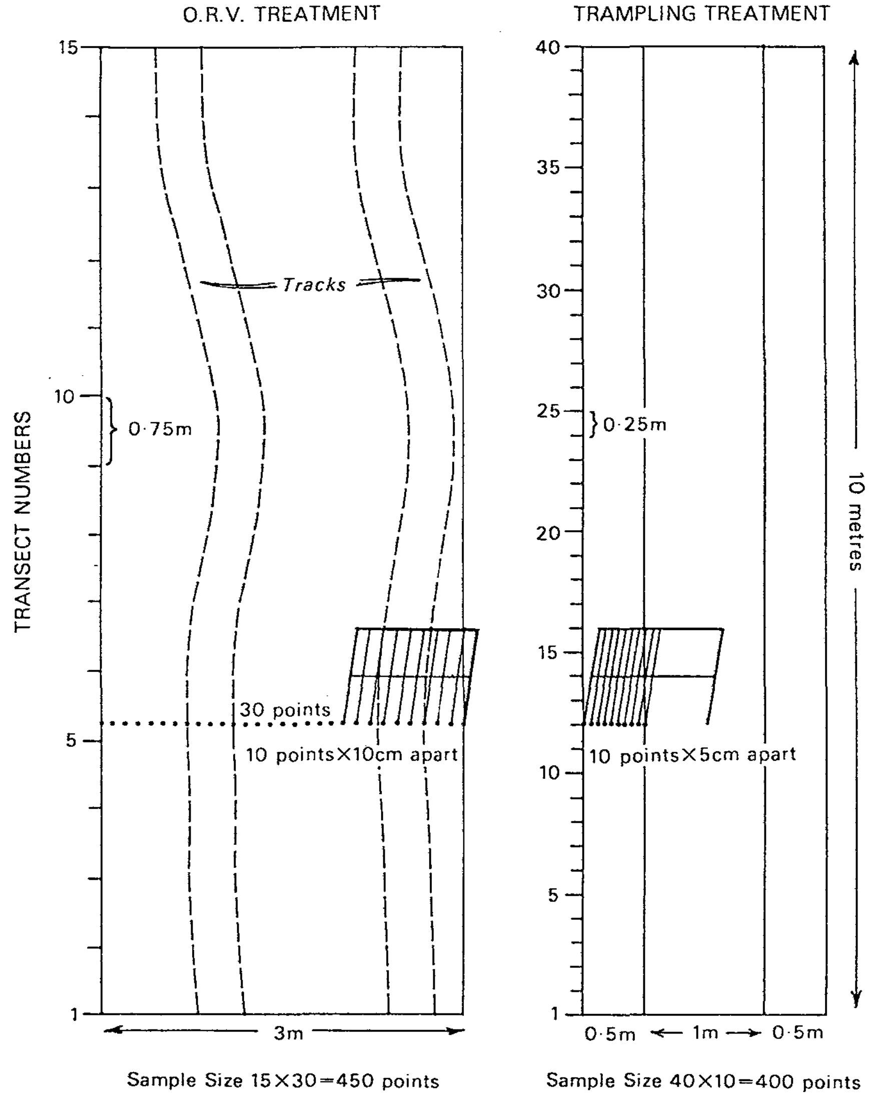


Figure 6.3 Sample plot layout for Off-road vehicle and trampling treatments, showing sampling technique.

Initially all plots were sampled during the period 24 April to 19 May 1987, and the initial treatments were also given during this period. Plots were then resampled at approximately 6 week intervals for the first 12 months, and more irregularly thereafter. At each sampling interval, all plots and controls were sampled within a few days of each other. The experiment was terminated on 15 December 1988, after 80 weeks and 7 sampling intervals.

For the "50% damage on one day" treatment, more samples were taken after the initial few passages, and the sample interval was increased with increasing passages. This was done because the previous study had shown that more damage occurred after the initial few passages (Chapter 5). This sample plot was not exposed to any further disturbance, but was resampled to determine recovery rates. Treatments exposed to repeated damage at various levels (Table 6.1) were sampled at each interval after the plot had been exposed to the required number of passages, as determined from the "50% damage on one day" treatment (Table 6.1).

Changes in soil density and compaction was estimated for all treatments by measuring the soil shear stress with a shear vane. Although Carter (1980a) used a similar instrument in Ireland, penetrometers are considered more reliable and may even be a better measure of compaction than soil bulk density (Liddle & Greig-Smith 1975a), and have been used successfully in other studies (Blom 1977). Unfortunately a penetrometer was not available, and results using the sheer vane are not very reliable.

DATA ANALYSIS

Change in plant height was determined for each successive sampling interval by calculating mean plant height and standard error for the entire sample plot. This was then expressed as a percentage change in height using the following formula:

$$\frac{\text{Height after exposure}}{\text{Initial height}} \times 100 - 100 = \%\ \text{change}$$

These values were plotted as graphs of percentage reduction in plant height against either number of passages or time interval. Although a total of 450 and 400 points were taken for the ORV and trampling treatments respectively, the actual sample size for each plot was dictated by the number of times a point struck a plant in the initial sample, for two reasons (Radloff, S. pers. comm.). Firstly, since average height was the desired measure, the inclusion of a large number of misses in the data set would dilute the real height of the vegetation. The initial misses were not considered real values, but subsequent misses at a point which previously struck a plant were treated as a zero measure of height, as the plant may have been destroyed during the treatment. Secondly, the analysis of complex data sets which contain many zero values is difficult. The number of times a plant was struck out of the total sample size was used to give a measure of the cover of the vegetation in each sample plot.

The total number of sample points taken at each recording interval for the treatments listed in Table 6.1 was 11 500, but only 3 350 struck plants. Thus, the total mean cover for the study area was 29%. The entire data set was captured into Lotus 123 as separate files according to the treatments (Table 6.1). These files were subdivided on the basis of sampling dates or number of passages, and individually analyzed using Statgraphics. Initially all values for each sample plot were analyzed together. To test the null hypothesis that no differences exist between the various treatments, a Scheffé-Multiple range test and a pairwise Analysis of Variance (ANOVA) was performed. For the one day treatments, the pairwise ANOVA was performed between the initial values and each subsequent treatment. For the recovery plots the initial value was compared with the values obtained at each sampling interval. For the repeatable damage, pairwise ANOVA's were performed between the initial value after damage and each subsequent value to determine when reductions in height became significant, and if so, whether they remained significant. Controls were also subjected to pairwise ANOVA's between each sampling period and the previous one, to see if any significant changes in height resulted from natural variations. In all cases significance was tested at a probability level of 0.05.

To test whether sample plots were homogenous, they were divided into subsets and analyzed using a one-way ANOVA. Trampling plots were divided into four sub-samples, by grouping 10 transects together, and ORV plots by grouping five transects together. The former therefore contained four sub-samples of 100 points each, and the latter three sub-samples of 150 points each (Fig. 6.3). The one-way ANOVA tested whether height between these blocks differed significantly (at $P<0.01$), and if this was the case, it meant that plots were heterogenous. Some of these were tested by means of a two-way ANOVA, but similar trends to that revealed by the one-way ANOVA showed that this was not necessary.

RESULTS

Data for all treatments (Table 6.1) are presented graphically as plots of percentage change in plant height (y axis) against number of passages (Figs. 6.4 & 6.5) or time in weeks (Figs. 6.6 to 6.14). Each graph is supported by a table showing results of the one-way ANOVA's, mean percentage cover and mean plant height (Tables 6.2 to 6.12).

Results of the one-way ANOVA between blocks used as a test of homogeneity, are given as "yes" or "no" in Table 6.1. More than half the *Sporobolus virginicus* sample plots were heterogenous, indicating that height of plants differed between subsets. This was mainly due to the patchy cover of this species (Plate 6.8), which did not affect the reliability of the data. All *Scaevola plumieri* sample plots were homogenous, except for the control plot, but all *Passerina rigida* plots were heterogenous (Table 6.1). This is to be expected, due to the contagious distribution of this species (see Plate 6.4). Two-way ANOVA's were not performed as pseudo-replication of the plots would be required, and this could not be done since all plots were not homogenous. One-way ANOVA's were therefore considered more reliable.

SINGLE DAY TREATMENTS

The *Passerina rigida* community had the lowest resistance to trampling, with a 47% reduction in height after only 5 passages (Plate 6.3). After the first passage the decrease in height was significant, but cover was only reduced by 14.5% (Table 6.2). *Scaevola plumieri* was the next most susceptible species, with 4 passages causing a significant decrease in height and 12 passages producing a similar decrease to that obtained after 5 passages for *P. rigida*. Thirty passages resulted in a 54.7% decrease in height. *Sporobolus virginicus* appeared most resistant, at least initially, and 12 passages were required to reduce height significantly. After 30 passages a similar decrease in height to that obtained for *S. plumieri* was recorded, and mean cover decreased from 27.7% to 17.8% (Fig. 6.4; Plates 6.6 & 6.7). It is also evident that most damage occurred after the initial few passages.

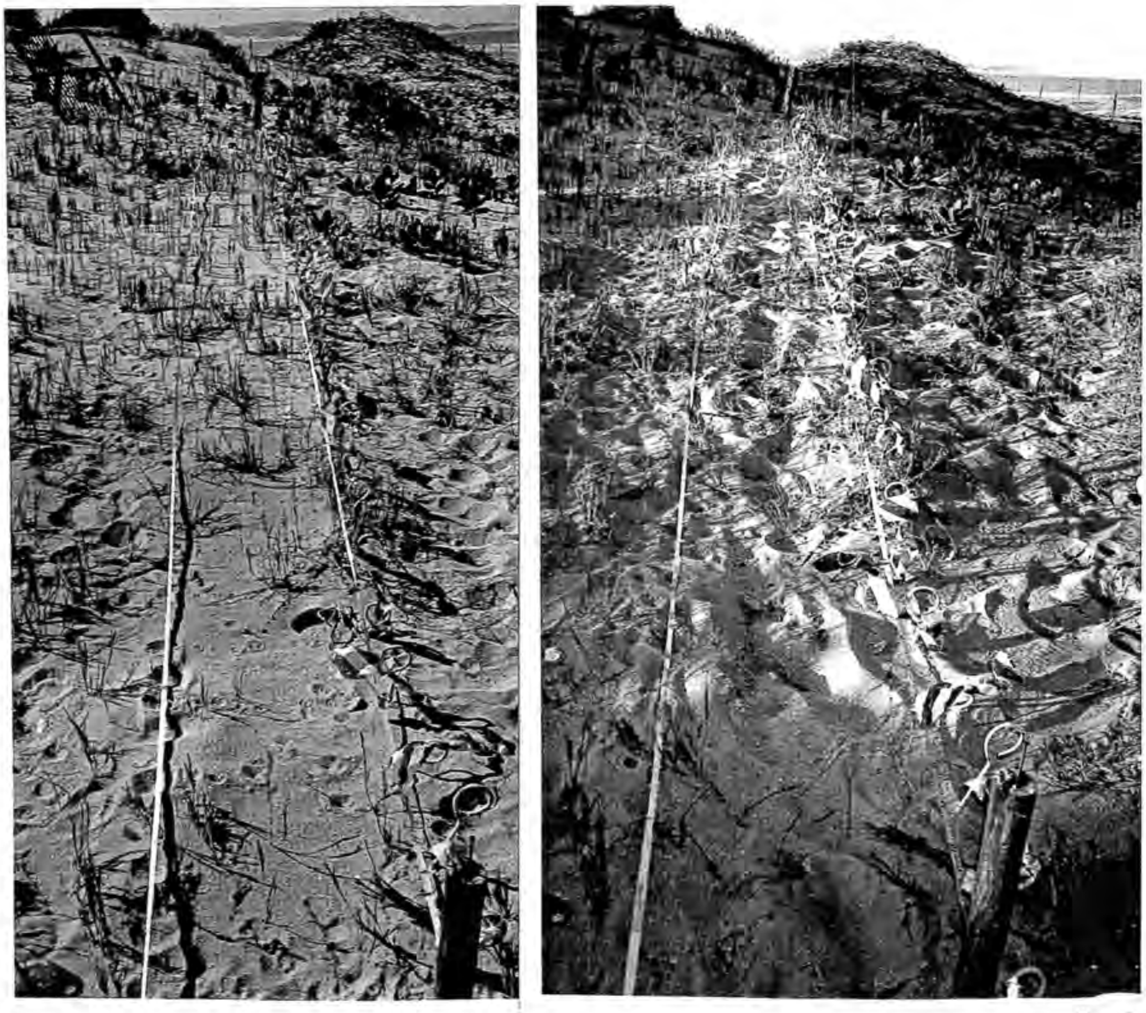


Plate 6.6 *Sporobolus virginicus* trampling sample plot, showing area before (left) and after (right) 30 passages. Disturbance to the substrate is less than for ORV impacts (compare with Plate 6.8). Height has been reduced by 5.95 cm to 2.75 cm.

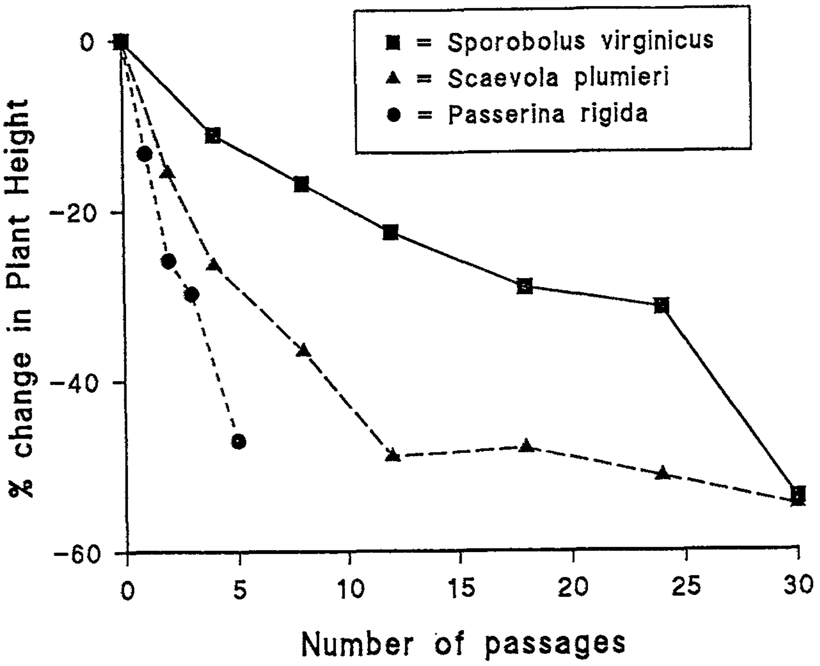


Figure 6.4 Percentage change in plant height for three species exposed to increasing trampling passages on a single day

Table 6.2 Change in plant height and mean percentage cover for three species exposed to increasing trampling passages on a single day, with corresponding statistical analysis.

No. of passages	Mean % cover	Mean plant height ±SE	% change in height	Scheffe range test	F - ratio	Sig level
			SPOROBOLUS VIRGINICUS			
0	27.7	5.95 ± 0.39	-	-	-	-
4	24.5	5.30 ± 0.39	- 11	N.S.	1.38	0.24
8	22.7	4.95 ± 0.40	- 16.9	N.S.	3.26	0.073
12	24.5	4.61 ± 0.35	- 22.6	Sig.	6.46	0.012
18	22.0	4.22 ± 0.35	- 29.1	Sig.	10.85	0.001
24	20.7	4.08 ± 0.39	- 31.5	Sig.	11.34	0.001
30	17.8	2.75 ± 0.32	- 53.8	Sig.	39.66	0.000
			SCAEVOLA PLUMIERI			
0	20.25	13.5 ± 1.07	-	-	-	-
2	19.25	11.41 ± 1.01	- 15.5	N.S.	2.09	0.149
4	18.25	9.95 ± 1.11	- 26.3	Sig	5.50	0.020
8	18.25	8.57 ± 1.02	- 36.5	Sig	11.25	0.001
12	16.00	6.89 ± 1.00	- 48.9	Sig	20.62	0.000
18	14.50	7.02 ± 1.01	- 48.0	Sig	19.63	0.000
24	13.75	6.57 ± 1.03	- 51.3	Sig	21.98	0.000
30	11.50	6.11 ± 1.01	- 54.7	Sig	26.94	0.000
			PASSERINA RIGIDA			
0	87.0	51.62 ± 1.98	-	-	-	-
1	85.0	44.82 ± 2.01	- 13.2	Sig	5.79	0.016
2	85.5	38.32 ± 1.79	- 25.8	Sig	24.71	0.000
3	77.5	36.28 ± 1.86	- 29.7	Sig	31.83	0.000
5	72.5	27.35 ± 1.74	- 47.0	Sig	84.61	0.000

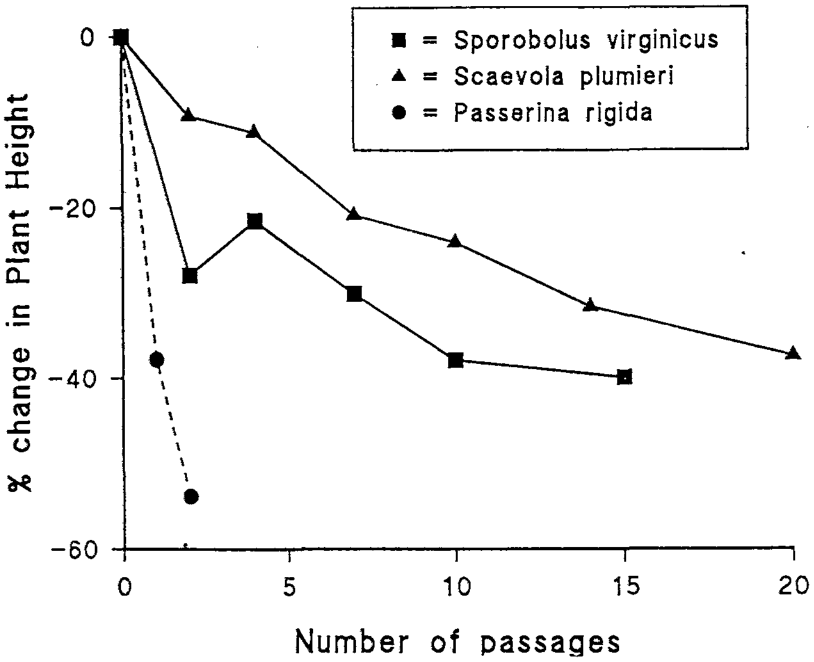


Figure 6.5 Percentage change in plant height for three species exposed to off-road vehicle passes on a single day,

Table 6.3 Change in plant height and mean percentage cover for three species exposed to increasing off-road vehicle passes on a single day, with corresponding statistical analysis.

No. of passages	Mean % cover	Mean plant height ±SE	% change in height	Scheffe range test	F - ratio	Sig level
			SPOROBOLUS VIRGINICUS			
0	42.7	7.91 ± 0.42	-	-	-	-
2	43.0	5.70 ± 0.37	- 27.9	Sig	15.49	0.000
4	43.8	6.21 ± 0.36	- 21.5	Sig	9.43	0.002
7	43.0	5.53 ± 0.33	- 30.1	Sig	19.61	0.000
10	39.3	4.91 ± 0.34	- 37.9	Sig	30.71	0.000
15	37.0	4.75 ± 0.36	- 39.9	Sig	32.17	0.000
			SCAEVOLA PLUMIERI			
0	18.6	7.04 ± 0.40	-	-	-	-
2	7.8	6.38 ± 0.21	- 9.2	N.S.	0.067	0.610
4	11.7	6.24 ± 0.29	- 11.2	N.S.	0.196	0.179
7	11.7	5.59 ± 0.16	- 20.9	N.S.	7.96	0.009
10	15.2	5.36 ± 0.23	- 24.1	Sig	9.73	0.021
14	17.0	4.82 ± 0.24	- 31.6	Sig	.67	0.000
20	15.7	4.39 ± 0.18	- 37.4	Sig	30.35	0.000
			PASSERINA RIGIDA			
0	79.3	38.63 ± 1.22	-	-	-	-
1	53.5	24.02 ± 1.02	- 37.8	Sig	84.45	0.000
2	47.1	17.84 ± 0.93	- 53.8	Sig	185.09	0.000

Plate 6.3 *Passerina rigida* recovery plot 9 weeks after exposure to 5 passages. Damage was more obvious a few weeks after impacting, as dead portions of the plants became clearly visible.

Plate 6.4 *Passerina rigida* recovery plot 5 weeks after exposure to only 2 ORV passes. Note damage to shrubs.

Plate 6.5 *Scaevola plumieri* recovery plot 5 weeks after exposure to 20 ORV passes. Vehicle tracks are clearly visible.

P. rigida was also least resistant to ORV effects, and seemed to be completely intolerant. Only 2 passes were required to reduce height by 53.8% and cover by over 30%, and a single pass caused a significant decrease in height (Table 6.3; Plate 6.4). Surprisingly, *S. plumieri* appeared more tolerant than *S. virginicus*, and 10 passes were required to reduce height significantly, whereas for the latter species 2 passes resulted in a significant decrease in height, and fifteen passes resulted in a similar decrease in height to 20 passes for *S. plumieri* (Fig. 6.5). For both these species, changes in cover was somewhat erratic and not very marked. Again, the greatest reduction in height occurred after the first few passes. For example, with *S. virginicus*, 2 passes caused a 27.9% decrease in height, and an additional 13 passes only reduced the height by a further 12% (Fig. 6.5; Plate 6.8).

Plate 6.7 *Scaevola plumieri* trampling sample plot, showing area before (left) and after (right) 30 passages. Damage was mainly caused by the leaves being broken off the stem (arrowed).

From the above it is clear that there is less tolerance to ORV effects. Height of *S. virginicus* was reduced by 39.9% after 15 passes, whereas 24 trampling passages only reduced height by 31.5%. This trend was more pronounced for *P. rigida*, with 2 passes of a vehicle causing a 53.8% reduction in height, whereas a similar level of trampling only reduced height by 25.8% (Tables 6.2 & 6.3). Such differences are to be expected, as the sheer forces exerted by a vehicle are far greater than those exerted by a human foot. The former extends to a depth of at least 13 cm (Zaremba *et al.* 1979), and the vertical force applied in sand has been measured at 18.1 kg cm^{-2} (Anders & Leatherman 1987b). This is much more than the estimated force of 0.2 kg cm^{-2} applied to the ground by a standing man (Liddle 1973 in Heath 1987). Nevertheless, the nature of the impact differs. With a vehicle, although the compressional forces are greater, they tend to be more even on level ground. The shearing action of the toe and compressional forces of the foot may cause more damage to certain plants, which will snap under direct pressure exerted at a particular angle. However, the even pressure of a wheel allows the plant to spring back after compaction, and it is suggested that this is one of the reasons why *S. plumieri* appeared more susceptible to trampling (Plate 6.7). Twenty four passages reduced height by 51.3%, whereas 20 vehicle passes reduced height by only 37.4% (Tables 6.2 & 6.3). Thus, it appears that plant morphology may also influence susceptibility to different types of impacts.

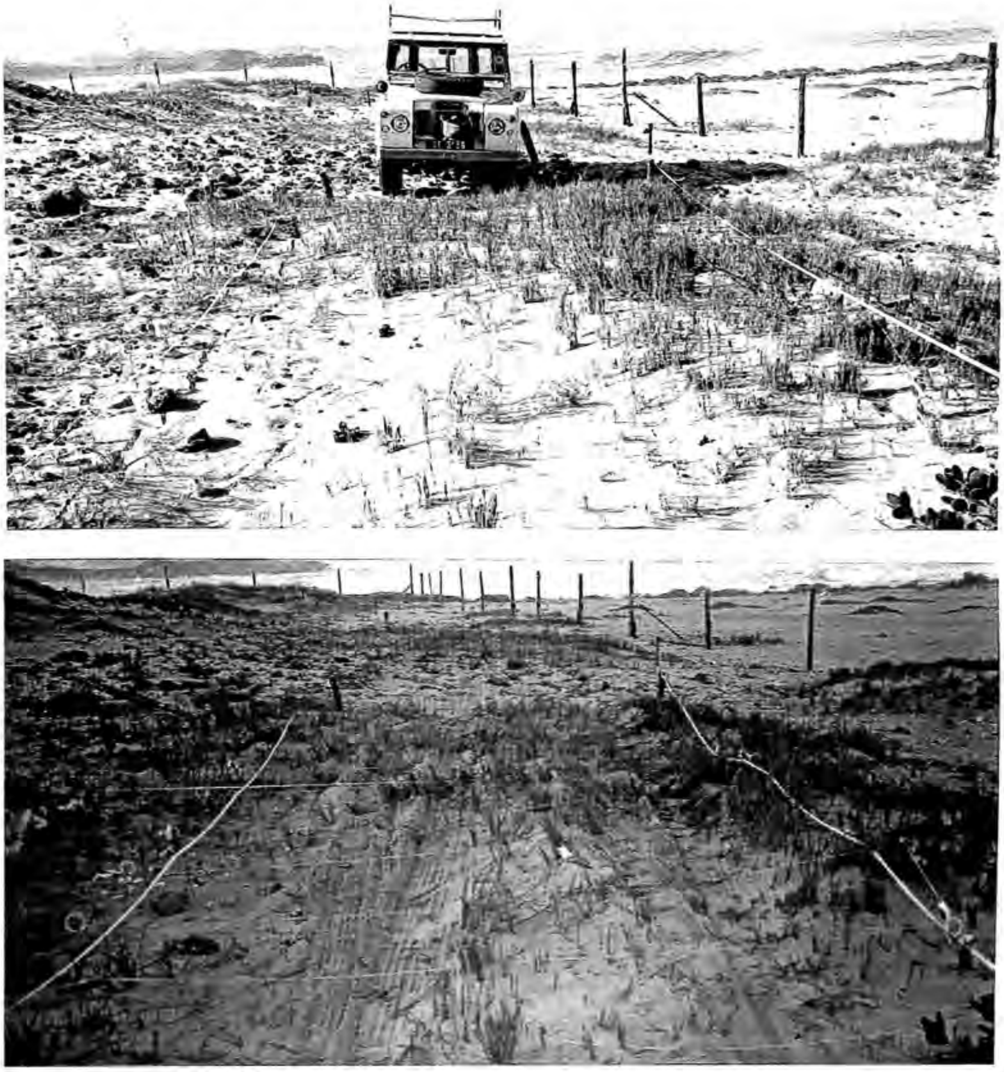


Plate 6.8 *Sporobolus virginicus* ORV sample plot, showing area before (top) and after (bottom) 15 passes. Note wheel ruts and loose sand on either side of ruts.

CONTROL PLOTS

The large degree of fluctuation in the height of vegetation in the control plots (Fig. 6.6) reflects both the natural variability of these communities and their response to various climatic and environmental factors; as well as stochastic events such as excessive sand movement, which occur often in this dynamic and unstable environment. Similar trends for the three species are apparent, although in some cases the response of one species is quite different to another. There was a steady and significant decrease in the height of *Sporobolus virginicus* over the winter months (June to August), but height increased in summer (December, 31 weeks), and reached a maximum at 45 weeks (Fig. 6.6). As was the case with the other two species, there was a decrease in height between 45 and 80 weeks. The spring and late summer growth phases can be related to the rains which fell during this period (Fig. 6.1). *Passerina rigida* showed a very similar trend, except for the slight increase in height at 9 weeks (Fig. 6.6). However, as expected, the fluctuations in height and therefore growth rate are less marked for this more stable, shrub dominated community. Nevertheless, the decrease in height over winter is significant (Table 6.4).

Scaevola plumieri showed an initial increase in height for the first 9 weeks, and growth fluctuated significantly until 31 weeks, after which height decreased steadily (Table 6.4). This is in contrast to the other two species, which showed a steady increase in height between 22 and 45 weeks. It is possible that changes in the actual height of the plants may be influenced by sand movement, as height was measured relative to the substrate level. Erosion may result in anomolous increases in height, and accretion decreases. However, the mean percentage cover shows similar trends to height, although this measure is not as precise or accurate (see Chapter 5; Sothern *et al.* 1985). It is most likely that the initial decrease in height of *S. virginicus* was due to sand inundating the sample plots, which are located close to the high water mark where sand movement is greatest (Fig. 6.1; Plate 6.1). Most of this movement occurs in the winter months when strong westerly winds are experienced (see Fig.2.2, pg 67), and excessive sand movement was noted in May and June 1987.

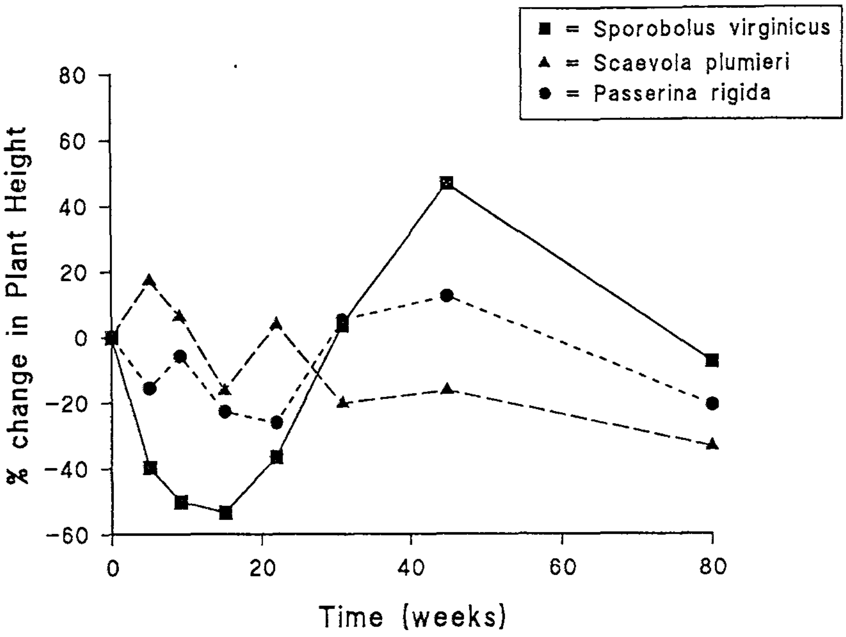


Figure 6.6 Percentage change in height for control plots.

Table 6.4 Natural fluctuations in cover and height of control plots, and corresponding statistical analysis.

Time period (weeks)	Mean % cover	Mean plant height ±SE	% change in height	Scheffe range test	F - ratio	Sig level
			SPOROBOLUS VIRGINICUS			
Initial	27.5	6.53 ± 0.41	-	-	-	-
5	24.0	3.94 ± 0.32	- 39.7	Sig	25.09	0.000
9	22.0	3.25 ± 0.34	- 50.2	Sig	32.21	0.000
15	19.0	3.04 ± 0.35	- 53.4	Sig	33.29	0.000
22	21.8	4.14 ± 0.37	- 36.6	Sig	24.79	0.004
31	33.5	6.77 ± 0.40	+ 3.6	N.S	3.47	0.154
45	44.7	9.59 ± 0.46	+ 46.8	Sig	21.73	0.000
80	19.8	6.04 ± 0.55	- 7.5	N.S	5.01	0.120
			SCAEVOLA PLUMIERI			
Initial	31.5	11.20 ± 0.74	-	-	-	-
5	35.0	13.14 ± 0.80	+ 17.3	N.S	3.16	0.077
9	27.25	11.92 ± 0.94	- 6.4	N.S	1.95	0.039
15	22.25	9.37 ± 0.82	- 16.3	N.S	3.28	0.620
22	31.75	11.62 ± 0.82	+ 3.8	N.S	0.77	0.253
31	28.75	8.93 ± 0.63	- 20.2	Sig	6.81	0.009
45	35.75	9.37 ± 0.61	- 16.2	N.S	3.20	0.621
80	21.5	7.46 ± 0.58	- 33.4	Sig	8.18	0.004
			PASSERINA RIGIDA			
Initial	54.7	32.32 ± 1.19	-	-	-	-
5	53.6	27.31 ± 1.15	- 15.5	Sig	9.15	0.062
9	51.6	30.49 ± 1.25	- 5.7	N.S	5.53	0.160
15	49.6	24.97 ± 1.07	- 22.7	Sig	11.32	0.000
22	49.6	23.87 ± 1.19	- 26.7	Sig	13.48	0.000
31	50.5	33.99 ± 4.19	+ 5.2	Sig	5.41	0.170
45	49.6	36.36 ± 2.54	+ 12.5	N.S	0.23	0.634
80	42.4	25.62 ± 1.50	- 20.7	Sig	10.51	0.000

RATES OF RECOVERY

Both *S. plumieri* and *P. rigida* did not fully recover from trampling, as average height was still significantly less than the initial value (Table 6.5). Results for *S. virginicus* are more erratic, with a very marked increase in height at 22 weeks, and again at 45 weeks. The latter increase corresponds to that noted in the control plot (Fig. 6.6), and was influenced by rainfall (Fig. 6.2). The increase at 22 weeks is difficult to explain, but there was a net increase in height after 80 weeks, indicating that this species is more tolerant. *S. plumieri* showed little recovery after 80 weeks, with height only increasing from 6.11 to 8.41 cm (Table 6.5). The decrease at 15 weeks was also noted in the control plot, and is not a result of the treatment (Figs. 6.6 & 6.7). *P. rigida* appeared to recover initially, but height decreased slightly at 15 weeks. After 80 weeks, height was still 40% less than before trampling, and this reduction remained significant for the duration of the study, indicating both low tolerance and resilience to trampling (Table 6.5).

For ORV treatments both *S. plumieri* and *S. virginicus* showed definite signs of recovery after 45 and 80 weeks respectively (Fig. 6.8). However, these final heights were very similar to, and therefore not significantly greater than, the initial values (Table 6.6). Height and cover of *S. virginicus* decreased rapidly and significantly for the 15 weeks after impacting (Fig. 6.8), but then showed a steady increase in height that closely corresponded to that noted for the control plot. It therefore appears that *S. virginicus*, although not tolerant to the impact, is able to recover more rapidly and fully from both human and vehicle induced changes, indicating a greater resilience to these effects. This is most likely related to the stoloniferous growth form of this grass. Brodhead & Godfrey (1979a) also found that the grass, *Ammophila breviligulata*, showed a fairly rapid response to ORV impacts, with full recovery after three years. Height of *S. plumieri* also decreased rapidly after 5 weeks, from -37.4% to -59.2%, and remained low for the subsequent 17 weeks (Table 6.6). Signs of recovery were only noted 31 weeks after impacting, with full recovery after 45 weeks. *P. rigida* did not show such a marked decrease in height for the 15 weeks after damage, but height and cover continued to decline for the duration of the study (Fig. 6.8).

This indicates that *P. rigida* has low tolerance and resilience, being unable to recover over a period of 18 months from 2 passes of a vehicle. It is interesting to note that *S. plumieri* recovered more successfully from ORV effects than from trampling (Figs. 6.7 & 6.8), lending support to the argument that it is more resistant to the former disturbance. The rapid decrease in height for the first 22 weeks after treatment for all plots is due to the death of some individuals which may have been sampled initially before signs of damage and necrosis was apparent. After 5 and 9 weeks damage to *P. rigida* from ORV's and trampling was clearly visible (Plates 6.3 & 6.4), as where vehicle tracks in the sparsely vegetated *S. plumieri* community (Plate 6.5). This indicates that sampling and measuring on a single day under-estimates the overall effects, and provides a best-case estimate of potential carrying capacity.

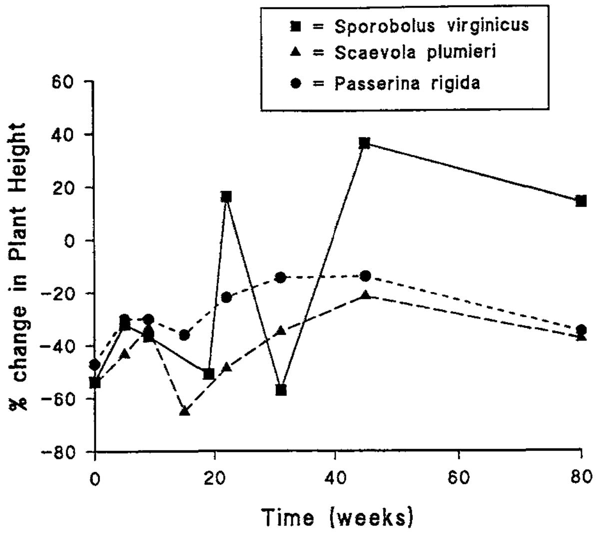


Figure 6.7 Percentage change in plant height showing recovery over an 80 week period following a trampling episoide.

Table 6.5 Change in plant height and percentage cover, for the 3 species investigated over an 80 week recovery period following trampling damage, with corresponding statistical analysis

Time period (weeks)	Mean % cover	Mean plant height ±SE	% change in height	Scheffe range test	F - ratio	Sig level
SPOROBOLUS VIRGINICUS						
Before	27.7	5.95 ± 0.39	-	-	-	-
After	17.8	2.75 ± 0.32	- 53.8	Sig	39.66	0.000
5	27.5	4.04 ± 0.43	- 32.1	N.S.	0.031	0.861
9	22.5	3.78 ± 0.39	- 36.5	Sig	10.64	0.013
15	17.0	2.86 ± 0.38	- 51.9	Sig	32.32	0.000
22	22.8	6.91 ± 0.84	+ 16.1	Sig	23.72	0.000
31	10.2	2.55 ± 0.41	- 57.1	Sig	35.8	0.000
45	32.5	8.11 ± 0.56	+ 36.3	Sig	9.88	0.002
80	22.0	6.77 ± 0.67	+ 13.8	N.S	1.13	0.289
SCAEVOLA PLUMIERI						
Before	20.25	13.54 ± 1.07	-	-	-	-
After	11.5	6.11 ± 1.01	- 54.7	Sig	26.94	0.000
5	14.25	7.64 ± 0.99	- 43.4	Sig	16.28	0.000
9	15.5	9.02 ± 1.18	- 33.2	Sig	8.05	0.005
15	10.25	4.72 ± 0.86	- 65.0	Sig	41.21	0.000
22	16.75	6.91 ± 0.84	- 48.8	Sig	23.72	0.000
31	17.0	8.77 ± 0.83	- 35.0	Sig	12.39	0.006
45	33.25	10.60 ± 0.81	- 21.5	Sig	4.82	0.029
80	17.25	8.41 ± 1.16	- 37.7	Sig	10.49	0.001
PASSERINA RIGIDA						
Before	87.0	51.63 ± 1.98	-	-	-	-
After	72.5	27.35 ± 1.74	- 47.0	Sig	84.61	0.000
5	83.0	33.54 ± 1.82	- 35.0	Sig	45.11	0.000
9	78.5	36.11 ± 1.89	- 30.1	Sig	32.19	0.000
15	78.0	32.96 ± 2.13	- 36.1	Sig	41.06	0.000
22	88.5	40.18 ± 2.35	- 22.2	Sig	13.84	0.000
31	94.5	44.17 ± 1.97	- 14.5	Sig	7.12	0.008
45	80.5	44.4 ± 2.22	- 14.0	Sig	5.89	0.016
80	71.5	30.97 ± 2.27	- 40.0	Sig	46.76	0.000

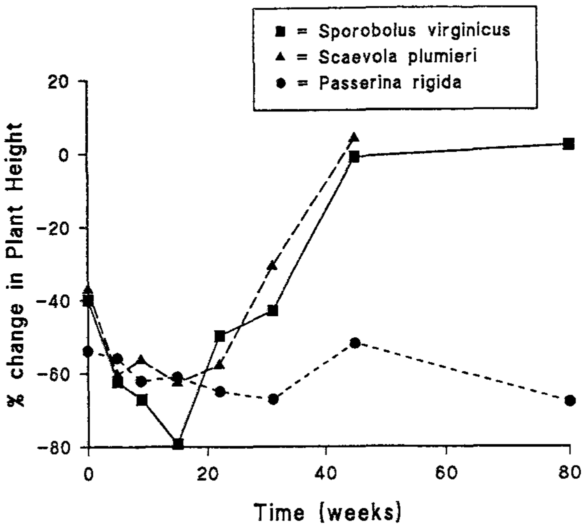


Figure 6.8 Percentage change in plant height showing recovery over an 80 week period subsequent to damage from an off-road vehicle.

Table 6.6 Change in plant height and percentage cover, for the 3 species investigated over an 80 week recovery period after ORV damage and corresponding statistical analysis.

Time period (weeks)	Mean % cover	Mean plant height ±SE	% change in height	Scheffe range test	F - ratio	Sig level
SPOROBOLUS VIRGINICUS						
Before	42.7	7.91 ± 0.42	-	-	-	-
After	37.0	4.75 ± 0.36	- 39.9	Sig	32.17	0.000
5	19.8	2.99 ± 0.31	- 62.2	Sig	87.64	0.000
9	19.1	2.61 ± 0.32	- 67.0	Sig	100.08	0.000
15	14.9	1.64 ± 0.21	- 79.2	Sig	175.69	0.000
22	21.1	3.98 ± 0.39	- 49.7	Sig	47.22	0.000
31	26.7	4.51 ± 0.37	- 42.9	Sig	36.58	0.000
45	40.4	7.84 ± 0.42	- 0.91	N.S	0.017	0.89
80	33.8	8.08 ± 0.46	+ 2.2	N.S	0.063	0.80
SCAEVOLA PLUMIERI						
Before	18.6	7.04 ± 0.36	-	-	-	-
After	15.7	4.39 ± 0.35	- 37.4	Sig	72.19	0.000
5	17.1	2.87 ± 0.35	- 59.2	Sig	73.71	0.000
9	15.5	3.16 ± 0.40	- 55.1	Sig	56.91	0.000
15	15.3	2.71 ± 0.33	- 61.5	Sig	84.11	0.000
22	17.6	3.06 ± 0.35	- 56.5	Sig	68.72	0.000
31	19.8	5.02 ± 0.54	- 28.7	Sig	11.65	0.000
45	29.1	7.54 ± 0.52	+ 7.1	N.S	0.21	0.64
PASSERINA RIGIDA						
Before	79.3	38.63 ± 1.22	-	-	-	-
After	53.5	17.84 ± 0.93	- 53.8	Sig	185.09	0.000
5	43.1	17.35 ± 1.02	- 55.8	Sig	179.51	0.000
9	35.5	14.67 ± 1.09	- 62.0	Sig	214.51	0.000
15	34.0	15.05 ± 1.11	- 61.0	Sig	204.54	0.000
22	32.8	13.56 ± 1.06	- 64.9	Sig	240.37	0.000
31	28.4	12.71 ± 1.13	- 67.1	Sig	243.37	0.000
45	37.7	18.61 ± 1.19	- 51.8	Sig	137.70	0.000
80	34.0	12.45 ± 0.94	- 67.8	Sig	289.73	0.000

LONG-TERM TRAMPLING TREATMENT

Results for the repeated treatments at a prescribed level of intensity (Table 6.1) are expressed graphically as the change in height relative to the value obtained after the initial treatment (Figs. 6.9 to 6.14). Corresponding data and statistical analyses are presented in Tables 6.7 to 6.12. In some cases data reveal variable trends, which may reflect the response of these communities to the many dynamic forces acting on them. It was therefore not always possible to clearly separate the effects of the treatment from these other influences.

At all three levels of trampling, the height of *Sporobolus virginicus* decreased steadily for the first 22 weeks, after which it increased and peaked at 45 weeks (Figs. 6.9). The latter corresponded to an increased growth rate noted in the control plot (Fig. 6.6). A significant decrease in height at 31 weeks was only noted for the 10% treatment, and this is difficult to explain. For both the 10 and 20% treatments, there was a net increase in height at the termination of the study, which was significant for the former. However, at the 35% level there is a net decrease (Table 6.7). Height of the sample plot was only greater than the initial value obtained before trampling for the 10% treatment (Table 6.7). However, for all three treatments the maximum reduction in height was similar (about -50 to -60%), but the maximum increase was greater at the higher levels of trampling (Table 6.7). These increases were also greater than those recorded for the recovery plot (Table 6.5; Fig. 6.7). Thus, the main response of an initial decrease in height followed by an increase is similar at all three levels of trampling, but the fluctuations in these values are larger at higher levels. This infers that another effect of trampling was to increase the variability within the *S. virginicus* community, which may in turn lead to instability. However, there was no significant and steady decrease in height and cover for any of the treatments.

At repeatable levels of 2 and 3 passages (10 & 20% respectively), *Scaevola plumieri* decreased in height for the first 15 and 22 weeks. For the 10% treatment height then increased and peaked at 31 weeks, only to decrease again (Fig. 6.10). Cover followed a similar trend, but none of these changes were significant (Table 6.8). The increase in height at 31 weeks for the 20% treatment became significant at 45 weeks, and average height of the vegetation in the sample plot was greater than before trampling (Table 6.8). Data at the highest level of trampling (7 passages) are surprising and difficult to explain. After an initial decrease in height the *Scaevola* in this plot seemed to be stimulated to grow, increasing steadily and sometimes significantly in height (Fig. 6.10; Table 6.8), despite the fact that in the control plot height decreased (Fig. 6.6). This cannot be due to any unusual characteristics in this plot, as it lay next to the 20% treatment (Fig. 6.1), and may be a consequence of the sampling technique or experimental design. Occasionally, marker poles had been disturbed, making it difficult to relocate the exact position of each 10cm transect within the plot. Results of the long term effect of trampling on *S. plumieri* seem inconclusive and may be masked by other influences. However, it appears from these results that the response of *S. plumieri* is slower than for *Sporobolus virginicus*, since the former is a woody shrub, but providing the physical damage is not too great, *Scaevola* may respond positively to the resultant increased sand movement which is known to stimulate its growth rate (Pammenter 1983; 1985).

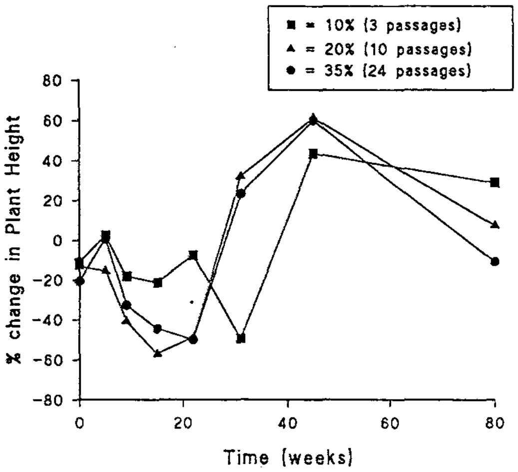


Figure 6.9 Damage to *Sporobolus virginicus* from repeated trampling at levels of 3,10 and 24 passages, given at each sampling period.

Table 6.7 Change in height and percentage cover of *Sporobolus virginicus* exposed to three levels of trampling over an 80 week period, with corresponding statistical analysis.

Time period (weeks)	Mean % cover	Mean plant height ±SE	% change in height	Scheffe range test	F - ratio	Sig level
			10 percent			
Before	20.75	6.10 ± 0.36	-	-	-	-
After	16.75	5.42 ± 0.57	- 11.2	N.S	1.04	0.31
5	20.0	5.55 ± 0.44	+ 2.4	N.S	0.04	0.85
9	19.0	4.44 ± 0.46	- 18.1	N.S	1.76	0.187
15	16.25	4.26 ± 0.45	- 21.4	N.S	2.52	0.114
22	18.75	5.01 ± 0.48	- 7.6	N.S	0.286	0.599
31	9.5	2.74 ± 0.47	- 49.5	Sig	13.19	0.000
45	36.75	7.76 ± 0.61	+ 43.2	Sig	7.92	0.006
80	24.25	6.97 ± 0.52	+ 28.6	Sig	4.12	0.044
			20 percent			
Before	23.0	4.70 ± 0.52	-	-	-	-
After	22.5	4.08 ± 0.38	- 13.2	N.S	0.93	0.35
5	15.25	3.45 ± 0.44	- 15.4	N.S	1.21	0.27
9	12.75	2.42 ± 0.38	- 40.7	Sig	9.61	0.022
15	10.75	1.75 ± 0.26	- 57.1	Sig	26.69	0.000
22	10.5	2.09 ± 0.32	- 48.8	Sig	16.24	0.000
31	19.5	5.38 ± 0.43	+ 31.8	Sig	5.17	0.024
45	33.0	6.57 ± 0.45	+ 61.0	Sig	17.81	0.000
80	20.25	4.37 ± 0.48	+ 7.1	N.S	0.224	0.642
			35 percent			
Before	20.25	5.21 ± 0.39	-	-	-	-
After	20.00	4.13 ± 0.39	- 20.7	N.S	3.74	0.055
5	18.00	4.16 ± 0.49	+ 0.7	N.S	0.002	0.96
9	14.00	2.78 ± 0.39	- 32.7	Sig	6.05	0.015
15	12.75	2.29 ± 0.32	- 44.5	Sig	13.4	0.000
22	11.25	2.04 ± 0.31	- 50.6	Sig	17.8	0.000
31	16.00	5.09 ± 0.52	+ 23.2	N.S	2.21	0.139
45	27.75	6.59 ± 0.46	+ 59.6	Sig	16.72	0.000
80	16.75	3.68 ± 0.42	- 10.9	N.S	0.63	0.436

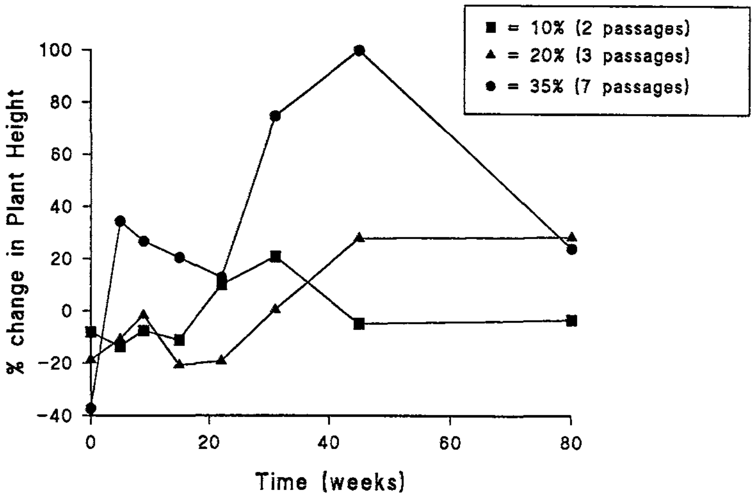


Figure 6.10 Damage to *Scaevola plumieri* from repeated trampling at levels of 2, 3 and 7 passages, given at each sampling period.

Table 6.8 Change in height and percentage cover of *Scaevola plumieri* exposed to three levels of trampling over an 80 week period, with corresponding statistical analysis.

Time period (weeks)	Mean % cover	Mean plant height ±SE	% change in height	Scheffe range test	F - ratio	Sig level
10 percent						
Before	12.9	13.51 ± 1.41	-	-	-	-
After	13.3	12.41 ± 1.58	- 8.1	N.S	0.26	0.610
5	14.3	10.72 ± 1.42	- 13.6	N.S	0.631	0.437
9	12.7	11.47 ± 1.38	- 7.6	N.S	0.202	0.659
15	11.5	11.04 ± 1.52	- 11.0	N.S	0.393	0.538
22	16.5	13.65 ± 1.82	+ 9.9	N.S	0.263	0.615
31	22.5	14.99 ± 1.79	+ 20.8	N.S	0.686	0.418
45	28.5	11.80 ± 1.45	- 4.9	N.S	0.081	0.780
80	18.0	11.98 ± 1.53	- 3.5	N.S	0.038	0.847
20 percent						
Before	24.0	6.15 ± 0.45	-	-	-	-
After	20.75	5.00 ± 0.43	- 18.7	N.S	3.42	0.066
5	19.25	4.46 ± 0.43	- 10.8	N.S	0.779	0.388
9	17.25	4.92 ± 0.45	- 1.6	N.S	0.017	0.898
15	14.75	3.97 ± 0.46	- 20.6	N.S	2.68	0.103
22	17.25	4.04 ± 0.36	- 19.2	N.S	2.88	0.091
31	16.75	5.02 ± 0.53	+ 0.4	N.S	0.001	0.976
45	32.75	6.39 ± 0.45	+ 27.8	Sig	5.01	0.026
80	19.5	6.41 ± 0.55	+ 28.2	Sig	4.19	0.042
35 percent						
Before	20.0	4.95 ± 0.37	-	-	-	-
After	14.5	3.11 ± 0.37	- 37.2	Sig	11.97	0.0007
5	16.75	4.18 ± 0.43	+ 34.4	N.S	3.49	0.063
9	14.7	3.94 ± 0.40	+ 26.7	N.S	2.307	0.131
15	12.0	3.75 ± 0.47	+ 20.5	N.S	1.13	0.290
22	13.5	3.51 ± 0.43	+ 12.8	N.S	0.48	0.496
31	14.0	5.43 ± 0.94	+ 74.6	Sig	5.22	0.024
45	23.25	6.20 ± 0.81	+ 99.4	Sig	34.05	0.000
80	11.5	3.85 ± 0.61	+ 23.8	N.S	1.07	0.303

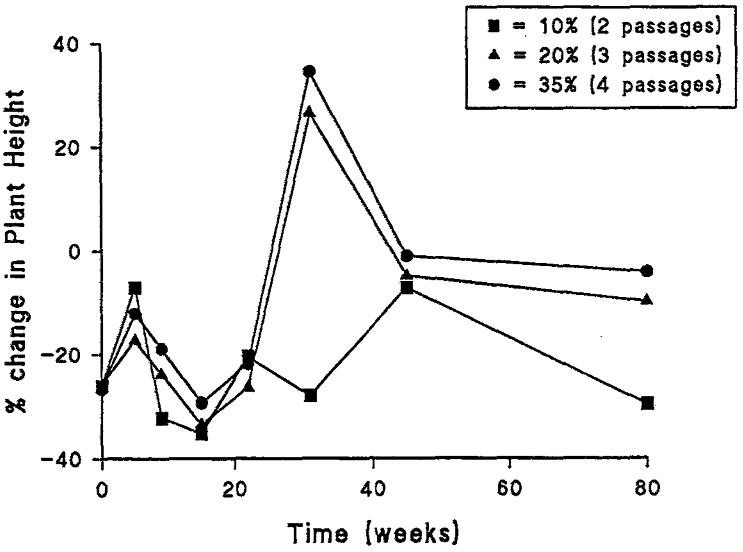


Figure 6.11 Damage to *Passerina rigida* from repeated trampling at levels of 2, 3 and 4 passages given at each sampling period.

Table 6.9 Change in height and percentage cover of *Passerina rigida* exposed to three levels of trampling over an 80 week period, with corresponding statistical analysis.

Time period (weeks)	% cover	plant height ±SE	% change in height	Scheffe range test	F - ratio	Sig level
10 percent						
Before	48.5	49.45 ± 2.60	-	-	-	-
After	47.5	36.89 ± 2.43	- 26.1	Sig	12.43	0.000
5	46.5	34.26 ± 2.41	-7.1	N.S	0.652	0.429
9	44.0	25.02 ± 2.11	- 32.2	Sig	13.56	0.000
15	38.0	23.90 ± 2.49	- 35.2	Sig	13.86	0.000
22	40.5	29.37 ± 2.68	- 20.4	Sig	4.29	0.039
31	36.0	26.58 ± 2.62	- 27.9	Sig	8.28	0.004
45	65.5	34.21 ± 2.26	-7.2	N.S	0.650	0.429
80	56.0	25.98 ± 2.17	- 29.6	Sig	9.31	0.001
20 percent						
Before	75.5	42.36 ± 1.71	-	-	-	-
After	72.5	31.34 ± 1.54	- 26.0	Sig	22.85	0.000
5	72.5	25.91 ± 1.31	- 17.3	Sig	7.24	0.007
9	75.0	23.87 ± 1.25	- 23.8	Sig	14.12	0.000
15	69.5	20.84 ± 1.12	- 33.5	Sig	30.35	0.000
22	67.0	23.07 ± 1.53	- 26.4	Sig	14.53	0.000
31	70.5	39.62 ± 1.74	+ 26.4	Sig	12.69	0.000
45	69.5	29.80 ± 1.79	-4.9	N.S	0.42	0.522
80	63.5	28.22 ± 1.80	-9.9	N.S	1.73	0.189
35 percent						
Before	62.5	39.65 ± 2.07	-	-	-	-
After	60.0	29.09 ± 1.95	- 26.6	Sig	13.78	0.000
5	61.5	25.57 ± 1.31	- 12.1	Sig	8.16	0.005
9	50.5	23.60 ± 1.26	- 18.9	Sig	15.34	0.000
15	55.0	20.57 ± 1.12	- 29.3	Sig	32.03	0.000
22	53.0	22.76 ± 1.52	- 21.8	Sig	15.67	0.000
31	69.0	39.10 ± 1.75	+ 34.4	Sig	11.03	0.001
45	67.5	29.41 ± 1.79	- 1.1	N.S	0.668	0.420
80	64.5	27.85 ± 1.79	- 4.2	N.S	2.16	0.140

Passerina rigida showed a similar response at all three levels of trampling, with height decreasing initially and then increasing slightly after 31 weeks (Fig. 6.11). The reduction in height and cover was no greater at 4 passages than at 1 passage (Table 6.9). The latter did not show the sudden increase in height at 31 weeks, conspicuous for the 20 and 35% treatments, which were located in adjacent plots (Fig. 6.2). For all treatments the final height was less than the initial height, and most reductions in height were significant (Table 6.9). The general trend of a reduction in height at all levels of repeated trampling is clear from Figure 6.9. It is also apparent that *P. rigida* is the most sensitive species, as it shows the greatest decrease in height, whereas *Sporobolus virginicus* is least sensitive.

LONG-TERM ORV TREATMENTS

Results of the 20% ORV treatment for *Sporobolus virginicus* are not shown graphically due to the large increases in height noted for this plot (Table 6.10). This plot is located in the south western portion of the sample area (Fig. 6.2), and immediately prior to sampling it was inundated with sand moving from west to east under the influence of the strong south westerly winter winds. Although all *Sporobolus* plots were affected, plot V3 was virtually buried, resulting in a significant under estimate of height and cover. The significant increase in height for the duration of the study reflects this species response to sand inundation, which masks the effects of 5 vehicle passes 8 times over an 80 week period (Table 6.10). It is clear that sand burial stimulates growth of *Sporobolus*, and possibly provides some protection from vehicle passes by burying rhizomes which are sensitive to vehicle tracks. Damage to rhizomes is one of the main causes of a decline in cover of *Ammophila breviligulata* (Brodhead & Godfrey 1979a). In the other two treatments, *Sporobolus* showed a response similar to that observed for trampling. There was a decrease in height until 22 weeks, after which height increased in response to rain during the growing season, as noted for the control plot (Figs. 6.6 & 6.12). The overall decrease in height was much less, and the increase greater, for the 10% treatment compared to the 35% (Table 6.10). *Sporobolus* appeared resilient to this low level of damage, but the cumulative effect of 10 passes at each sampling period resulted in a net decrease in height.

Scaevola plumieri showed a similar decrease in height, but this continued for at least 31 weeks, and the increase in height after this period was never significant (Table 6.11). At the level of 10% damage (2 passes) height increased after 31 weeks, and was slightly higher than after impacting, but never reached the pre-impact height of 7.55cm (Table 6.11). The 20% treatment resulted in a greater decrease in height than the 35% treatment, with a steady and significant decline terminating in a height of 90.5% less than that measured after the first 7 passes (Fig. 6.13; Table 6.11). This sample plot was located on a slope, and the sliding, sideways movement of the vehicle caused, as it accelerated up the slope, extensive damage to the substrate and vegetation (Plate 6.9). The 35% treatment sample plot was located on level ground (Plate 6.10), and damage to the vegetation was therefore not as extensive. Height was only reduced by a maximum of 22.3% (Table 6.11). Thus, the effect of 7 passes on a slope was almost 5 times greater than the effect of 17 passes on a level area. A similar observation was made by Brodhead & Godfrey

(1979a) and has important management implications since *Scaevola plumieri* usually forms steep hummock dunes along this coastline (Chapter 1).

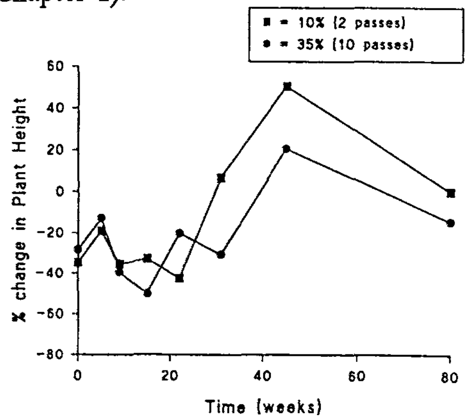


Figure 6.12 Damage to *Sporobolus virginicus* from repeated Off-road vehicle passes at levels of 2 and 10 passes given at each sampling period. (Note that 20% damage is not included).

Table 6.10 Change in height and percentage cover of *Sporobolus virginicus* exposed to three levels of Off-road vehicle impact over an 80 week period, with corresponding statistical analysis.

Time period (weeks)	Mean % cover	Mean plant height ±SE	% change in height	Scheffe range test	F - ratio	Sig level
			10 percent			
Before	25.1	8.27 ± 0.53	-	-	-	-
After	21.3	5.39 ± 0.48	- 34.8	Sig	16.2	0.001
5	17.1	4.36 ± 0.61	- 19.1	N.S	1.74	0.183
9	16.4	3.48 ± 0.45	- 35.4	Sig	8.34	0.004
15	12.7	3.62 ± 0.40	- 32.8	Sig	7.84	0.005
22	16.5	3.10 ± 0.43	- 42.5	Sig	12.49	0.000
31	17.3	5.75 ± 0.64	+ 6.7	N.S	0.208	0.654
45	27.1	8.11 ± 0.50	+ 50.4	Sig	15.25	0.000
80	15.5	5.39 ± 0.48	0.0	N.S	1.98	0.16
			20 percent			
Before	10.2	3.51 ± 0.27	-	-	-	-
After	8.7	2.23 ± 0.29	- 36.5	Sig	10.36	0.002
5	7.3	3.29 ± 0.47	+ 47.5	N.S	3.64	0.059
9	8.0	2.82 ± 0.46	+ 26.4	N.S	0.99	0.332
15	9.5	4.41 ± 0.48	+ 97.7	Sig	14.06	0.000
22	10.2	6.72 ± 0.63	+ 201.3	Sig	39.71	0.000
31	13.3	6.41 ± 0.58	+ 187.4	Sig	39.84	0.000
45	28.0	5.00 ± 0.60	+ 124.2	Sig	16.05	0.000
80	20.0	9.13 ± 0.75	+ 309.4	Sig	70.77	0.000
			35 percent			
Before	28.0	7.50 ± 0.41	-	-	-	-
After	29.3	5.37 ± 0.30	- 28.4	Sig	17.36	0.000
5	24.7	4.68 ± 0.41	- 12.8	N.S	1.89	0.17
9	19.3	3.25 ± 0.38	- 39.5	Sig	19.18	0.000
15	15.8	2.67 ± 0.36	- 50.3	Sig	32.71	0.000
22	18.9	4.28 ± 0.43	- 20.3	Sig	4.41	0.036
31	19.3	3.72 ± 0.38	- 30.7	Sig	11.72	0.000
45	27.1	6.48 ± 0.45	+ 20.7	Sig	4.13	0.043
80	17.1	4.58 ± 0.51	- 14.7	N.S	1.82	0.178

Plate 6.9 *Scaevola plumieri* sample plot for 20% ORV repeatable treatment, showing damage after first 5 passes. The large number of tracks is due to the vehicle sliding on the slope.

It was not possible to expose *Passerina rigida* to repeated levels of 10 and 20%, since a single pass caused 37% damage. One plot was therefore treated at this level, and the other exposed to 2 passes, which resulted in 54% damage (Table 6.1). For the 35% treatment, height continued to decrease for the duration of the study (Fig. 6.14), and cover also decreased steadily (Table 6.12). Surprisingly, the maximum decrease in height was far greater for the 35% treatment, whereas the 50% treatment showed signs of increased growth at 45 weeks. It is unclear whether height would have continued to increase, as data for 80 weeks is not available. However, this is unlikely as the control plot also decreased at 80 weeks (Fig. 6.6). It appeared that most of the damage had already taken place after the first two passes, and that subsequent passes were no longer able to reduce height significantly. In both cases, height was much less than the original value before treatment, and these sites will continue to deteriorate, even at these low levels of use. Recovery is also very slow (Fig. 6.8), and vehicles appear to cause irreparable damage to *P. rigida* dominated communities.

At all three levels of ORV impact, height of the three species was less after 80 weeks than the pre-treatment height, except for *Sporobolus virginicus* at 20% (Table 6.10), for the reasons given. However, the recovery plots showed that both *S. virginicus* and *Scaevola plumieri* were fairly resilient and able to recover if they were not exposed to any further vehicle passes (Fig. 6.8). This suggests that these species are only able to recover from ORV effects if they are not damaged during their period of recovery, and sustained impacting, even at low levels, will prevent them from recovering. This is also the case for *Passerina rigida*, except that it is more susceptible and unable to recover from very low levels of impact, even if it is not disturbed any further. As expected, the lowest level of repeated damage (10%) had the least influence on height, with plants reaching similar values to the initial value before impact (Tables 6.10 & 6.11).

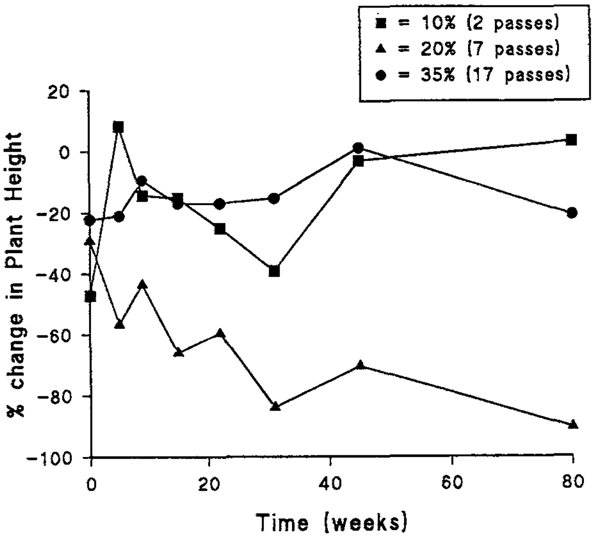


Figure 6.13 Damage to *Scaevola plumieri* from repeated Off-road vehicle passes at levels of 2, 7 and 17 passes given at each sampling period.

Table 6.11 Change in height and percentage cover of *Scaevola plumieri* exposed to three levels of Off-road vehicle impacts over an 80 week period, with corresponding statistical analysis.

Time period (weeks)	Mean % cover	Mean plant height ±SE	% change in height	Scheffe range test	F - ratio	Sig level
10 percent						
Before	27.8	7.55 ± 0.31	-	-	-	-
After	14.2	3.77 ± 0.38	- 47.2	Sig	42.51	0.000
5	18.2	4.09 ± 0.45	+ 8.5	N.S	0.29	0.593
9	14.2	3.22 ± 0.39	- 14.6	N.S	1.03	0.315
15	12.5	3.21 ± 0.43	- 14.8	N.S	0.98	0.335
22	14.9	2.81 ± 0.33	- 25.5	N.S	3.61	0.058
31	11.1	2.30 ± 0.38	- 40.0	Sig	7.56	0.006
45	16.7	3.66 ± 0.39	- 2.9	N.S	0.041	0.841
80	15.3	3.88 ± 0.36	+ 2.9	N.S	0.030	0.864
20 percent						
Before	31.3	11.35 ± 0.67	-	-	-	-
After	30.9	8.04 ± 0.54	- 29.2	Sig	14.67	0.000
5	13.8	3.49 ± 0.48	- 56.6	Sig	39.27	0.000
9	15.8	4.53 ± 0.53	- 43.6	Sig	21.39	0.000
15	12.9	2.74 ± 0.41	- 65.9	Sig	61.0	0.000
22	13.1	3.25 ± 0.47	- 59.6	Sig	43.82	0.000
31	3.8	1.29 ± 0.37	- 83.9	Sig	105.09	0.000
45	6.9	2.38 ± 0.49	- 70.4	Sig	59.27	0.000
80	1.8	0.76 ± 0.30	- 90.5	Sig	136.17	0.000
35 percent						
Before	16.9	9.80 ± 0.64	-	-	-	-
After	20.2	7.61 ± 0.66	- 22.3	Sig	5.67	0.018
5	19.3	6.00 ± 0.65	- 21.1	N.S	2.98	0.086
9	17.8	6.89 ± 0.67	- 9.5	N.S	0.57	0.458
15	13.6	6.31 ± 0.76	- 17.1	N.S	1.66	0.199
22	18.9	6.31 ± 0.67	- 17.1	N.S	1.91	0.169
31	19.1	6.43 ± 0.62	- 15.5	N.S	1.71	0.193
45	27.1	7.68 ± 0.50	+ 0.9	N.S	0.009	0.927
80	19.1	6.02 ± 0.48	- 20.9	N.S	3.76	0.054

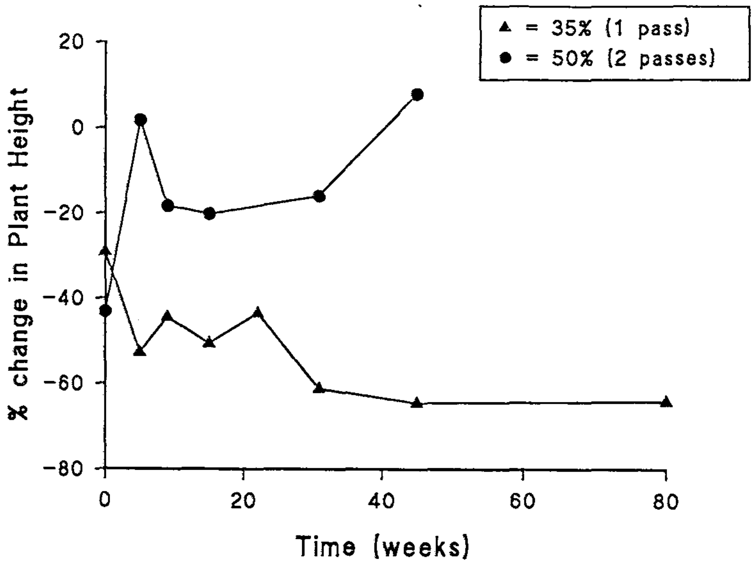


Figure 6.14 Damage to *Passerina rigida* from repeated Off-road vehicle passes, at levels of 1 and 2 passes given at each sampling period. (Note different levels of damage).

Table 6.12 Change in height and percentage cover of *Passerina rigida* exposed to two levels of Off-road vehicle impacts over an 80 week period, with corresponding statistical analysis.

Time period (weeks)	Mean % cover	Mean plant height ±SE	% change in height	Scheffe range test	F - ratio	Sig level
20 percent						
Before	50.7	58.47 ± 2.15	-	-	-	-
After	48.1	41.43 ± 2.14	- 29.1	Sig	31.65	0.000
5	33.7	19.58 ± 1.94	- 52.7	Sig	57.28	0.000
9	30.7	23.01 ± 2.23	- 44.4	Sig	35.58	0.000
15	31.5	20.46 ± 2.00	- 50.6	Sig	51.32	0.000
22	35.9	23.43 ± 2.12	- 43.5	Sig	35.66	0.000
31	22.2	16.09 ± 2.08	- 61.2	Sig	72.06	0.000
45	36.7	14.72 ± 1.42	- 64.5	Sig	108.18	0.000
80	28.5	14.84 ± 1.68	- 64.2	Sig	95.69	0.000
35 percent						
Before	50.7	23.67 ± 0.92	-	-	-	-
After	40.2	13.47 ± 0.78	- 43.1	Sig	71.580	0.000
5	41.1	13.71 ± 0.86	+ 1.8	N.S.	0.046	0.830
9	37.8	11.0± 0.75	- 18.3	Sig	0.023	0.023
15	34.7	10.75 ± 0.77	- 20.2	Sig	0.013	0.013
22	33.7	10.00 ± 0.69	- 25.8	N.S	1.000	1.000
31	35.1	11.31 ± 0.79	- 16.0	N.S	0.052	0.052
45	42.7	14.55 ± 0.87	+ 8.0	N.S	0.361	0.361
80	-	-	-	-	-	-

Plate 6.10 *Scaevola plumieri* sample plot for 35% ORV repeatable treatment, showing damage after first treatment of 10 passes. Damage is less than shown in Plate 6.9, since area is more level.

CHANGES TO SOIL SURFACE COMPACTION

Only selected data on changes to soil compaction, as measured with a sheer value, are presented in Table 6.13, to reveal the most important trends. Trampling in the loose sand did not result in compaction, as reported by Liddle (1975a) and numerous other workers, who found that an increase in compaction was directly related to the amount of pedestrian traffic. In fact the sand became less compact with increasing passages (Table 6.13; Plate 6.6). This will result in increased sand movement, a reduction in the field capacity or water-holding ability of the soil, and possible exposure or loss of seeds in the sand. The main influence of vehicles was to form distinct tracks or ruts in the sand (Plates 6.8 & 6.9), which influence the microclimate and prevent vegetation from recolonizing (Liddle & Moore 1974). However, soil compaction within the tracks did not occur, as reported by Liddle & Moore (1974). The most noticeable effect was that sand pushed up on either side of the track was less compact than that in the track (Table 6.13). Since no compaction occurred within the track, but sand became loose along the edges, the main effect of the vehicle passes was similar to that of trampling, namely to loosen and destabilize the substrate. This was the case for all treatments, where the sand on the edges of the tracks was nearly half as compact as sand within the tracks (Table 6.13). The general effect of both vehicles and trampling on unconsolidated foredunes is therefore to loosen the sand and make it more mobile. The main effect would be increased erosion, but species such as *Scaevola plumieri* may be stimulated to grow under these conditions. However, the physical damage caused to these plants reduces this ability.

Table 6.13 Changes in soil sheer strength (KPa) for *Scaevola plumieri* and *Sporobolus virginicus* after trampling and vehicle impacts. The latter was recorded both in the tracks and along the edge. Data for *Passerina rigida* not shown as plant roots influenced values.

TRAMPLING			
SCAEVOLA PLUMIERI		*SPOROBOLUS VIRGINICUS*	
PASSAGES	VALUE (KPa)	PASSAGES	VALUE (KPa)
0	6.22 ± 0.49	0	2.80 ± 0.33
2	5.37 ± 0.31	4	2.84 ± 0.38
4	4.51 ± 0.41	8	2.90 ± 0.27
8	4.48 ± 0.29	12	2.34 ± 0.23
12	3.31 ± 0.38	18	1.85 ± 0.19
18	3.83 ± 0.46	24	1.79 ± 0.15
24	3.01 ± 0.32	30	1.70 ± 0.18
30	3.15 ± 0.44		

VEHICLE					
SCAEVOLA PLUMIERI			*SPOROBOLUS VIRGINICUS*		
PASSAGES	TRACK (KPa)	EDGE (KPa)	PASSAGES	TRACK (KPa)	EDGE (KPa)
0	3.38 ± 0.54	-	0	3.10 ± 0.26	
1	3.18 ± 0.45	2.76 ± 0.31	2	2.94 ± 0.19	0.99 ± 0.18
4	2.86 ± 0.28	3.82 ± 0.35	4	2.90 ± 0.15	1.16 ± 0.11
7	2.50 ± 0.28	1.90 ± 0.19	7	3.22 ± 0.22	1.4 ± 0.16
10	3.21 ± 0.37	1.09 ± 0.15	10	3.30 ± 0.23	1.5 ± 0.18
20	3.78 ± 0.28	0.96 ± 0.12	15	3.60 ± 0.16	1.3 ± 0.15
MEAN	3.15 ± 0.18	2.11 ± 0.54		3.18 ± 0.10	1.27 ± 0.09
Mean 10%	2.26 ± 0.15	1.56 ± 0.32		3.14 ± 0.42	1.85 ± 0.63
Mean 20%	1.60 ± 0.15	0.91 ± 0.17		2.78 ± 0.40	1.60 ± 0.08
Mean 35%	3.27 ± 0.33	1.67 ± 0.12		2.5 ± 0.63	1.67 ± 0.47

DISCUSSION

TRAMPLING

Most trampling studies in coastal areas, which have followed an experimental approach (*vide* Liddle 1975a), have been undertaken on dune grasslands in Europe (Trew 1973; Liddle & Greig-Smith 1975b; Liddle 1975a; Boorman & Fuller 1977; Hylgaard 1980; Sothern *et al.* 1985) and other communities such as heathland (Hylgaard & Liddle 1981; Williams *et al.* n.d.; Harrison 1981). The vegetation of these communities generally forms a low, dense and relatively diverse sward, whereas foredune communities are much less dense and have a lower diversity (Chapter 1). The main foredune pioneer that has been investigated in detail is *Ammophila breviligulata*, which has been studied experimentally by Hylgaard (1980) and Nickerson & Thibodeau (1983), and analytically by McAtee & Drawe (1980), and McDonnell (1981). Bowles & Maun (1982) experimentally investigated the sensitivity of an open dune community (*Calamovilfa longifolia*) and a heath-grassland community to measured amounts of trampling. However, no information on the sensitivity of dune species to trampling is available in South Africa.

In this study all three species were found to have a low resistance to trampling, with as few as 5 passages causing a 50% reduction in the height of *Passerina rigida* (Table 6.2). Even the grass, *Sporobolus virginicus*, was not resistant to moderate levels of trampling, with 30 passages reducing height by over 50%. The height of *Ammophila breviligulata* at Cape Hatteras was reduced significantly after 200 shod passages evenly spaced over a period of 45 days, but 2000 barefoot passages were needed to produce a similar decrease in height (Nickerson & Thibodeau 1983). About 50 shod passages was needed to damage all shoots of the *Calamovilfa longifolia* open dune community at Lake Huron, and 3 months later no quantitative differences between the control and trampled plots existed (Bowles & Maun 1982). Nevertheless, striking qualitative differences, such as number of dead or broken leaves was evident. This open dune community required four treatments of 50 passages to produce a significant result, but one treatment of 50 passages in the heath-grassland community caused significant effects, with a pathway plainly visible. Dune grasslands investigated by Liddle (1975a) and Liddle & Greig-Smith (1975b) at Aberffran in North Wales were reduced in height by 55% after 384 passages, and trampling of a short *Festuca rubra* turf in South Wales at levels of 500 passages a year produced very little bare ground, but did reduce the cover of more sensitive species. At a low intensity of 100 passes on a single day, no increase in bare ground occurred (Williams *et al.* n.d.; Sothern *et al.* 1985).

Liddle (1991) provides a review of the tolerance of various communities to trampling, expressed as the number of passages required to reduce the ground cover or biomass of the vegetation by 50%, of a number of communities. Eucalyptus woodland was the most susceptible, requiring only 12 passages, and a sand dune pasture in Wales the most tolerant, with 1445 passages required. The most susceptible coastal community given by Liddle was a sand dune grassland in Scotland, which required 119 passages. Clearly then, dune vegetation in South Africa has a very low resistance to trampling, and this is significant in view of the widespread distribution of *Scaevola plumieri* and *Sporobolus virginicus* along this coastline (Chapters 1 & 3; Tinley 1985). It is also important to note that both these species are cosmopolitan, occurring on foredunes along the Gulf and Caribbean Sea of Mexico (Moreno-Casasola & Espejel 1986); Baja California, Mexico (Johnson 1977) and Equatorial West Africa, Kenya, Florida and other localities in the USA (Doing 1985).

The *Passerina rigida* community confined to southern African coastlines, was much more susceptible. In the previous study (Chapter 5) the shrub, *Chrysanthemoides monilifera* was also found to have a low resistance and tolerance to trampling, lending support to the observation that plant species differ in their ability to tolerate trampling (Hylgaard & Liddle 1981). The pioneering work of Bates (1935) showed that this ability is related to the morphology of the species, as mentioned earlier (Chapter 5). The upright branches of *P. rigida* are easily snapped when walking through the vegetation, and the leaves of *Scaevola plumieri* are very brittle, being easily damaged when trodden on. It is possible that the low, rhizomatous growth form of *Sporobolus virginicus* results in less damage. However, plants may become buried, an effect noted for *Ammophila breviligulata* exposed to vehicle impacts (Brodhead & Godfrey 1979a). This range in tolerance can result in changes to the species composition of dune grassland, with more resilient species attaining dominance under trampling stress (Liddle 1975a; Sothern *et al.* 1985). However, changes in diversity or species composition are unlikely to occur in these communities, since they are dominated almost exclusively by a single species.

OFF-ROAD VEHICLES

Passerina rigida was also most susceptible to ORV effects, but in contrast to the results of the trampling study, *Scaevola plumieri* was more resistant than *Sporobolus virginicus*, and it is suggested that this is related to its morphology. However, one would still expect a grass species to be more resilient to ORV effects, as this is the case for trampling (Chapter 5; Liddle 1975a; 1991). It was also evident that most of the damage occurred after the first few passages (Fig. 6.5), and similar results where noted by Brodhead & Godfrey (1979a) and Ranwell & Boar (1986) for *Ammophila breviligulata*. Similarly, coastal grasslands near East London were found to be damaged most by the first few passes, but were generally more resilient. Repeated levels of 10, 26 and 50 passes of a vehicle were applied, but damage was significant at all three levels tested (Avis *et al.* in prep.).

Most studies on the impact of ORV's on foredune vegetation is limited to *A. breviligulata*. Cover of this species was significantly reduced ($p < 0.05$) after 70 passes over foredunes at Cape Cod, with no significant difference between fore and reardunes (Brodhead & Godfrey 1979a). Biomass was also reduced to very low levels after 50 to 100 passes, and effectively to zero in the track (Godfrey *et al.* 1978). The seaward advance of the vegetation was also significantly reduced (Brodhead & Godfrey 1979a), with only 1 pass per week for 12 weeks producing a significant loss of vegetation (Anders & Leatherman 1987b). One could expect at least similar, but possibly worse effects on coastal foredunes in South Africa, since all three species are less tolerant than *A. breviligulata* to vehicles. They are also much more susceptible than dune turf, which required 200 vehicle passes to reduce cover by 50% (Liddle 1973 in Ranwell & Boar 1986). The susceptibility of *Passerina rigida* is similar to that noted for salt marsh species such as *Salicornia* spp., which was destroyed by 1 to 5 passes, leading Brodhead & Godfrey (1979b) to conclude that this severe environmental impact warranted a complete ban on vehicles in such areas. The consequence of this damage to foredune vegetation is increased wind erosion and destabilization of the dunes, which may migrate across stable areas, and the displacement of sand downslope (Godfrey *et al.* 1978). A steepening of the foredune profile, which may become less effective at dissipating wave energy and lead to accelerated dune erosion has also been noted (Anders & Leatherman 1987b). Furthermore, vehicle traffic has been attributed to the lack of embryo dunes on barrier islands in Texas (McAtee & Drawe 1981).

RATES OF RECOVERY

Liddle and Thyer (1986) have termed this resilience, and defined it as "the potential to regenerate after damage". Both Bayfield (1979) and Hylgaard (1980) stressed the importance of assessing recovery capacity when assessing the vulnerability of habitats to human impacts for planning and management proposals. The *Ammophila arenaria* and *Empetrum nigrum* communities sampled by Hylgaard in Denmark returned to their original state after one year, and Nickerson & Thibodeau (1983) recorded good recovery of *A. breviligulata* after one year, even for plots which received 2000 passages. Full recovery was noted for *A. breviligulata* on foredunes exposed to 175 vehicle passes after three years, but on rear dunes, tracks were still visible (Godfrey *et al.* 1978). The more rapid recovery of this species on foredunes may be related to its ability to grow better in shifting sand (Brodhead & Godfrey 1979a). The *Calamovilfa longifolia* heath exposed to 50 passages in Bowles & Maun's (1982) study showed complete recovery after one year, but heavier treatments (200 passages) affected growth in the following season. Harrison (1981) showed that all semi-natural grasslands and heathlands, except for *Calluna* heathland, recovered in a few weeks of autumn growth after 2000 passages.

From the above it is evident that recovery rates differ widely, and are not only dependent on the plant morphology and the type of community, but also the habitat, and type and severity of the impact. Dune grasslands are more tolerant and recover more rapidly (Liddle 1975a) and *A. breviligulata* recovered more rapidly after trampling (Nickerson & Thibodeau 1983). Severity of impacts on *Calamovilfa longifolia* heath affected recovery (Bowles & Maun 1982), and recovery rates of dune grasslands in Wales exposed to trampling, motorcycle and horse impacts differed (Sothern *et al.* 1985).

In this study rates of recovery were not affected by the type of impact, but differed for the three species. However, trends were difficult to elucidate owing to the large amount of natural fluctuation in these communities (Fig. 6.6). *Sporobolus virginicus* was able to recover from both trampling and ORV impacts, but none of the species fully recovered after 18 months. It appears that in addition to vulnerability (Liddle 1975b), recovery may also be related to primary productivity. Foredune systems are tolerant to changing environmental conditions and therefore less susceptible to damage, since areas least tolerant of changing environmental conditions are more susceptible (Godfrey *et al.* 1978). However, they are not productive systems, such as dune grasslands, and therefore have a slower recovery rate than those communities. There were no real differences in rates of recovery following a trampling or vehicle impacting episode. In fact, *Scaevola plumieri* appeared to recover more rapidly after ORV impacts, whereas it was unable to recover after trampling. Height of *Passerina rigida* continued to decline for the duration of the study, and it appears that these communities, with the exception of *Sporobolus virginicus*, have a lower resilience than *Ammophila* and other foredune communities (Brodhead & Godfrey 1979a; Hylgaard 1980; Bowles & Maun 1982).

LONG TERM IMPACTS

The levels of repeated impacts were relatively low when equated to number of passages or vehicle passes per month (Table 6.14), and are also very low when compared to similar studies. Bowles & Maun (1982) originally applied 50 passages to a heath-grassland community, but found that 300 repeated passages were needed to cause a significant effect. Nickerson & Thibodeau (1983) exposed *Ammophila breviligulata* foredunes to 20, 200 and 2000 passages over a period of 45 days, and repeated treatments one year later. Sothern *et al.* (1985) considered 50 trampling passages a year on grassland a low level, and 300 a high level of trampling. At Cape Cod, Brodhead & Godfrey (1979a) exposed *Ammophila breviligulata* foredunes to medium (10 vehicle passes/day for 27 days) and heavy (25 passes/day for 27 days) levels of impact and found a significant drop in biomass after 70 passes. The first few passes were the most damaging, and continued ORV impacts resulted in an overall decline in biomass.

Table 6.14 Number of human trampling passages and vehicle passes per month for the various treatments.

COMMUNITY	LEVEL	NO. TRAMPLING PASSAGES PER MONTH	NO. VEHICLE PASSES PER MONTH
Sporobolus virginicus	10%	1.5	1
	20%	4.5	2
	35%	10.5	4.5
Scaevola plumieri	10%	1	1
	20%	1.5	3
	35%	3	7.5
Passerina rigida	10%	0.5	-
	20%	1	-
	35%	2	0.5
	50%	-	1

The effect of repeated treatments was similar for both trampling and vehicles, namely, to prevent or retard the recovery of the various communities. This effect was least pronounced for *Sporobolus virginicus*, and most dramatic for *Passerina rigida.* The former was the only species which consistently showed a slight increase in height over time, with this increase being more noticeable at the lower levels of damage. At the 10% level of repeated trampling, *Sporobolus* showed a net increase in height, suggesting that this low level of disturbance stimulated growth. Liddle & Greig-Smith (1975b) concluded that low levels of trampling could stimulate plant production. However, even at levels of 1 vehicle pass per month, pre-impact height was never achieved (Table 6.10). The rapid growth of this species following sand inundation suggests that this community is more productive, and may therefore be less susceptible to damage. Little information on the response of dune vegetation to environmental fluctuations, such as precipitation, which has been shown to be important on beach plains (van Tooren *et al.* 1983) and dune slacks (Grootjans *et al.* 1991) in the Netherlands is available locally. This thesis (Chapters 2 & 4) and the work of McLachlan *et al.* (1987) and Lubke & Avis (1982a) has shown that these communities are dynamic and responsive to fluctuations in factors such as rainfall and sand movement.

Both repeated treatments of trampling and vehicles resulted in a steady decrease in the height of *P. rigida* at all levels, but the response of *Scaevola plumieri* differed. Height was not always reduced due to trampling, as was the case for vehicles, and repeated trampling did not seem to cause more harm to the *Scaevola* plants than trampling on a single occasion. It appears that these continuous low levels of trampling are not more harmful than slightly higher levels on a single day. However, this would be difficult to prove, given the large amount of natural fluctuation in these communities (Fig. 6.6). It is more likely due to the fact that the first few passes inflict maximum damage, with incremental damage being less, as most harm is already done (Godfrey *et al.* 1978). Nevertheless, one would expect a reduction in cover and height over time, as noted by Sothern *et al.* (1985) for trampling, and Anders & Leatherman (1987b) for ORV impacts. On North Padre Island, Texas, areas with highest levels of traffic had lowest values of cover and biomass (McAtee & Drawe 1980).

From these results it appears that *Sporobolus virginicus* is able to withstand low levels of trampling and ORV passes and *Scaevola plumieri* only very low levels (1 to 2 ORV passes per month). However, even these low levels of impacting restrict plant growth, with vegetation rarely obtaining pre-impact height. *Passerina rigida* is extremely susceptible, and cannot withstand any disturbance.

GENERAL ECOLOGICAL EFFECTS

The vegetation of trampled areas is usually distinct, with high traffic areas supporting species of earlier successional stages (Bates 1935). This led Westoff (1967 in Liddle & Greig-Smith 1975b) to comment that vegetation characteristic of ecotones is also found on paths, and that the path itself is a special kind of ecotone which exhibits a slow gradient of wear from the centre to the edge. Trampling and vehicle disturbances therefore effect the successional stages of communities, and the species composition of coastal grasslands is affected by long term vehicle impacts, with diversity decreasing significantly and a single species dominating in high use areas (Avis *et al.* in prep.). McAtee & Drawe (1980) found that foredunes exposed to high traffic supported pioneer species, whereas in less disturbed sites higher successional stages were present, but paths through fixed dune vegetation cannot be equated with a successional stage (Page *et al.* 1985). Austin (1977) found that trampling influenced the successional relationships between species of lawn grass; and it also exerts a strong influence on species composition, as the disturbance causes asymmetric competition between species (Ikeda & Okutomi 1992).

The effect of trampling and vehicle disturbances on community organization and succession; and the influence of successional stage on the communities tolerance to these disturbances, is both complex and contradictory. From work at Cape Cod, Godfrey *et al.* (1978) found that stable areas least tolerant to changing environmental or physical stress (namely communities of higher successional stages) were damaged the most. Conversely Goldsmith (1974 in Liddle 1975b) found that as plant succession proceeded, the vegetation became more tolerant to trampling, leading Liddle (1975b) to postulate that more productive ecosystems (successionally advanced) were more tolerant to trampling. In this study *Passerina rigida*, which has been shown to be a common species in the intermediate stages of succession towards Dune Thicket (Chapters 2 & 4), was more susceptible than the earlier successional communities, supporting the conclusions drawn by Godfrey *et al.* (1978). Similar results where noted for *Chrysanthemoides monilifera* (Chapter 5). In this regard, the work of Sousa (1980) on the response of intertidal communities to disturbance is worth noting. He found that the amount of damage suffered by the different successional stages, and their rates of recovery, could be attributed to the life history characteristics of the component species rather than emergent properties of the assemblage. Thus, when assessing the susceptibility of various communities to environmental perturbations such as trampling, one needs to adopt an individualistic view (Gleason 1926), and focus on the susceptibility of individual species, rather than on the community as a unit. However, Page *et al.* (1985) present evidence of overall community reactions to perturbation effects, and suggest that species of semi-fixed dunes are not capable of fast reaction to change and fast recovery from disturbance. In the previous study (Chapter 5), the species composition of a forest layer, rather than the successional stage of the community, was the most important factor influencing susceptibility. It appears from this study that successional stage influences recovery rates and not susceptibility, as early successional species are most likely to recover more rapidly, since they are exposed more frequently to perturbations and are therefore more responsive. It is for this reason that *Sporobolus virginicus* and *Ammophila breviligulata* (Brodhead & Godfrey 1979a), common on dynamic foredunes, are able to recover more rapidly than *Passerina rigida* and vegetation of more stable dunes (Brodhead & Godfrey 1979a&b).

MANAGEMENT IMPLICATIONS

In the absence of local scientific information on the ecological impacts associated with recreational use, particularly ORVs, Schneier (1986) recommended that all non-essential ORV use be prohibited except in terms of a permit system. Local authorities are the agencies who can enforce legal control of ORV use on beaches. However, their regulations may only relate to specific areas, and enforcing legislation is a problem due to a shortage of manpower (Rabie 1980). A total ban of ORV use is therefore thought by some to be the only solution (Anon 1983). In Natal more moderate enforcement has been suggested (Brokensha 1982), such as controlling access, preventing use during certain time periods and controlling numbers, which is possible in terms of current legislation (Rabie 1980). Such policy decisions are the responsibility of the relevant authorities, but in making these decisions their gambit must be to consider the ecological consequences of uncontrolled recreational use.

Burden & Randerson (1972) felt that data from trampling studies were useful for calculating acceptable levels of use to help formulate definitive management policies that would maintain an area in the desired condition, whilst allowing maximum use. Such an approach has been applied by Carlson & Godfrey (1989) in Massachusetts, using standard ecological survey methods. In this case it was not possible to reduce visitation to levels of natural carrying capacity, which is very low (Godfrey & Godfrey 1978), as such a policy would not have conformed with the goals of the relevant authority. By recognizing this conflict between access and protection, as discussed earlier (Chapter 5) and by Vogt (1979), Carlson & Godfrey (1989) increased the ecological carrying capacity of the reserve by implementing a human impact management plan. This entailed fencing sensitive areas, providing human access through raised boardwalks and vehicle access using sand-level wooden ramps, and implementing a public education programme. The latter is important as beach users are generally unaware that degradation of dune vegetation may bring about coastal erosion (Eastwood & Carter 1981).

The present study has shown that common dune species are sensitive to both trampling and ORV effects, but they are able to withstand very low levels of human trampling (2 to 10 passages per month). However, even in low use zones, such levels will only account for incidental and accidental usage, and here as well as in higher use zones some form of control is necessary. Shrub species such as *Passerina rigida* are completely intolerant of any disturbance, and certain forest layer communities are also highly susceptible (Chapter 5). Coastal grasslands in this area are, however, more resilient (Avis *et al.* in prep.). Current levels of vehicle use are still low, ranging from 0.24 to 0.77 vehicles per km. However, on public holidays and weekends 2 vehicles per km have been counted (Els & McLachlan 1990), and these levels are sufficient to cause a significant decrease in height of *Scaevola plumieri* foredune vegetation (Table 6.3). Two or 3 passes per month are sufficient to reduce height of *S. plumieri* and *Sporobolus virginicus* significantly, and prevent recovery (Tables 6.7 & 6.8). The correct management approach should therefore concentrate on channelling and attracting beach and ORV users to specific less sensitive areas (*vide* Burden & Randerson 1972). This approach is in line with the current coastal zone management policy of preventing ribbon development (Council for the Environment 1991), and should not be difficult to achieve as ORV users naturally concentrate in areas where fishing is good (Els & McLachlan 1990).

Specific recommendations pertaining to trampling and beach access to achieve the above principles, based on the results of this and other studies, are as follows:

* In high use zones, access through sensitive vegetation must be by means of elevated wooden boardwalks, constructed to allow natural processes to continue (Carlson & Godfrey 1989). For more resilient vegetation such as coastal grassland, pathways need not be elevated. However, the substrate must be hardened or reinforced to protect it from erosion.
* Sensitive vegetation backing popular beaches may need to be fenced to protect it from trampling (Council for the Environment 1991). In high use zones resilient vegetation may need to be protected, as damage is unsightly and leads to erosion and blowouts (Avis *et al.* in prep.).
* In low use zones vegetation will not need to be protected, as it is able to withstand levels of trampling likely to be experienced in such areas (see Tables 6.7; 6.8 & 6.14). The natural resilience and malleability of these communities provides sufficient protection. However, the threshold value of about 5 and 10 passages per month over a specific area for *Scaevola plumieri*

and *Sporobolus virginicus* respectively should not be exceeded. In low use zones it may be more desirable for people not to follow specific paths, provided these areas are infrequently walked on (Nickerson & Thibodeau 1983), at low levels of trampling may not always be detrimental (McDonnell 1981).

- Access points must be clearly demarcated and signposted (Council for the Environment 1991). The latter should include information on the need to protect sensitive vegetation, and messages should be positive and instructional. This is important as it has been found that people are more inclined to accept rules if they know the reasons (Carlson & Godfrey 1989).
- The design of access points must not only consider ecological factors, but should also consider the interaction between the walkers and the nature and position of paths (Liddle 1975a). They should provide the shortest possible route from parking and other areas to the beach, having due regard for natural vegetation and ecological processes.

Specific recommendations pertaining to ORV use of beach and dune environments are as follows:

- Impose a permit system to restrict ORV use to ecologically acceptable levels (Schneier 1986). Els & McLachlan (1990) found that 69% of anglers supported such a measure. Rabie (1980) suggested controlling access by means of lockable gates or booms, but although possible in terms of current legislation, this does not seem a practical solution.
- Prohibit driving in dune areas and above the high tide mark (Brokensha 1982). Driving below the high water mark is acceptable as invertebrate fauna are tolerant to ORV impacts (van der Merwe & van der Merwe 1991). The low resilience of foredune communities (Figs. 6.5 & 6.8) makes this an important recommendation, which has the support of 71% of recreation club members, and 73% of anglers (Els & McLachlan 1990).
- The protection of the drift-line and seaward edge of the vegetation is also important, and can be achieved by not allowing driving 2 hours before or after high tide (Brokensha 1982), or to only allow driving within three hours of low tide. Support for this recommendation was only 11% (Els & McLachlan 1990), and enforcement would therefore be very difficult. It would be easier to close narrow beaches, which force drivers to run along the toe of the dune at high tide, to ORV use (Leatherman & Godfrey 1979). This suggestion of closing certain beaches was supported by recreation club members (83%) and other beach users (68%), but not by anglers (15%, Els & McLachlan 1990). Since 68% of anglers visit specific beaches because of good fishing, their needs should be considered.
- Driving should be restricted to the area between the high and low tide (Brokensha 1982), as this hard sand has a greater carrying capacity and research has recently shown that the macrofauna have a high tolerance for vehicular traffic (van der Merwe & van der Merwe 1991). Overall support for this recommendation was only 31%, being lowest amongst anglers (Els & McLachlan 1990), and enforcement would be very difficult.
- To prevent excessive and unnecessary driving along the beach, access roads perpendicular to the

coast should be built at isolated, favourite angling spots (Rabie 1980; Schneier 1986).

* All access tracks through dune vegetation must be carefully planned to avoid sensitive areas (Leatherman & Godfrey 1979), and surfaced with gravel or a board and chain roadway (Schneier 1986; Council for the Environment 1991). In certain cases wooden ramps may be necessary. They should also be orientated in such a way that prevailing winds cannot create blowouts, but should avoid sharp turns and climbs up steep grades. Tracks must also be controlled and maintained, and deteriorated routes should be closed off (Leatherman & Godfrey 1979).

* Sensitive areas, such as Dune Scrub which has been shown to have no tolerance to ORV's (Figs. 6.5 & 6.14), should be closed and in high use zones protected from ORV use (Godfrey *et al.* 1978; Leatherman & Godfrey 1979).

* The concept of "no carrying capacity" needs to be adopted when planning for ORV use of dune areas, since only a few passes are necessary to cause damage (Fig. 6.5), and recovery is slow (Fig. 6.8).

* If possible, ORV traffic should be restricted or eliminated entirely from the sensitive dune environment (Godfrey *et al.* 1978), but a number of large, easily accessible areas could be designated for unrestricted use by ORV's. These sacrifice areas will need to be carefully selected (AAAS Committee on Arid Lands 1974 in van der Merwe 1988). However, it is unlikely that such areas exist in the coastal zone, due to the inter-relationships between various ecological processes.

* The public should also be educated into the harmful effects of ORV's, as this will reduce the need for penalties. However, the public are generally not averse to the imposition of heavy penalties (76% support, Els & McLachlan 1990).

* Other control measures, suggested by Els & McLachlan (1990), and their level of acceptance include: Imposing speed limits (46%); closing beaches at certain times of the year (38%); limiting the number of vehicles on the beach at any one time (27%); prohibiting driving at night (27%); paying for access to beach (20%) and banning ORV's on beaches altogether (6%).

Most of the above control measures can be accommodated in Article 10 of the Seashore Act (Rabie 1980) and the Administrator of the Cape Province has recently forbidden ORV use above the high water mark (Schneier, S.C. pers. comm.). However, the main problem is the ability to enforce the various control measures, given the current lack of manpower (Rabie 1980; Anon 1983). Thus, the practicality and enforcement of these measures and the ecological sensitivity of the coastal environment will need to receive equal consideration.

CONCLUSIONS

From this study it is evident that dune forming pioneer species, common along the Southern African coastline, have a low resistance to trampling and off-road vehicle effects. They are generally more tolerant to trampling, but *Scaevola plumieri* appeared to be slightly more tolerant to ORV effects, due mainly to its growth habit. The three species investigated differed in their resilience and tolerance to these perturbations, with *Passerina rigida* being least tolerant, and *Sporobolus virginicus* most tolerant. However, very low levels of passages and ORV passes (4 and 2 respectively) were sufficient to cause a significant decrease in height, and the greatest amount of damage occurs after the first few passes. Rates of recovery are generally low, with no species achieving its pre-impact height after 18 months. *S. virginicus* had the greatest resilience, and showed signs of recovery after both trampling and ORV treatments. *S. plumieri* recovered most rapidly from ORV damage, but *P. rigida* was unable to recover, and height continued to decrease for the duration of the study. Repeated disturbances at very low levels (1 to 5 passages; 1 to 3 passes per month) did not have a significant cumulative effect, but growth and recovery was significantly reduced at higher levels. Lower numbers of vehicle passes than trampling passages were required to cause similar reductions in height, and again *S. virginicus* was most resilient, and *P. rigida* least, to long-term effects.

The main effect of both trampling and vehicle disturbances on the substrata was to loosen rather than compact the already loose sand. This would result in increased sand movement which at very low levels, may benefit species such as *S. virginicus* and *Scaevola plumieri*. Species were also far more susceptible to damage on steep slopes, and level areas afforded greater resistance to both trampling and vehicle effects. Results concur with those of Leatherman & Godfrey (1979) that dunes have no carrying capacity for ORV's, and implications for management are stricter control of vehicle use on beaches, and where possible and necessary the implementation of strategies aimed to increase the natural carrying capacity of these systems.

CHAPTER SEVEN

A REVIEW OF COASTAL DUNE STABILIZATION IN THE CAPE PROVINCE OF SOUTH AFRICA

INTRODUCTION

Dune stabilization or reclamation can be defined as the process of limiting or preventing the movement of shifting sands by covering the surface with artificial material or by establishing a vegetation cover. This movement of sand is a natural and intrinsic component of the dynamic coastal ecosystem, and the shape of dunes and beaches are constantly changing by erosion or accretion in response to the variable climatic and environmental factors experienced along the coast. It was only when man started developing and exploiting the coastline that these natural drift sands posed a threat, and the need arose to prevent sand movement.

A limited amount of information on coastal dune stabilization in South Africa has been published (Keet 1936; King 1939; Walsh 1968; Stehle 1988), and most recent accounts are contained in unpublished government reports (Dept of Forestry 1980; Stehle 1980; 1981a&b). The aim of this Chapter is, therefore, to consolidate the historical accounts on dune stabilization in South Africa, and discuss both the past and present methods employed. The introduction of alien vegetation, and problems associated with dune stabilization are also addressed.

HISTORICAL DEVELOPMENT OF THE METHODS OF DUNE STABILIZATION

EARLY ATTEMPTS AT STABILIZATION : 1830 - 1875

In the Western Cape, problems of drift sand formation due to the removal of shrubs and grass for firewood and thatch, arose in the mid-eighteenth century, but it was not until 1845 that an organized dune stabilization programme was initiated. This was undertaken by the Central Roads Board to protect what was known as the "hard road" which stretched across the Cape Flats from Cape Town to the Eerste River (Fig. 7.1).

These early methods simply involved sowing seed and planting seedlings directly in the sand. Both indigenous species such as the Hottentot fig, (*Carpobrotus edulus*) and Pipegrass (*Ehrharta villosa*) and aliens such as Port Jackson Wattle (*Acacia saligna*) were used. Later this work was expanded, with more alien species such as Long Leafed Wattle, (*A. longifolia*), Sweet Hakea, (*Hakea sauveolens*), Australian Myrtle, (*Leptospernum laevigatum*) and Cluster Pine, (*Pinus pinaster*) and other pines being introduced (Shaughnessy 1986). Table 7.1 lists the earliest records of species used for dune stabilization in South Africa.

Table 7.1 Earliest records* of species used for dune stabilization in South Africa, and areas where first planted. Species in Table 7.2 not listed here where first used in the eastern Cape during the mid 1970s.

* Sources: Shaughnessy, 1980[1] & 1986[2]. Stehle, 1981a[3] * 1982[4]

? Date unknown

SPECIES	COMMON NAME	ORIGIN	ALIEN	AREA FIRST PLANTED	YEAR FIRST PLANTED	PERIOD USED	SOURCE
Acacia saligna (Labill.) Wendl.	Port Jackson Wattle	Australia	Yes	White sands	1883	1833 - 1874	1
Carpobrotus edulis (L.) L.Bol.	Hottentot fig	S Africa	No	White sands	1833	1833 - present	1
Secale africanum Stapf.	Rye grass	Europe	Yes	White sands	1833	1833 - ?	1
Acacia cyclops A. Cunn	Rooikrans	Australia	Yes	White sands	1850	1850 - 1974	1
Acacia longifolia (Andr.) Willd.	Long-leafed Wattle	Australia	Yes	White sands	1850	1850 - 1974	1
Pinus pinaster Ait.	Cluster pine	Europe	Yes	White sands	1850	1850 - 1940	2
Myrica cordifolia L.	Waxberry	S Africa	No	White sands	1850	1840 - present	1
Ehrharta villosa Schult. F.	Pipegrass	S Africa	No	White sands	1850	1850 - present	1
Leptospermum laevigatum F. Muell.	Australian myrtle	Australia	Yes	White sands	1852	1852 - ?	2
Hakea sauveolens R. Br.	Sweet hakea	Australia	Yes	W Cape	1857	1857 - 1936	2
Casuarina equisetifolia G. Forst.	Beefwood	Australia	Yes	W Cape	1857	1857 - 1930	1
Eucalyptus diversifolia Bonpl.	Gum tree	Australia	Yes	W Cape	1857	1857 - ?	1
Cassia corymbosa Lam	Common cypress	Australia	Yes	White sands	1857	1857 - ?	1
Chrysanthemoides monilifera (L.) T.Norl.	Bitou	S Africa	No	White sands	1858	1858 - present	1
Acacia melanoxylon R. Br.	Black Wattle	Australia	Yes	White sands	1867	1867 - 1974	1
Ammophila arenaria (L.) Link.	Marram grass	Europe	Yes	W Cape	1876	1876 - present	4
Cladoraphis cyperoides (Thunb) S.M. Phillips	Steekgras	S Africa	No	W Cape	1890	1890 - present	4
Passerina rigida Wikstr.	Gonnabos	S Africa	No	W Cape	1896	1896 - present	4
Colpoon compressum Berg	Basbos	S Africa	No	Strandfontein	1899	1899 - present	4
Mundia spinosa L. (DC.)	Skilpadbessie	S Africa	No	Strandfontein	1899	1899 - present	4
Agropyron distichum (Thunb.) Beauv.	Seawheat	S Africa	No	W Cape	1900	1900 - present	3
Rhus crenata Thunb.	Dune crow-berry	S Africa	No	South coast	1930	1930 - present	3
Metalasia muricata (L.) D.Don.	Blombos	S Africa	No	De Mond	1939	1939 - present	4
Sutherlandia frutescens R. Br.	Camphor bush	S Africa	No	De Mond	1939	1939 - present	4

Concern regarding sand drifts on the road to Simonstown also developed and two screens about 420 m apart were constructed east of the road. Hottentot fig was planted between these screens and a fence of poplar cuttings constructed along the road. This was maintained until 1857. In the same year, R. Smith was appointed Superintendent of Plantations, and a fairly intensive afforestation programme of the White Sands area was undertaken (Fig. 7.1). *Acacias* and other Australian trees such as Australian Beefwood (*Casuarina* sp.) and Gumtrees (*Eucalyptus* spp.), were used. Smith isolated the major areas of drift sand on the Cape Flats and recommended more extensive plantings of alien species. Various drift sand areas in the Western Cape were stabilized by Smith until 1864 when he was replaced as Superintendent by A. Mathieson, who was expected to maintain the existing plantations and not initiate new drift sand stabilization (Shaughnessy 1980).

From the 1850's the technique used in France was employed. This involved the placing of rows of half-meter high brushwood at random distances apart on the bare sand. Seeds of indigenous species such as Waxberry (*Myrica cordifolia*) and Pipegrass as well as Cluster Pine were then sown in between these rows of brushwood (Stehle 1982).

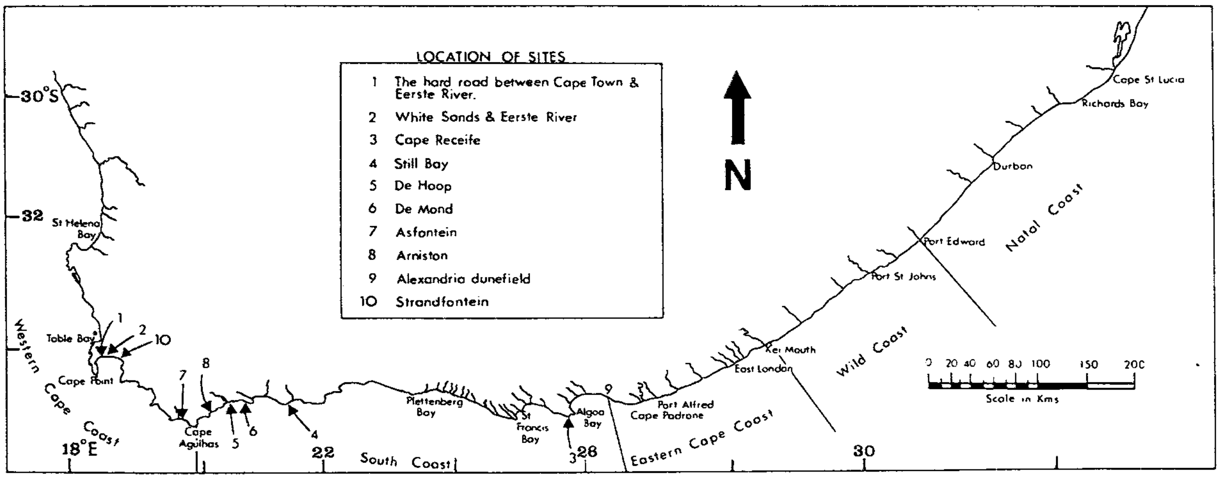


Figure 7.1 Map of the southern African coastline, showing the location of the stabilization sites mentioned in the text and the various regions of the coastline.

STABILIZATION METHODS INTRODUCED BY JOSEPH LISTER : 1875 - 1900

In 1875 stabilization became a function of the Cape Forestry Department whose policy was to stabilize drift sand areas with tree plantations which could then be harvested, thus making these areas economically viable. To achieve this end a new stabilization technique was developed by Joseph Storr Lister, who had 5 years previous experience as a forester in India. His method involved the spreading of city refuse at a density of about 110 tons per hectare over the area to be stabilized (King 1939). Besides temporarily stabilizing the sand, this refuse, which contained a large amount of horse dung, provided additional nutrients for the seedlings. Various plants were used, but Port Jackson Wattle was the most common species planted. He strongly supported the planting of this tree, as he believed it could be commercially harvested for its tannin. A further advantage was that it was not attacked by the

Australian scale insect, (*Icerya purchasi*) which had been accidently introduced from Australia and spread rapidly amongst the *Acacia* plantations. Consequently, from 1877 until 1888, Lister concentrated on planting Port Jackson Wattle in the Western Cape (Shaughnessy 1980), and in 1888 when transferred to the Eastern Cape, he employed the same techniques to stabilize the drift sands around Cape Recife near Port Elizabeth (Figs. 7.1 & 7.2).

A major disadvantage of this technique was the need to construct a railway line from the city's refuse dump to the stabilization site for the transport of the refuse, which made the method uneconomical. It became essential to employ a new technique, and in 1896 Marram grass, (*Ammophila arenaria*) was used on a wide scale as a substitute for refuse to temporarily stabilize the sand before seeding (Stehle 1981b).

In 1892, Lister was succeeded by David E. Hutchins who introduced further changes in the treatment of drift sands. All stabilization previously undertaken had been initiated at the area closest to the stable vegetated zone. Hutchins proposed that the drift sands be stabilized with Marram grass at their origin along the shoreline. The essential feature of this method was the formation of a "*dune littorale*" as was done by the French at Gascony (McNaughton 1895). This "French method" was adopted in 1896, and in 1897 it was officially decided to discontinue the use of city refuse (Shaughnessy 1980). Unsuccessful attempts were also made to plant seedlings of indigenous species such as Basbos (*Colpoon compressum*) and Gonnabos (*Passerina rigida*) in between the Marram grass. As success was only achieved with Waxberry the use of indigenous vegetation was abandoned in 1904.

THE METHOD OF LARGE SCALE DUNE STABILIZATION : 1900 -1970

Dune stabilization methods changed little from 1900 to 1970 when control of drift sands fell under the jurisdiction of the Department of Forestry, who initiated various dune stabilization work along the South African coastline. In 1901, stabilization at Still Bay was commenced and completed 50 years later with 445 ha stabilized (Fig. 7.1). At De Hoop, 2100 ha of drift sand was threatening villages in the area, and in 1934 the landward margin of sand was successfully stabilized with both indigenous and alien species. Stabilization of the De Mond Forest Reserve was commenced in 1942 and by 1958, 283 ha had been successfully stabilized, mainly with indigenous vegetation (Fig. 7.1). During this period the Department of Forestry promoted the stabilization of all sand drifts (Walsh 1968). For example, it was felt that the entire 21 500 ha of bare sand along the 45 km stretch of coastline from Asfontein, east to Arniston should be stabilized (Fig. 7.1). This programme was very successful and by 1934 a total area of 66 886 ha had been stabilized along the Cape coastline, mainly with alien species, although indigenous vegetation had been used in some areas (Keet 1936). Large scale stabilization and afforestation was also undertaken in Natal during the early 1940's, using Australian Beefwood. Primarily these plantations were established to stabilize shifting sands, but also to provide timber (Weisser 1978a).

During this period the method used was essentially three-fold, the first stage being the erection of barriers to arrest the flow of sand at its source. These barriers faced the prevailing wind and were aligned to follow the trend of the coastline. They were constructed of wooden poles or strips of Marram grass 40-60 meters wide. The Marram grass grew as it accumulated sand while the wooden barriers were physically raised as sand accumulated around them, care being taken to ensure that the crest of the developing foredune remained even. When the dune reached a sufficient height to prevent most sand reaching its crest (above 40 m), it was rounded off by establishing a second barrier a few meters behind and parallel to the crest (Keet 1936). However, later it was found that low dunes covered with vegetation were preferable as they were cheaper, easier to maintain and as effective in trapping sand (Walsh 1968). It was also found that a bush barrier consisting of brushwood interlaced between stakes placed one metre apart was more suitable than wooden poles. The siting of these artificial foredunes above and parallel to the spring high tide mark was found to be crucial for successful stabilization.

The second stage in the stabilization process consisted of thatching the surface of the sand behind the artificial foredune with brushwood or by sowing grass. This was commenced from the down-wind side of the dune, with each branch placed with its stump overlapping the top of the branch behind it. To reduce expense, the less exposed dune valleys were covered more lightly than the dune crests. About 7 to 9 kg of Pipegrass seed was sown per hectare, and one Marram grass set of 3-4 tufts was planted per square meter. Planting and sowing was commenced at the base of the windward slope of the dune during the rainy season, with an even surface maintained. These pioneer grass species are not permanent as accumulating sand initially stimulates their growth, but once they have stabilized the dunes and sand movement ceases, they die out.

The third and final stage in the process of stabilization involved the introduction of woody species, mainly Australian *Acacias*, by sowing seed amongst the grasses which provided protection for the young seedlings (Keet 1936). Later the planting of grasses was found to be unnecessary, and the method simply consisted of covering the entire area behind the artificial foredune with *Acacia* branches, the seeds of which fell from the pod onto the sand where they germinated, the resultant prolific growth stabilizing the area within three years (Plate 7.1). Additional sowing was seldom necessary and indigenous vegetation was rarely used as in most cases it was suppressed and killed by the alien vegetation (Walsh 1968).

Plate 7.1 Dunes permanently stabilized with Rooikrans at Sundays River Mouth on the Eastern Cape coast. Note the dense growth of the Rooikrans, and the alternating strips of cleared and vegetated areas. Brushwood from the felled trees has been packed on the sand.

CURRENT METHODS OF STABILIZATION : 1970 - PRESENT

The threat to indigenous vegetation by the invasion of Rooikrans (*Acacia cyclops*) was raised for the first time in 1936 (Keet 1936). However, the general consensus was that there were no indigenous species which could substitute for the aliens despite the successful stabilization in 1942 of the De Mond area with indigenous species such as Waxberry and Blombos (*Metalasia muricata*). There seemed to be a general apathy regarding the replacement of Rooikrans with indigenous species to the extent that in 1957 experiments were initiated to determine the suitability of using other alien species instead of Rooikrans.

It was not until 1974 that it was decided that the use of alien species should be phased out and only indigenous species and the non-invasive alien, Marram grass be used (Stehle 1981a). At this time the Department of Forestry reviewed its general policy on dune stabilization and decided that the old methods based on the French model be revised as they interfered too much with the natural ecological processes governing the stability of the beach and dune environment. Furthermore, the injudicious stabilization of vast areas of drift sand was restricting the natural cycle of deposition and erosion of sediments between the beach and surf zone. In many cases these stabilized areas experienced storm damage and needed constant repairs (Stehle 1981b).

Consequently the policy on dune stabilization was changed again, and in 1980 the Directorate of Forestry adopted the view that drift sands were natural areas and should be preserved as such (Cobby 1988). Only when farmland or settlements were threatened would dune stabilization be considered, and then only with indigenous species. The elimination of the already established *Acacia* species also received greater attention, and artificial foredunes were to be built only when absolutely necessary, and then only if they had no negative effects on the sediment exchange between beach and surf zone (Department of Forestry 1980). More importantly, it became mandatory that a management plan containing information on the area requiring stabilization, why it should be undertaken and what methods were to be used, be prepared. The present policy is to only stabilize areas when absolutely necessary, and it is likely that many stabilization sites along the coast would not have been treated had this policy been introduced in the nineteenth century (Burns & Reyneke 1983).

Plate 7.2 A sand dune along the Alexandria coastline being temporarily stabilized by brushwood packing before seeding and planting.

The techniques employed to temporarily stabilize the sand before planting or seeding have not changed markedly. Barriers are still constructed at the seaward margin of the stabilization site to afford it some protection, but large foredunes are no longer created. These sand-arresting barriers are constructed using one meter wide nylon shadecloth (40% shade) attached to poles driven into the sand at one meter intervals. The area to be stabilized is still covered with brushwood, although the process is more mechanized and brushwood is spread as sparsely as possible to reduce costs (Plate 7.2). Approximately 650 cubic meters per hectare of deseeded Rooikrans brushwood is used if available. Although less suitable, baled hay is also used, with 1000 bales per hectare spread evenly over the bare sand. The direct planting of Marram and other grass species onto the bare sand prior to seeding instead of brushing is no longer practised (Stehle 1980; Lubke & Avis 1986a), and Marram is only used to create sand-arresting barriers.

Once the area has been temporarily stabilized with brushwood, vegetation is established by seeding and/or planting young indigenous plants. Seeds are sown at a total density of about 150 to 200 kg per hectare depending on the species, and sowing is repeated every year for 3 to 5 years. Seedlings, established in nurseries under shadecloth, are planted about two meters apart (Lubke & Avis 1986a). In an attempt to simulate the process of dune succession, the seeding and planting is divided into three stages, and Table 7.2 lists the species used at each of these stages. In the Alexandria area planting trials using a number of indigenous species revealed that Waxberry was the most successful species (Plate 7.3). Its rapid growth rate and spreading growth pattern makes it the most useful indigenous species to use, and it should be utilized more intensively for future stabilization (see Chapter 8).

Plate 7.3 A stabilization area along the Eastern Cape coastline which has been packed with brushwood, seeded and planted with various species. The more densely covered area was planted with Waxberry.

Once the area has been seeded and planted, it is maintained for a number of years. Fences, brushwood and plants are replaced when they become covered by sand as the successful stabilization of an area using indigenous vegetation takes at least five years (Plate 7.4).

Plate 7.4 A 7 year old area on the Alexandria coastline which has been permanently stabilized with indigenous species. Note the dense cover of the indigenous species.

Table 7.2 Indigenous species used in the three stages of dune stabilization in South Africa (Adapted from Lubke & Avis 1986a).

SPECIES	COMMON NAME	1 Moisture requirements	2 Means of propagating	Month seed is harvested	NOTES
Stage One **Pioneers**					
Ehrharta villosa Schult. F.	Pipegrass	L	P or S	Oct - Dec	Good in mobile sand
Ammophila arenaria (L.) Link.	Marram grass	L	P	-	Accumulates sand
Carpobrotus species	Hotnotvye	M	C	-	Along edge of forest
Scaevola plumierii (L.) Vahl.	Seeplakkie	L	P	Mar	Ideal foredune species
Arctotheca populifolia (Berg.) T. Norl.	Sea pumpkin	L	P or S	Aug - Oct	Close to high tide mark
Ipomea pes-caprae (L.) R.Br.	Dune morning glory	L	P or S	Mar - Apr	Pioneer of open sand
Gazania rigens (L.) Gaertn.	Daisy	M	P or S	-	Foredune areas
Agropyron distichum (Thunb.) Beauv.	Seawheat	L	P or S	Dec	Very similar to Marram
Tetragonia decumbens Mill.	Klapiesbrak	L	P	-	Foredune areas
Stage Two **Dune Slack Species**					
Scirpus nodosus Rottb.	Dune slack sedge	H	S	All year	Grows well in slacks
Chironia bacifera L.	Christmas berry	M	S	Dec - Mar	Grows in slacks & open areas
Helichrysum cymosum (L.f.) D. Don.	Dune everlasting	H	S	Sep - Jan	Hardy slack species
Psoralea repens L.	Dune creeper	M	S or P	Oct - May	Grows in slacks & forest margins
Shrubs					
Stoebe plumosa (L.) Thunb.	Slangbos	L	S	Feb - Mar	Excellent shrubs that grow well from seed and spread rapidly in open areas
Metalasia muricata (L.) D. Don.	Blombos	L	S	Jun - Jul	
Chrysanthemoides monilifera (L.) T.Norl.	Bitou	L	S	Jun - Jul	
Passerina species	Gonnabos	L	S	Dec	Pioneer dune forest species, very good in open areas and slacks, but seeds are slow to germinate
Mundia spinosa L. (O.C.)	Skilpadbessie	L	S	Dec - Feb	
Myrica cordifolia L.	Waxberry	L	S	May - Aug	
Rhus crenata Thunb.	Dune crow-berry	L	S, C or P	May - Jul	
Brachylaena discolor DC.	Silverleaf	L	P or C	Aug - Oct	Spreads well over sand
Scutia myrtina (Burm.F.) Kurz	Cat's claw	M	P	May	Useful pioneers of dune forest to be used only after a shrub cover has been achieved
Tarchonanthus camphoratus L.	Camphor bush	M	P	Jan - Oct	
Olea exasperata Jacq.	Sand olive	M	P	-	
Euclea racemosa Murray	Dune ghwarrie	M	P	Feb - May	
Stage Three **Trees**					
Sideroxylon inerme L.	White milkwood	M	P	Dec - Feb	
Mimusops caffra E.Mey. Ex A.DC.	Red milkwood	H	P	Dec - Apr	Large trees that can only be planted once the area has been well covered by shrubs and is stable
Cordia caffra Sond.	Septee	M	P	Jan	
Pterocelastrus tricuspidatus (Lam.) Sond.	Cherrywood	H	P	Jul - Mar	
Cassine aethiopica Thunb.				Jun - Jan	
Maytenus procumbens (L.F.) Loes.	Kububerry	H	P	Aug - Jan	
	Dune kokoboom	H	P		

[1] L = Low, M = Medium, H = High

[2] P = Plants, S = Seeds, C = Cuttings

PROBLEMS ASSOCIATED WITH DUNE STABILIZATION

Despite the obvious advantage of stabilizing drift sand areas threatening human settlements and farmland, a number of disadvantages also exist. The most obvious of these has stemmed from the use of alien species which have invaded the natural vegetation. The three Australian *Acacia* species, namely *Acacia cyclops*, *A. longifolia* and *A. saligna*, used widely for dune stabilization have been classified by Wells *et al.* (1986) as species capable of transforming natural habitats and landscapes due to their high invasive potential. Stirton (1978) states that the major danger of these species is their ability to form stands of dense, impenetrable tall shrubs or short trees (pole thicket) at the expense of the indigenous vegetation (Plate 7.1). This suppressive effect prevents the growth of indigenous vegetation under the trees, "thus resulting in areas which can be likened to ecological deserts" (Stirton 1978). Their strong competitive ability due to the lack of natural enemies gives them many advantages usually only attributed to annual weeds, as they are able to invade disturbed areas with ease. As a result, the vegetation of many coastal and adjacent areas has become infested with these species (Jacot Guillarmod 1988).

Australian Beefwood has a very low invasive potential, but it produces copious leaf litter and the roots are very fibrous, covering several square meters of ground around each tree. This is due to a symbiotic relationship with a bacterium of the genus *Frankia*, and results in no other species being able to grow under the trees (Benge 1982). Thinning or felling of this species is therefore essential before indigenous vegetation can return, and has been initiated by the Directorate of Forestry in Natal (Weisser 1978a). However, the ability of these trees to coppice compounds the problem.

In addition to the threat to indigenous vegetation other harmful effects of using aliens include the increase in periodicity of fires due to the flammable nature of many of these species, the draining of soil water resources by increased transpiration, erosion due to the lack of an understory, the loss of cultivated land and the associated loss in public and private monies to remove them (Jacot Guillarmod 1988).

As a result of these problems, the Directorate of Forestry is now actively involved in removing alien species from the natural vegetation and from older stabilization sites along the coast (Lubke & Avis 1986b). This is best exemplified at Sundays River Mouth, located at the western end of the Alexandria dunefield (Fig. 7.1) where a large dune stabilization programme was initiated in 1957. This started with the creation of an artificial littoral dune using brushwood fencing and Marram grass. Once the sand supply from the beach was cut off the area behind this dune was stabilized using alien species such as Rooikrans and Australian Beefwood. Removal of this vegetation was initiated in 1978 by clearing 20m wide strips of vegetation and leaving 10 m strips intact. This method ensured that the area remained stable and it was hoped that indigenous vegetation would colonize the cleared areas (Plate 7.1).

By 1983 very few species had invaded these areas and a field trial was initiated to determine what factors were responsible for this lack of colonization. The main limiting factor was found to be the low soil moisture level due to the low rainfall in the area, with grazing of young plants by large mammals and a lack of nutrients being of secondary importance. In areas such as this, regular sowing and planting of indigenous species would be required before success is achieved. Clearly the major problem associated with this approach is the expense involved, as the present cost of stabilizing one hectare is approximately R10 000 (± US $4000.00). Therefore it is important to assess whether the area that will benefit from the protection warrents the economic expenditure required. In other words, a cost-benefit analysis should be undertaken. In this case the results showed that the additional expenditure was not warrented, and no further stabilization or attempts at establishing indigenous vegetation have been undertaken since 1984.

Another major problem associated with stabilizing large sand drifts, particularly dunes which move across a headland, has only recently been realized. These headland bypass dunes (Tinley 1985) are often responsible for supplying sand to beaches downdrift, and by stabilizing these dunes the supply of sand is cut off, resulting in beach erosion. This has occurred at both St. Francis Bay and Port Elizabeth, and the latter area will be used as a case study to explain these consequences in more detail.

In 1870 the danger of drift sand to the settlement of Algoa Bay was realized and in 1893, Lister started to stabilize the Cape Recife peninsula (Fig. 7.1). By 1909 the entire area now known as the Port Elizabeth Drift Sands Forest Reserve had been stabilized using the techniques described earlier (Fig. 7.2). Thus, the threat of silting up the harbour posed by these drift sands was removed (Lubke 1985), and King (1939) stated that Lister had "transformed over 4500 ha of barren waste into a thriving plantation which is restoring fertility to the soil and, at the same time, is yielding a handsome revenue from the sale of fuel".

Lubke (1985) is of the opinion that stabilization of the peninsula has been responsible for the loss of sand from Port Elizabeth's beaches, which was found to be the case at St. Francis Bay. However, Braine (1902) and Crews (1984a&b) have suggested that the area was previously stabilized and went through two stages of natural destabilization, but present only dubious historical and no substantial supportive data. Lord *et al.* (1985) reported that this was unlikely, and their study showed that the stabilization of the Cape Recife area is responsible for the loss of sand from the Humewood and Summerstrand beaches (Fig. 7.2). They estimated from aerial photographs and wind data that the supply of wind driven sand into Algoa Bay averaged 170 000 m^3 yr^{-1} before stabilization of the driftsands. At present, the only active dunefield is a small system in the Cape Recife Nature Reserve, which provides about 26 000 m^3 yr^{-1}. The transport of sand by sea around Cape Recife was estimated as being less than 25 000 m^3 yr^{-1}. They therefore concluded that at the present time the beaches have an annual nett loss of about 80 000 m^3 of sand per annum.

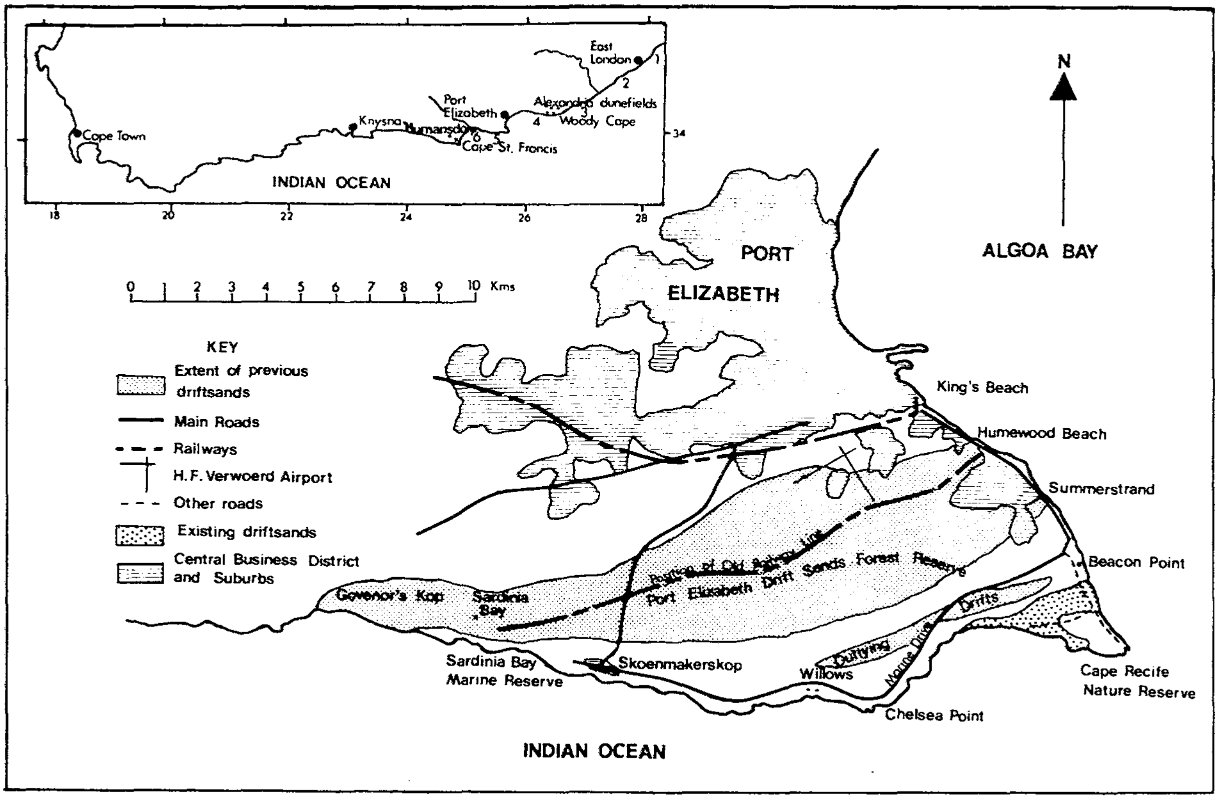


Figure 7.2 Map of Port Elizabeth and the Cape Recife area. Extent of drift sands are taken from King (1939). Subsequently the outlying drifts were also stabilized, as were some of the dunes in the Nature Reserve (from Lubke 1985).

The two ways to counter this erosion are both costly. The first would be to increase the supply of sand to the beach, while the second would be to reduce the wave energy in the vicinity of the beach (Lord *et al.* 1985). The former could be achieved by destabilizing dunes at Cape Recife, the latter by constructing sea walls along the beachfront (Crews 1984b). The Port Elizabeth Municipality decided on the costly construction of movable groins in an effort to replenish the beaches. Clearly, this erosion problem has stemmed directly from the stabilization of the Cape Recife headland bypass dunes and care must be taken when large drift sand areas are stabilized in future.

This ability to successfully stabilize drift sands has resulted in further problems. It provides a means for development within the unstable dunes and an excuse to clear vegetation very close to the open dunes, since methods are well established to restabilize these areas. The Directorate of Forestry has also found that farmers clear the coastal vegetation for additional grazing land and leave an inadequate buffer of vegetation between pastures and the drift sands. This results in blowouts which require stabilizing. As the region from the high water mark to the edge of the coastal forest falls under the jurisdiction of the Directorate of Forestry, the stabilization of these blowouts is their responsibility and many farmers take advantage of this system, and stabilization should not be undertaken if the farmers negligence resulted in the destabilization.

Unfortunately, there are many examples of developments along the South African coastline where the remedial action of dune stabilization has become necessary. Developments which require extensive dune stabilization are still proposed, as for example the construction of a road across mobile sand dunes to a parking area located just behind the beach at Boesmansriviermond (Fig. 7.1). To prevent sand covering the road and parking area about 60 ha of dunes to the west would need to be stabilized. La Cock *et al.* (1992) undertook a study of the area to determine if this development was both feasible and justifiable. This study showed that the dunes in the area have a net eastward movement of 3 m yr^{-1}, and that this sand is an important sediment source for the beaches. This development would not only ruin the natural beauty of the area, but the unnecessary dune stabilization would also prevent sand moving across the dunefield, resulting in similar problems to those experienced at Port Elizabeth and St. Francis Bay.

CONCLUSION

The present techniques employed for dune stabilization have proved very efficient in establishing indigenous vegetation. The use of indigenous species has not only afforded protection to areas which appeared to be threatened by drift sand, but has also helped conserve the natural flora by preventing the spread of alien species. The use of seedlings appears to have helped expedite the process, and in some areas an attractive and functional vegetation cover has been achieved (Plate 7.4). The success of stabilization programmes using indigenous vegetation has been investigated more fully in Chapter Eight. However, the need for dune stabilization is questionable, and the most important consideration is to decide whether the area threatened by sand drift warrants a costly stabilization programme. The Directorate of Forestry presently manages drift sand areas as special ecosystems, as it was decided in 1980 that it was neither desirable from the ecological point of view nor financially feasible to carry out total stabilization of the large areas under its control, since these areas are ecologically stable.

Hopefully the correct management of coastal areas and controlled development practices will help to reduce the need for dune stabilization, and the removal of alien species from the natural vegetation will help alleviate the problems associated with their spread. However, dune stabilization will always be required as a management tool in the coastal zone. Consequently, the general public and coastal landowners must be made aware of the problems associated with stabilization using alien species and with unplanned development along the coastline. Indeed, certain coastal property owners still favour the use of alien species such as Rooikrans for stabilizing and vegetating their property (Crews 1984b). Publications on coastal management and dune stabilization have been produced for many years in Australia, Europe and the USA (*vide* Jagschitz & Wakefield 1971; Beach Protection Authority Queensland, various publications) and there has always been a need for such publications in South Africa. Recently pamphlets produced in our laboratory outlining the techniques to use for dune stabilization, and factors to consider when developing within the coastal zone, have been made available to the general public (Avis 1986; Lubke & Avis 1986a) and videos on the techniques of dune stabilization have also been produced (Lubke & Avis 1991). Prior to this the stabilization techniques were contained in unpublished reports and there still exists a need for more general information to be distributed on this basis. Consequently, the Department of Environment Affairs has produced a series of brochures outlining the principles of coastal zone management (DEA n.d.).

CHAPTER 8

A SURVEY OF COASTAL DUNE STABILIZATION IN SOUTH AFRICA : QUANTIFICATION AND EVALUATION

INTRODUCTION

The stabilization or reclamation of areas of mobile sand using vegetation, both within the coastal zone and elsewhere, is an important management tool which has been used in South Africa (Chapter 7; Stehle 1988; Lubke & Avis 1986), the United States (Jagschitz & Bell 1966; Davis 1975), the United Kingdom and Europe (Adriani & Terwindt 1974; Wilcock & Carter 1977; Carter 1980b; Ranwell & Boar 1986; Doody 1989; Skarregaard 1989), the Middle East and North Africa (Dougrameji & Kaul 1972; Zollner 1986); Australia (Craig 1985; Beach Protection Authority Queensland, various publications) and New Zealand (Restall 1964; Wendelken 1974). Although the process is relatively costly, it is effective and produces a natural and aesthetically pleasing barrier to mobile sands. However, as discussed earlier (Chapter 7), there are a number of disadvantages associated with the technique.

In South Africa large scale stabilization programmes are restricted to the coastal zone, and are undertaken by centrally funded Government agencies, mainly the Directorate of Forestry of the Department of Waters Affairs and Forestry. An ecological approach towards dune stabilization is now adopted, with a management plan being drafted for areas requiring stabilization, and only indigenous species are used (Chapter 7). It is likely that had this approach been adopted in the past, many areas along the coastline would not have been stabilized. It is important to note that coastal areas are geologically sensitive as these systems are finely tuned in terms of cause and effect, being in close dynamic equilibrium with the wave and wind regime. They are therefore prone to mismanagement (Rust 1988), and any serious human interference (such as dune stabilization) will be reflected by some adjustment to the beach profile. Thus, a clear understanding of the controlling environmental factors are imperative if man is to correctly manage the area.

Most of the literature mentioned above either describes the techniques used for stabilization (Jagschitz & Bell 1966; Ranwell & Boar 1986; Skarregaard 1989) or discusses the results of experimental investigations undertaken to improve existing, or develop new techniques (Adriani & Terwindt 1974; Gadgh *et al.* n.d.; Craig 1985; Stanley & Watt 1990). Few studies actually evaluate quantitatively the success of these programmes, except for Hansen and Vestergaard (1984) and Zollner (1986). In South

Africa considerable funds have been spent on dune stabilization, but no objective studies have been undertaken to evaluate the success of these programmes. Such a study was therefore initiated to quantitatively assess the success achieved using current techniques for stabilizing coastal dunes with indigenous vegetation. From these data it has been possible to glean information on those species most suited to dune stabilization along the coast. The overall process, and principle, of dune stabilization is also discussed.

STUDY AREA

The 260 km of coastline east of the Sunday's River Mouth (lat.33°43'S; long.25°52'E) to the Kei River Mouth (lat.32°43'S; long.28°24'E) has over 200 km of sandy beaches backed by dunes. The coastline is linear trending, subtropical to temperate with a bimodal rainfall and diverse flora (Fig. 8.1). The geomorphology, climate and vegetation has already been discussed (Chapter 1). However, it is relevant to discuss the physiography in more detail, as this is an important consideration with regard to dune stabilization. Wind deposited dunes dominate the area from Sunday's River Mouth to the Keiskamma River Mouth (Fig. 8.1; see Plate 1.1, pg 20). Further east, the continental shelf becomes narrower and the limited availability of sand results in smaller dunefields. The sandy, shelving beaches are predominantly wave built and rest on low rocky platforms. Because they shelve gently, sand is usually exposed at low tide and may be transported by saltation and surface creep to form dunes (Rust 1988; Marker 1988). The variety of bare dune types formed include barchanoid, transverse, reversing, buttress barchanoid and longitudinal dunes, and vegetated dunes are mainly foredunes, retention ridges and various parabolic types (classification after Tinley 1985).

The vegetation is Succulent Thicket from Sundays River to Bushmans River, and from here to East London it is predominantly Dune Scrub or Thicket with patches of Forest. North east of East London Dune Forest becomes more common, and is best represented at Kei Mouth (Chapter 1).

Within this coastal area a total of 18 stabilization sites were sampled in detail, and a description of each is given in Table 8.1. Most of the stabilized dunes are either parabolic blowouts or buttress barchanoids, and it is only in the larger sites that transverse dunes and foredunes are found. Due to the configuration of the coastline, most sites face south or south east, but as one moves west, the aspect changes to southwest due to the half-heart shaped Algoa Bay (Fig. 8.1). Most dunes have steep (>30% slope) or moderate (15-30%) slopes, with only a few flat areas (<15%). A brief description of the natural vegetation surrounding or abutting each site is also given in Table 8.1, but is not discussed further as it has already been described in detail (Chapter 1).

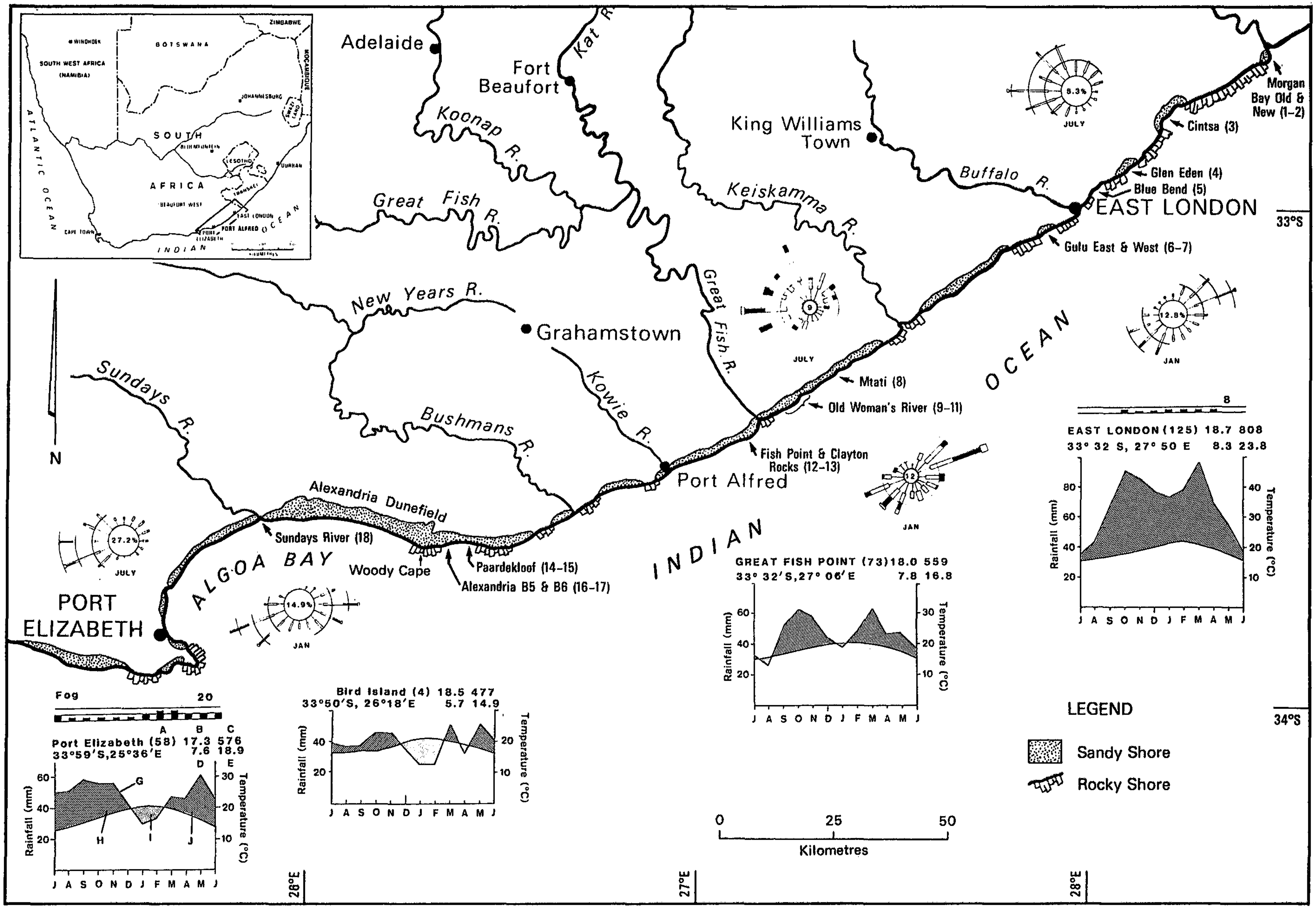


Figure 8.1 Map of the coastline showing the location of the 18 stabilization sites sampled and Walter Leith climate diagrams for Port Elizabeth, Bird Island, Great Fish Point and East London. Wind roses for January (summer) and July are also shown for these locations.

Table 8. 1 Summary description of the physiography and vegetation at each stabilization site

Stabilization Site	**Dune types**	**Aspect**	**Slope**	**Natural Vegetation**	**Comments**
Morgan Bay New area	Parabolic & buttress barchanoid	SSW	Steep	*Mimusops/ Sideroxylon* Forest	Close to mouth of river
Morgan Bay Old area	Parabolic blowout	SW	Moderate	as above	Immediately behind above site.
Cintsa	Eroded mature foredune	SE	Steep	*M. caffra* forest	Edge of site eroded by high tide
Glen Eden	Edge of tranverse dune	SE	Flat	Dune Scrub	Small area close to forest
Blue Bend	Parabolic blowout	E	Moderate to steep	*B.discolor/ M.caffra* Dune Scrub	Active blowout recently stabilized.
Gulu East	Parabolic; foredune; buttress barchanoid	SW	Moderate to steep	As above	East of Gulu River
Gulu West	As above	S	As above	As above	West of Gulu River
Mtati	Buttress barchanoid & transverse	S & SE	Steep	*B.discolor; M.caffra; S.inerme* dominated Dune Thicket	West of Mtati River
Old Woman's River East	Parabolic blowout	E &SE	Moderate		Blowout above aeolionite ridge
Old Woman's River Middle	Parabolic & buttress barchanoid	E & SE	Moderate to steep		Active blowout area in forest.
Old Woman's River West	Parabolic & buttress barchanoid	E & SE	Steep	as above	Active erosion of stabilization area
Fish Point	Transverse, reversing, buttress barchanoid & parabolic	SE	flat - steep	As above but invaded by *A.cyclops*	East side older than west
Claytons Rocks		SE	As above	As above	Immediately west and joined to Fish Point
Paardekloof B7 & B8	Transverse & barchanoid	S to SW	Moderate to steep	Sparse Dune Thicket with patches of Dune Fynbos	Large expanse of unvegetated dunefield surrounds site
Alexandria B5 compartment	Transverse, barchanoid and parabolic	S to SW	Moderate to steep		Edge of thicket far from high water mark
Alexandria B6 compartment		S to SW			As above. Has test plot using *M.cordifolia*
Sunday's River Mouth slack	Dune hollow	S	Flat	Kaffrarian Thicket	Behind large artificial foredune

METHODS

HISTORICAL INVESTIGATION

To directly compare the success of species establishment and growth at each site it is important to know in what year stabilization was commenced, and what areas were covered with brushwood, seeded and/or planted each year. Some of this information was recorded by the respective forest officers, and documents for the past 30 years (1955 to 1985) were perused at the offices of the Regional Directorate of Forestry, King William's Town. The following documents were used to extract relevant information:

* The annual reports for the district;
* Proposed and completed annual plans; and
* Production control sheets.

SAMPLING TECHNIQUES

From a pilot survey it was found that the best measure to determine the success of species establishment and growth was a visual estimate of cover and density in 1 m^2 quadrats. The latter was difficult to determine for grasses, and a value of 99 was given for quadrats with a large but indeterminate number of individuals. Quadrats were randomly placed within each site, the number of samples depending on the size of the site, with smaller areas being more intensively sampled. Soil samples were also taken at random, and pH and conductivity was determined using the techniques described previously (Chapter 2). The position of quadrats were recorded on a sketch map of the area, and notes were made on the aspect and slope of the dunes (determined with an Abney level) and dominant species in the natural vegetation. From this information it was possible to produce a sketch map of the vegetation at each site to facilitate data interpretation, but these are only presented for some sites when considered relevant.

DATA ANALYSIS

Initially the cover values for each of the 18 stabilization sites were individually analyzed using TWINSPAN (Hill 1979a) to isolate species assemblages; and DECORANA (Hill 1979b) to determine whether these groups were associated in any way. The merits of using these techniques have been discussed earlier (Chapter 1). However, results were found to be unreliable, primarily due to the sparseness of the vegetation cover, which ranged from 8 to 52%, and low density of individuals at certain sites. Modifications to the pseudospecies cut levels did not improve the analyses, and data on individual sites was expressed better when the following information was calculated and compared with the observed results: total mean percentage cover; total mean density; total number of species; Simpson's diversity (ℓ) and dominance (Ds); mean soil pH and conductivity; and importance value of all the species found at each site (Table 8.3). The latter was calculated using the techniques described earlier (Chapter 3) and data for the five most common species at each site are presented as Table 8.3. Simpson's diversity and dominance was calculated for each site, and for subsamples of 15 quadrats each, this being the smallest sample size. The diversity of the subsample which had the closest value to that calculated for the entire area is presented in Table 8.3, the requirement being that samples should be the same size for direct comparison of diversity.

The importance values of all the species at each site were combined into a single data set which was re-analyzed using TWINSPAN, to determine the synecological relationships between species and to see if the various sites were distinct enough to be separated on the basis of their floristic composition. DECORANA ordination was undertaken in an attempt to elucidate what major factors controlled the distribution of species and sites along the coastline.

RESULTS

HISTORICAL INVESTIGATION

Results of the historical investigation to assess the amount of work undertaken at each stabilization site is presented in Table 8.2, which has been divided according to the following main activities:

* packing of brushwood to temporarily stabilize sand,
* area sown with seed (hectares) or the quantity of seed sown (in kilograms). When known the species sown is also indicated,
* number of seedlings or area planted (in hectares) with seedlings,
* brushwood fence construction (in metres),
* areas cleared of alien species,
* maintenance, mainly taking the form of repacking areas covered with sand following periods of strong winds.

Unfortunately, detailed records for many of the sites have not been kept, particularly the smaller areas in the East London district. However, detailed observations were kept for the Gulu, Mtati, Fish River/Clayton Rocks and Old Womans River sites, and some general observations can therefore be made.

Brushwood fences are usually constructed during the early stages of the stabilization programme, and in the larger sites up to 7 km of fences were sometimes erected. Work usually commences with the packing of brushwood over the dunes, and this activity occurs regularly each year (see Plate 7.2, pg 241). The sowing of seeds or planting of seedlings was done less regularly, as planting or sowing is only undertaken once a sufficiently large area has been packed or sufficient seed is available. It is important to note that initially alien species were planted. In 1977 at Mtati, alien species such as *Acacia cyclops* and *Eucalyptus gomphocephala* were planted, whereas the following year *A. cyclops* and *A. saligna* were cleared at the Gulu sites (Table 8.2). This occurred before the present policy of using only indigenous species was enforced (Chapter 7), and it is clear that more recently only indigenous species were used (Table 8.2).

This lack of detail in some cases makes the interpretation of the floristic data gathered for this study, and the evaluation of the success achieved at each site, more difficult to assess. Nevertheless, in all cases a concerted and real effort was made to stabilize the sites, and the success achieved is evaluated on the basis of this assumption.

Table 8.2 Available information kept by the Directorate of Forestry on annual work undertaken at each stabilization site. Abbreviations of species planted are as follows: NR - No Records, but work could have been undertaken. A.c - *Acacia cyclops*; C.e. - *Casuarina equisetifolia*; A.s. - *Acacia saligna*; E.g. -*Eucalyptus gomphocephela*; G.r. - *Gazania rigens*; C.e. *Carpobrotus edulis*; A.a. - *Ammophila arenaria*; A.t. - *Atriplex* sp.

SITE ACTIVITY	MORGAN BAY(1+2)	CINTSA	GLEN EDEN	BLUE BEND	GULU EAST & WEST	MTATI	OLD WOMAN'S RIVER AREAS	FISH POINT & CLAYTON ROCKS	PAARDEKLOOF B7 & B8	ALEXANDRIA B5 & B6	SUNDAY'S RIVER
Area packed with brushwood (in hectares)	1982 - 1	1978 - 1.2 1982 - 1	1973 - 1 1974 - 2 1975-80 - NR 1981 - 1	1980 - 4 1981-83 NR	1965 - 1.2; 1966 - 2; 1967 - 2.6; 1968 - 1.2; 1969 - 1.0; 1970 - 1.2; 1971 - 1.0; 1972 - 4.2; 1973 - 4; 1974 - 5; 1975 - 8.5; 1976 - 7.5; 1977 - 7.7; 1978 - 7.0; 1979 - 9; 1980 - 6; 1981 - 6; 1982 - 1.	1977 - 4 1978 - 31 1979 - 11 1982 - 11	1969 - 1; 1970 - 5; 1971 - 2.1; 1972 - 4.2; 1973 - 3.6; 1975 - 1; 1976-79- NR; 1980 - 15ha; 1981 - 20ha.	1968 - 3; 1969 - 6.5; 1970 - 3.1; 1971 - 2.5; 1972 - 8.7; 1973 - 12.5; 1974 - 27; 1975 - 24; 1975 - 28; 1977 - 12; 1980 - 0.7; 1981 - 7.	1977 - 2.2 1979 - 0.5 1980 - 15	1978-82 - NR 1982 - 16	1968 - 5.5 1969 - 6.9 1970 - 41 1971 - 3.1 1973 - 3 1974 - 2 1976 - 4 1981 - 1
Area sown with seed (hectares) or quantity used (Kg)	1983 - ?	1982 - indig seed	1974 - 2 1981 - 1	NR	1965 - 45kg; 1968 - 4; 1969 - 1; 1971 - 1; 1972 - 20; 1974 - 5; 1976 - 8.9; 1977 - 7.7; 1979-82 - 82kg.	1978 - indig 535kg 1979 -343kg 1982 -968kg	1971 - 2.1 ha 1980 - 634kg (15ha) 1981 - 1565kg	1969 - 3.2ha; 1970 - indig 3ha; 1971 - indig & Ac 2.5 ha; 1974 - indig & Ac 48ha; 1976 - 90kg; 1978 - 127kg; 1980 - 90kg.	1979 - 0.5ha 1980 - 46kg	1978-82 NR 1982 - 309kg 1983 - 197kg	1970 - 10ha 1971 - 4ha 1973 - 3ha 1981 - 20kg
Seedings planted (number or area)	NR	NR	NR	1980 - 5300	1975 - A.c & C.e.; 1976 - C.e (6383) 1978 - indig (9300) 1978 - C.e. (7.0ha); 1979 - indig (22542) 1980 - indig (8000) 1982 - indig (4462)	1977 -A.c (4ha) 1977 - E.g/C.e(4100) 1978 -indig (5275) C.e (1259) & E.g (1259) 1979 -indig (30855) & E.g (1205) 1982 -indig (23816)	1970 - A.c (6000) 1980 - indig (50 818) 1981 - G.r (35 236) & C.d (19 248)	1973 - A.a (0.8ha) 1974 - A.c & indig (25 000) 1976 - 35 000 1978 - C.e (2 749) 1982 - indig (8 000)	1977 - 2 053 1978 - 949 1980 - 1 056 1982 - 11 247 1983 - A.a (2319) & indig (2125)	1978-82 - NR 1982 -20 464 1983 - 7 674	1969 - indig 6.9ha; 1971 - A.a 4ha; 1976 - 4ha 1978 - A.t ? 1982 - indig (1017)
Fence construction (in metres)	NR	1979 -250 1983 -200	NR	NR	1967 - 1000; 1968 - 6335; 1969 - 150; 1983 - 200	NR	1968 - 3 650 1969 - 900	1968 - 430 1969 - 1000	1979 - 450	NR	1968 - 550 1975 -1400
Area cleared of aliens	NR	NR	NR	NR	1978 - 11.3ha of A.c & A.s	1980 - 6ha	NR	1980 - 50ha	NR	NR	NR
Maintenance	NR	NR	NR	NR	1966 - 10ha repacked 1975 - 3.6ha repacked	NR	1982 - 4.3ha repacked	1970 - 13ha repacked	NR	NR	1972 - 3ha repacked 1975 - 1ha repacked

DETAILED ANALYSIS OF THE STABILIZATION SITES

A brief description of each site has already been given (Table 8.1), but more detailed information on the edaphic and floristic properties of individual sites provides information on suitable species, the species diversity in relation to age and past history, the overall success achieved and the reasons for the stabilization (Table 8.3). Individual sites are therefore discussed in more detail below.

Morgan's Bay Sites

The climate along this region of the coastline is more favourable than further west, with an annual precipitation of 808 mm falling mainly in the summer months (Fig. 8.1). There is no dry period, and temperatures are moderate, with winds blowing mainly parallel to the coast in summer. Winter winds tend to blow from the west. The Cintsa, Glen Eden, Blue Bend and Gulu sites experience this climate.

These sites are situated a few hundred metres west of the Ntshala River in a parabolic blowout dune orientated in a north easterly direction (Fig. 8.2). The older site is slightly larger than 1 hectare in extent and was 15 years old at the time of sampling. It is situated in a hollow in the coastal forest, and due to its age is mostly dominated by woody species such as *Metalasia muricata* (Plate 8.1), and has a relatively high soil pH (Table 8.3). Species richness and Simpson's diveristy are high, and the highest total mean percentage cover was recorded for this site.

The younger site was 2 years old when sampled, and is about 1 hectare in extent. It is found in front of the older site on an active blowout (Plate 8.2). Soil conductivity and pH are similar to the old site, but soil organic matter, species diversity and richness are lower. The total mean percentage cover was the lowest recorded for all sites (Table 8.3) and many patches of bare sand occur (Fig. 8.2). This area is dominated by the succulent creeper, *Carpobrotus edulis* and *Mariscus congestus*, a sedge common along this stretch of the coastline. The creeper *Cynancum natalitium* is common along the margin closest to the forest (Fig. 8.2), as noted previously in natural vegetation (Chapter 1).

Cintsa Bay Site

This small site of 1 hectare is situated 31 km north east of East London. Attempts were made to stabilize the steep south-east facing slope of a relic foredune as it was collapsing due to undercutting of the dune at high tides, and destruction of the vegetation as a result of recreational pressure (Plate 8.3). The site was only six years old at the time of sampling, and soil pH and conductivity were relatively high due to the high incidence of salt spray. Organic matter was relatively high considering the age of the site. Simpson's diversity was the lowest recorded with only 6 species found. Simpson's dominance was therefore high due to the predominance of the shrub, *Chrysanthemoides monilifera* (Table 8.3) which must have been planted. Other common species include *C. natalitium* and the shrub, *Passerina rigida*, which is found on natural foredunes (Chapter 1), and plays a very important role in succession towards Dune Thicket (Chapters 2 & 4). Despite the relatively high total mean cover in 1985 when data was collected, Thicket (Chapters 2 & 4). Despite the relatively high total mean cover in 1985 when data was collected, almost all vegetation had disappeared when the area was revisited in 1992, thus indicating the importance of an ongoing maintenance programme. This loss of vegetation was mainly due to erosion and slope failure, which was prevalent at the time of sampling (Plate 8.3).

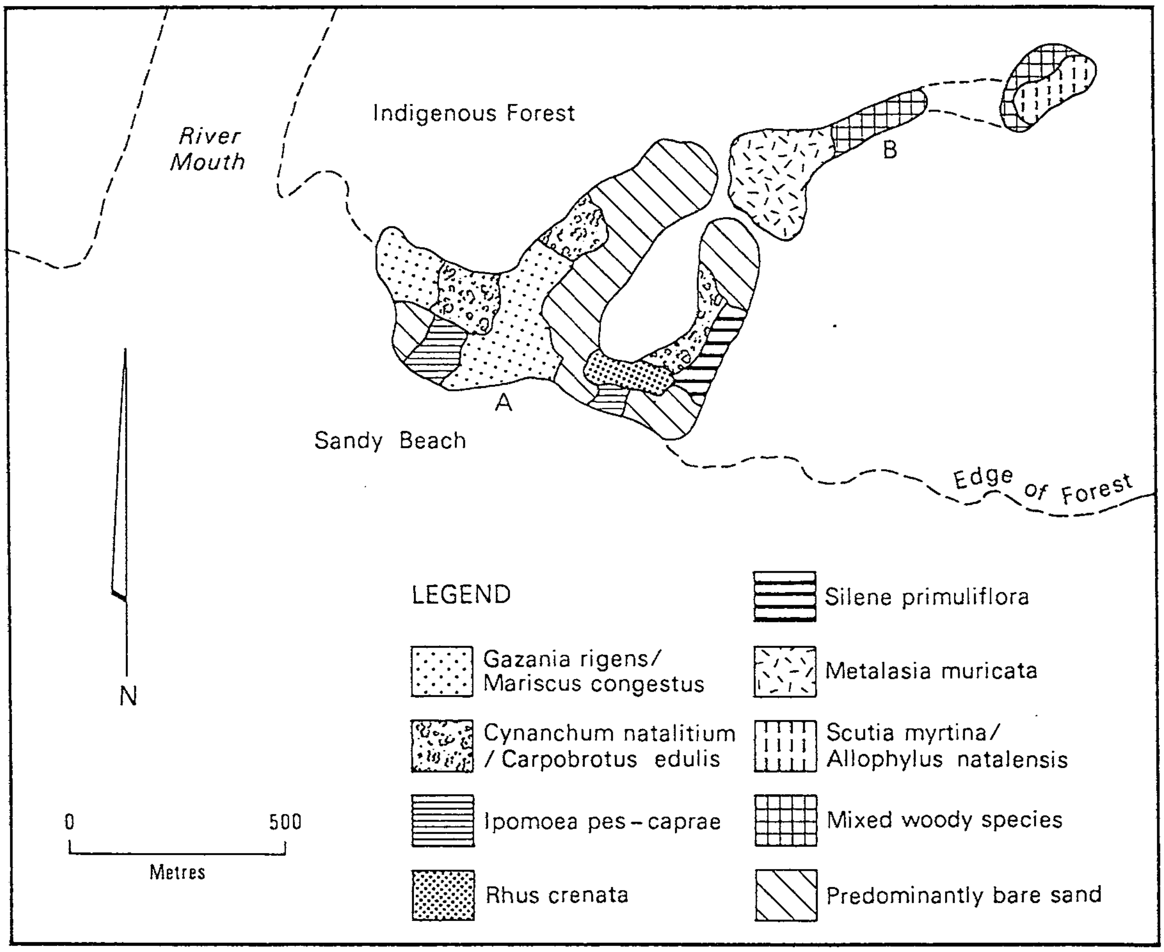


Figure 8.2 Map showing the vegetation of the Morgan's Bay Young (A) and Old (B) stabilization sites. Note the large bare areas which have a very sparse plant cover.

Glen Eden Site

This site is situated immediately north-east of the Bulura River behind a car park constructed on a flat aeolionite outcrop. The reason for stabilizing the 3 hectare area is unclear, as it is protected by this rocky outcrop. This site is relatively old (12 years), and was stabilized with Australian beefwood, *Casuarina equisetifolia* and *Acacia cyclops*. Despite the allelopathic and inhibitory effects reported in the literature for the former species (Benge 1982) and discussed earlier (Chapter 7), the highest species diversity was recorded at this site, although species richness was not very high (Table 8.3). Total mean cover was also high and the area was dominated by the grass, *Stenotaphrum secundatum*. This species seemed to thrive under the *Cassuarina* and *Acacia* canopy, together with more typical forests species, such as *Oplismnus hirtillus*, which was only recorded at this site. This observed higher density contrasts with that noted at Gulu (see below & Avis 1985).

Plate 8.1 Morgan's Bay Old area, looking north-east into parabolic dune, now completely stabilized after 15 years (1984).

Plate 8.2 Morgan's Bay New area, looking south-west down a recently stabilized blowout towards the sea. The village of Morgan's Bay is in the right background. Vegetation cover is still very sparse after 2 years (1984).

Plate 8.3 Slope failure of the Cintsa Bay stabilization site due to wave attack. The dominant vegetation above the erosion scarp is *Chrysanthemoides monilifera*.

Plate 8.4 Aerial view of the Blue Bend stabilization site, showing parabolic shape of blowout dune.

Blue Bend Site

This typical parabolic dune (Plate 8.4) found at Bonza Bay one kilometre north east of East London, was stabilized to prevent the blowout encroaching onto adjoining residential land. It was only six years old when sampled, and is 5 hectares in extent. Soil pH and conductivity are relatively high as the seaward slope is exposed, but organic matter is low as the site is young (Table 8.3). Simpson's diversity is relatively high, and 19 species were recorded. As noted previously (Avis 1986), species density was relatively high due to the smaller size of these younger plants, but mean cover was only 19.1%. A large number of seedlings were planted in 1980 (Table 8.2), and these woody species such as *Rhus crenata* and *Chrysanthemoides monilifera* could be clearly identified in the field as having been planted. They dominate this site, together with the Dune Everlasting, *Helichrysum praecinctum*. The forest margin species, *Cynanchum natalitium* is also common (Table 8.3).

Gulu East and West Sites

The Gulu River opens into the sea 20km west of East London (Fig. 8.1), and has a sandy beach on each side. The mobile sands from these foredunes, parabolic and buttress barchanoid dunes was thought to be responsible for silting up the river mouth; and to prevent further siltation , it was decided in 1965 to stabilize the dunes. The area is characterized by a number of blowouts orientated perpendicular to the coast due to the resultant onshore winds (Daines 1991). These areas were 20 years old at the time of sampling, making them the oldest sites investigated. Gulu East is much smaller (25 ha) than Gulu West (40 ha), which is over two kilometres long (Fig. 8.3).

Initially seed of indigenous species and *Acacia cyclops* was planted, but later this alien species was removed (Table 8.2). In 1975 over 6000 *Casuarina equisetifolia* trees were planted, due to its non-invasive and rapid growth rate. Indigenous shrubs such as *Rhus crenata* and *Passerina rigida*, together with pioneer species were either planted or seeded, and usually formed a number of distinct plant communities (Fig. 8.3). Stabilization was initiated closest to the mouth, and the area furthest west is younger and therefore colonised by pioneer species (Plate 8.5). In other areas woody species such as *P. rigida, Metalasia muricata* and *Chrysanthemoides monilifera* were planted and have become dominant (Table 8.3), forming distinct communities (Fig. 8.3; Plate 8.6). Although trees such as *Brachylaena discolor* were planted, they had not yet become dominant, possibly indicating that planting them too early may not be successful. Total mean cover is high when compared to other sites, but total mean density is similar, indicating that the individual plants are larger. Soil conductivity and pH is low for both sites, and organic matter relatively high due to the age of the area and possible build up of detritus (Table 8.3). Simpson's diversity is high, as is the species richness, indicating that indigenous species are establishing naturally.

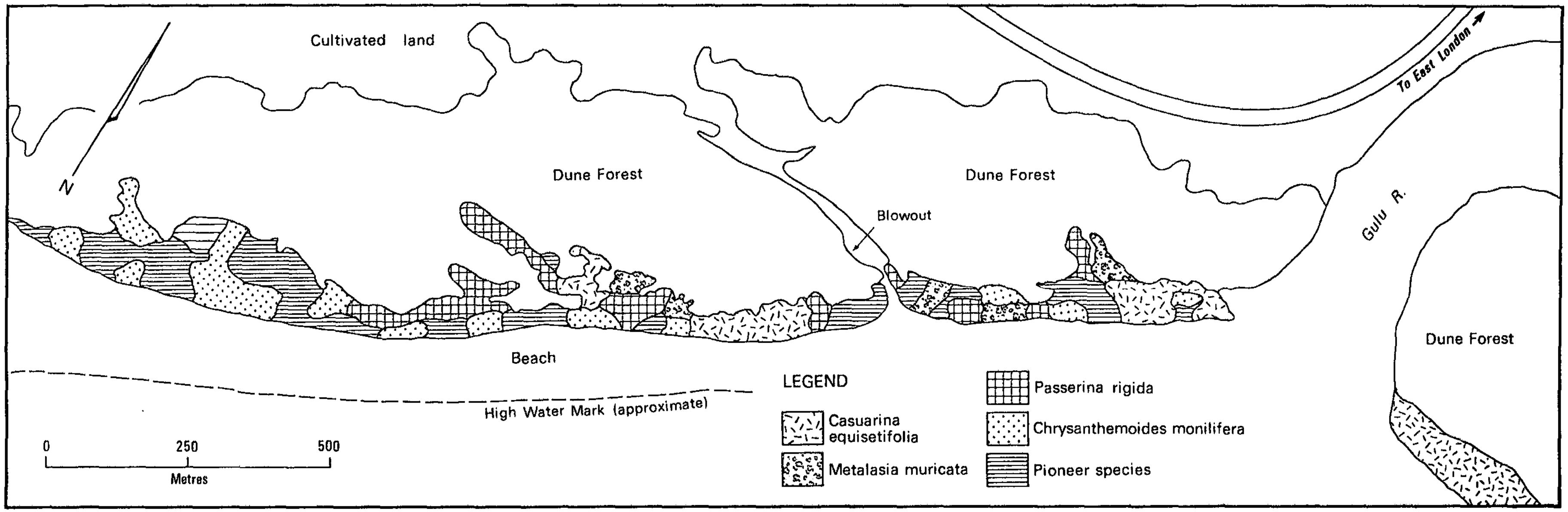


Figure 8.3 Map showing the vegetation of the Gulu East and West stabilization sites. Note the patches of *Casuarina equisetifolia*.

Plate 8.5 Five year old portion of Gulu West, with sparse cover, except for *Chrysanthemoides monilifera* (foreground) which was planted along the edge of this site to create a foredune.

Plate 8.6 The oldest portion of Gulu West, dominated by woody species such as *Passerina rigida* and *Chrysanthemoides monilifera*. The alien, *Acacia cyclops* is also common, as are stands of *Casuarina equisetifolia* (background).

The use of *C. equisetifolia* at this site, a species used extensively on the Natal coast (Chapter 7), raises a number of interesting points. *Casuarina* patches are distinct from those planted with indigenous vegetation, and have a species diversity of less than half that of the latter areas (Avis 1985). Their rapid growth rate; ability to rapidly utilise available nutrients; production of dense, fibrous roots covering several square metres of soil around each tree (Chapter 7); and copious leaf litter with an allelopathic effect on most other species results in competitive exclusion. The only species which appeared able to survive was the composite, *Senecio litorosus*. Thus, despite being non-invasive this alien species is not suitable for dune stabilization as, unlike *Ammophila arenaria*, it persists and will need to be physically removed to enable indigenous species to become established.

Mtati Site

The Mtati, Old Woman's River and Fish Point/Clayton Rocks sites experience a similar climate (Fig. 8.1). Mean annual precipitation is less than that experience at East London, and bimodal, with late spring (October) and autumn (March) months receiving a greater amount of precipitation. There are also short dry periods in August and January, but temperature is similar to that found further east. Winds generally blow parallel to the shore, with easterly winds more common in summer, and westerly winds more common in winter (Fig. 8.1; Chapters 1 & 2; Daines 1991).

The Mtati Site is located 5 km east of the Mpekweni River, and stretches for about 1 km until the Mtati River. It is 57 hectares in extent and over 200 m wide in places. Both buttress barchanoid and transverse dunes are found, and the seaward side is about 200 m from the high tide mark (Plate 8.7). The area was stabilized to prevent sand blowing over the high relic foredune, covered with Dune Thicket, onto the coastal road (R72) which was sited too close to the dunes. It was 8 years old at the time of sampling, and the sand had average pH and organic matter content values, and fairly low conductivity (Table 8.3).

Stabilization was initiated with the packing of a 4 ha area with brushwood and planting *Acacia cyclops* and *Eucalyptus gomphocephela*. Thereafter, mainly indigenous species were used, but the latter species and *Casuarina equisetifolia* were also planted periodically (Table 8.2). A total of 37 species were recorded, but Simpson's diversity was slightly below average. Total mean cover is fairly high for an 8 year old area, but total mean density is low (Table 8.3). *Ehrharta villosa* and *Stoebe plumosa* are distinctly dominant, as these species were sown and planted extensively at this site, where they have become well established. Other common shrubs besides *S. plumosa* include *Passerina rigida* and *Myrica cordifolia* (Table 8.3; Plate 8.7).

Table 8.3 Edaphic and floristic properties at 17 stabilization sites sampled from the east (left of table) to the west (see Fig. 8.1) (Note that soil data at Alexandria B5 and B6 and Paardekloof is lacking) Floristic data are presented as the importance value of the 5 most common species (dominants) at each site. Life form is also shown. F: forbs; C: creeper or vines; S: Shrubs; G: grasses; R: rushes and sedges; T: trees.

STABILIZATION SITE	Morgan's	Bay	Cintsa	Glen	Blue	Gulu	Gulu	Mtati	Old	Woman's	River	Fish	Clayton	Paarde-kloof	Alex		Sunday's
	New 1	Old 2	3	Eden 4	Bend 5	East 6	West 7	8	East 9	Mid 10	West 11	Point 12	Rocks 13		B5	B6	River Mouth
Size (hectares)	1.3	1.2	1.0	3	5	?	?	57	6.2	7.5	?	134		40	16.5		12
Sample size	60	45	20	17	40	154	270	404	70	191	150	400	420	245	160	150	55
Year started	1982	1970	1978	1973	1980	1965	1965	1977	1968	1968	1968	1968	1968	1977	1978	1978	1981
Age (time of sampling)	2	15	17	12	5	20	20	8	17	17	17	17	17	8	7	7	4
Mean pH ± S.E.	8,99 0,064	8,88 0,131	9,05 0,003	-	9,15 0,036	7,91 0,091	7,90 0,062	7,96 0,055	7,96 0,005	7,53 0,085	7,78 0,170	7,95 0,085	7,61 0,15	-	-	-	8,04 0,108
Mean conductivity µS cm^{-1} ± S.E.	128,33 13,5	136,33 6,69	132,3 15,38	-	116,0 2,27	85,12 5,99	104,52 8,42	82,85 4,04	98,0 15,4	133,0 31,0	145,5 9,1	102,63 8,36	134,2 23,9	-	-	-	166,6 39,7
% Organic matter	0,58	0,97	0,93	-	0,41	0,97	1,01	0,97	0,96	0,93	0,89	0,97	1,12	-	-	-	1,1
Species richness	17	34	6	22	19	33	37	37	23	31	32	40	40	35	42	21	15
Simpson's diversity	0,871	0,912	0,696	0,925	0,843	0,902	0,915	0,814	0,628	0,872	0,910	0,822	0,889	0,831	0,810	0,622	0,846
Simpson's dominance	0,128	0,087	0,304	0,075	0,157	0,098	0,085	0,186	0,372	0,128	0,089	0,178	0,111	0,169	0,190	0,378	0,153
Total Mean % cover	8,08	52,24	36,9	51,6	19,1	27,0	34,3	18,46	14,52	12,46	13,51	25,23	22,64	21,91	17,01	16,58	12,55
Total Mean density	5,72	11,21	3,44	6,98	8,57	3,70	4,05	3,81	5,01	4,00	3,95	3,36	3,63	6,95	4,78	7,08	5,71
SPECIES IV SCORE *Ehrharta villosa* (G)						28		67	103	37		58	21	52	60	42	
Passerina rigida (S)		24	51			41	48	18	57		27						
Chrysanthemoides monilifera S			142		40		28		32		37			31		32	
Stoebe plumosa (S)								62		41		35	36	29	21		
Silene primuliflora (F)								19	15		25			36	23	105	
Helichrysum praecinctum (F)					58					29				43	29		42
Carpobrotus edulis (C)	52	24			29					26	45						
Metalasia muricata (S)		25				25	25						20				
Senecio litorosus (F)						28	27								41	21	
Myrica cordifolia (S)								21				31	22				37
Casuarina equisetifolia (T)				21		30	42										
Cynanchum natalitium (C)	34		68		25												
Gazania rigens (F)	39																41
Ficinia aphylla (G)		37															42
Rhus crenata (S)					25							20					
Polycarena cuneifolia (F)									17	23							
Mariscus congestus (G)	40																
Senecio elegans (F)	32																
Anthospernum littoreum (F)		28															
Brachylaena discolor (T)			11														
Ipomeae pes-caprae (C)			8														
Stenotaphrum secundatum (G)				63													
Rhoicissus digitata (C)				39													
Oplisminus hirtillus (F)				34													
Digitaria eriantha (G)				21													
Heteroptilis suffructicosa (F)											27						
Stipagrostis zeyheri (G)												34					
Scirpus nodosus (R)													20				
Ammophila arenaria (G)																22	
Helichrysum argenteum (F)																	46

The Old Woman's River Sites

Three sites were stabilized a few kilometres east of the Great Fish River, close to a stream known as Old Woman's River (Fig. 8.1). All have steep slopes with active blowouts and buttress barchanoid dunes at the base (Table 8.1), and were stabilized due to the apparent threat they posed to adjoining farm lands. Stabilization was initiated in 1968, by packing areas with brushwood and sowing *Acacia cyclops* seeds. Later seedlings were planted and only recently were indigenous seeds and seedlings used (Table 8.2). Soil pH, organic matter and conductivity values are similar to other sites of comparative age, but species diversity differed, being significantly lower at Old Woman's River East (Table 8.3). This is due to the overall dominance by Pipegrass (*Ehrharta villosa*), which must have been used extensively. Simpson's dominance is therefore highests for this site, and species richness lowest. Total mean cover and density values are relatively low considering the age of these sites. However, as only indigenous vegetation was sampled it is likely that these areas are younger, as early stabilization made use of alien species (Table 8.2). Furthermore, active sand movement was still occurring, as many plants had been buried by sand.

Other common species at Old Woman's River East include the shrubs, *Passerina rigida* and *Chrysanthemoides monilifera*, and herbaceous species such as *Silene primuliflora*. The middle area is dominated by *Stoebe plumosa*, with *Ehrharta villosa* and *Helichrysum praecinctum* common. The west site is dominated by *Carpobrotus edulis* and *C. monilifera*, but *P. rigida* and *S. primuliflora* are also common. *Gazania rigens* was only recorded at Old Woman's River West, where it had an importance value of 12.4. Its failure to dominate, despite so many seedlings being planted (35 256, Table 8.2) indicates that it is not a very suitable species.

Most of Old Woman's River West, which is a typical site in this area, is covered by pioneer species, mainly *Carpobrotus edulis* (Fig. 8.4). These areas are sparse and many quadrats contained no species. Woody species mainly occur in areas closest to the indigenous thicket, with *C. monilifera* either occurring together with *P. rigida* or *Stoebe plumosa*. The latter species was most common in an area sheltered by a patch of indigenous vegetation (Fig. 8.4). The tops of both parabolic blowouts were sparsely covered with pioneer species, due to active sand movement.

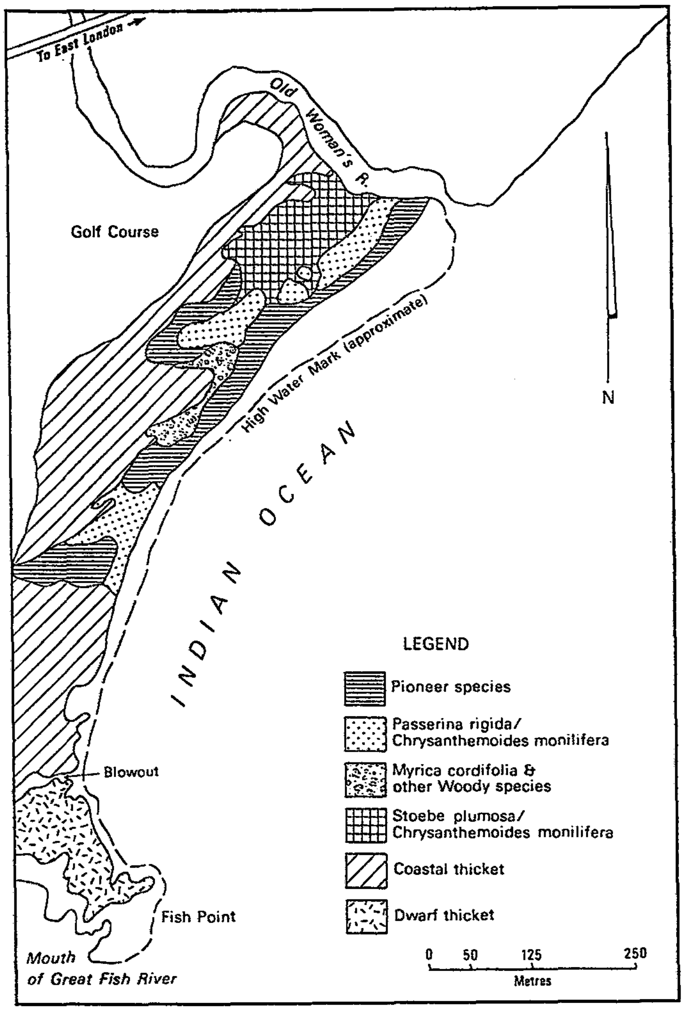


Figure 8.4 Map showing the vegetation of the Old Woman's River West site.

Fish Point and Clayton Rocks

These sites are located a few kilometres west of the Great Fish River (Fig. 8.1), and stabilization was initiated separately in 1968. However, at the time of sampling the two 17 year old sites had joined together to form one large stabilization area of 134 hectares in extent. This large scale programme was initiated to prevent blowouts from encroaching onto adjacent agricultural land. It was thought that this would be successful only if the extensive transverse, reversing and buttress barchanoid dunes were stabilized, thus trapping the supply of sand to the blowouts, which are orientated parallel to the coast due to the angle of the onshore winds (Daines 1991).

Soil pH, organic matter content and conductivity are comparable to other sites. Species richness for the two areas is identical, but Simpson's diversity is lower at Fish Point, due to the dominance of *Ehrharta villosa* (Table 8.3). Total mean cover is higher than the Old Woman's River sites, which are of comparable age; but total mean density is less, indicating that fewer larger plants occur, owing to the fact that indigenous species were planted when stabilization was first initiated (Table 8.2). The invasive species which had been planted earlier were cleared in 1980, except for *Casuarina equisetifolia*.

The Fish Point site is dominated by the grasses, *E. villosa* and *Stipagrostis zeyheri*, as well as the shrubs *Stoebe plumosa* and *Myrica cordifolia*. These shrubs, as well as *Metalasia muricata* and *E. villosa* dominate the Clayton Rocks area (Table 8.3). The abundance of the sedge, *Scirpus nodosus* is due to the presence of a large slack in the western portion of the Clayton Rocks area.

Alexandria Compartments B7 & B8 - Paardekloof

No large areas stabilized with indigenous vegetation are found between the previous site and the Bushman's River (Fig. 8.1). However, west of this area, a large number of sites occur in the Alexandria dunefield, and a total of 41 areas were earmarked for stabilization during the 10 year period from 1980 (Stehle 1980). Many of these were not stabilized due to policy changes and financial constraints, and only four sites were sampled (Fig. 8.1). They are all exposed to similar climatic conditions with the lowest mean annual precipitation and lowest number of days with greater than 10 mm rainfall recorded for this area of the coastline. The mean annual diurnal range in temperature is also less, and temperatures are warmer in summer, when a definite dry season occurs (Fig. 8.1). Winds are similar to those experienced at Port Elizabeth, and result in a net westerly movement of sand.

The Paardekloof area is situated east of Woody Cape, closer to Cape Padrone than compartments B5 & B6 (Fig. 8.1). It is a large area of 40 hectares in extent, with a wide dunefield dominated by transverse and barchanoid dunes, and was 8 years old at the time of sampling. However, more activity took place in 1980 (Table 8.2), and most of the area was probably 5 to 6 years old. Initially two areas were stabilized separately, but these eventually joined together as stabilization progressed. The area has a relatively high species richness and Simpson's diversity, and total mean cover and density are also high (Table 8.3), despite the lower rainfall in this area (Fig. 8.1). The success achieved at this site is most likely due to the extra work that was put into stabilizing these areas, in order to meet the goals set in the management plan of Stehle (1980).

The area is dominated by (*Ehrharta villosa*), which grows well in shifting sand and contributes significantly to the high density and cover values recorded. The herbs, *Helichrysum praecinctum* and *Silene primuliflora* are also common, as both do well in exposed areas. The most abundant shrubs are *Stoebe plumosa* and *Chrysanthemoides monilifera* (Table 8.3; Plate 8.8).

Plate 8.7 View looking west towards Fish Point of the Mtati stabilization site. The dominant cover is the grass, *Ehrharta villosa*, and shrubs are mainly *Passerina rigida* and *Stoebe plumosa*. Note the small blowout on the top of the dune ridge (right background).

Plate 8.8 Paardekloof site on the Alexandria coast, dominated by *Ehrharta villosa* and *Stoebe plumosa*.

Alexandria Compartments B5 & B6

These two areas are located less than 1 km west of Paardekloof (Fig. 8.1), and were large parabolic dunes stabilized to prevent sand encroaching onto adjoining farmland. Although only 7 years old, they have a high total mean cover and density, which is very similar for both areas (Table 8.3). However, species richness and Simpson's diversity is far greater in area B5 than B6, and the only explanation for this is that a greater variety of species must have been planted in the former area. This highlights the difficulties experienced when trying to make direct comparisons between sites. Area B6 also has a lower diversity due to the significant dominance by *Silene primuliflora*. Species composition is fairly similar, with *Ehrharta villosa*, *S. primuliflora* and *S. litorosus* being common to both. *Helichrysum praecinctum* is only important in B5, and *Chrysanthemoides monilifera* in B6 (Table 8.3; see Plate 7.4, pg 242). The latter area also contains a large amount of *Ammophila arenaria*, which was used to create an artificial foredune.

Sunday's River Mouth Slack

The majority of the Sunday's River site was stabilized with alien species, as described earlier (Chapter 7). These form dense thickets of *Acacia cyclops* and *Eucaplyptus gomphocephela*. However, the dune slack area immediately in front of the alien vegetation was stabilized with indigenous vegetation over 17 years ago. More recently (1981) the area immediately behind the artificial foredune was also stabilized (Table 8.2), and it is this area which was sampled. Despite the low rainfall, the dune slack has a water table close to the surface, and total mean cover and density are high for an area this young (Table 8.3). Species richness is low, but diversity is high as no single species dominates. Pioneer species such as *Gazania rigens* are common, as well as *Ficinia aphylla* which colonises dry slacks (Chapter 1). Other species include *Myrica cordifolia* and *Helichrysum praecinctum* and *H. argenteum*. In the older slack, *M. cordifolia* dominates and forms a dense cover.

CLASSIFICATION AND ORDINATION OF THE SITES

Multivariate analysis of the importance value data for all species in the 17 sites resulted in an objective classification (Fig. 8.5) and ordination (Fig. 8.6) of the stabilization sites. The first division separated sites 2 and 4, both with high diversity and cover values (Table 8.3). The Glen Eden site contains many ground cover species usually associated with forests, and the Morgan Bay Old area is dominated by woody shrubs and trees which were not common elsewhere. The second division separated the three sites found north east of the Buffalo River (sites 1, 3 & 5) into a distinct group (Fig. 8.5). All are of similar age, but the diversity and species richness of the Cintsa site is lower, whereas cover is higher (Table 8.3). Nevertheless, species composition is similar as the areas are exposed to the same climatic regime and were stabilized by the same forester using similar techniques.

The sites found in the Alexandria area near Woody Cape (Fig. 8.1; sites 14 to 17) were separated into a distinct group at the third level of division. Sites in this group do not have similar diversity and species richness values, despite being of comparable age and having similar cover values (Table 8.3). Again they are grouped according to their species composition, which is similar, with species such as *Ehrharta villosa, Silene primuliflora* and *Helichrysum praecinctum* being common.

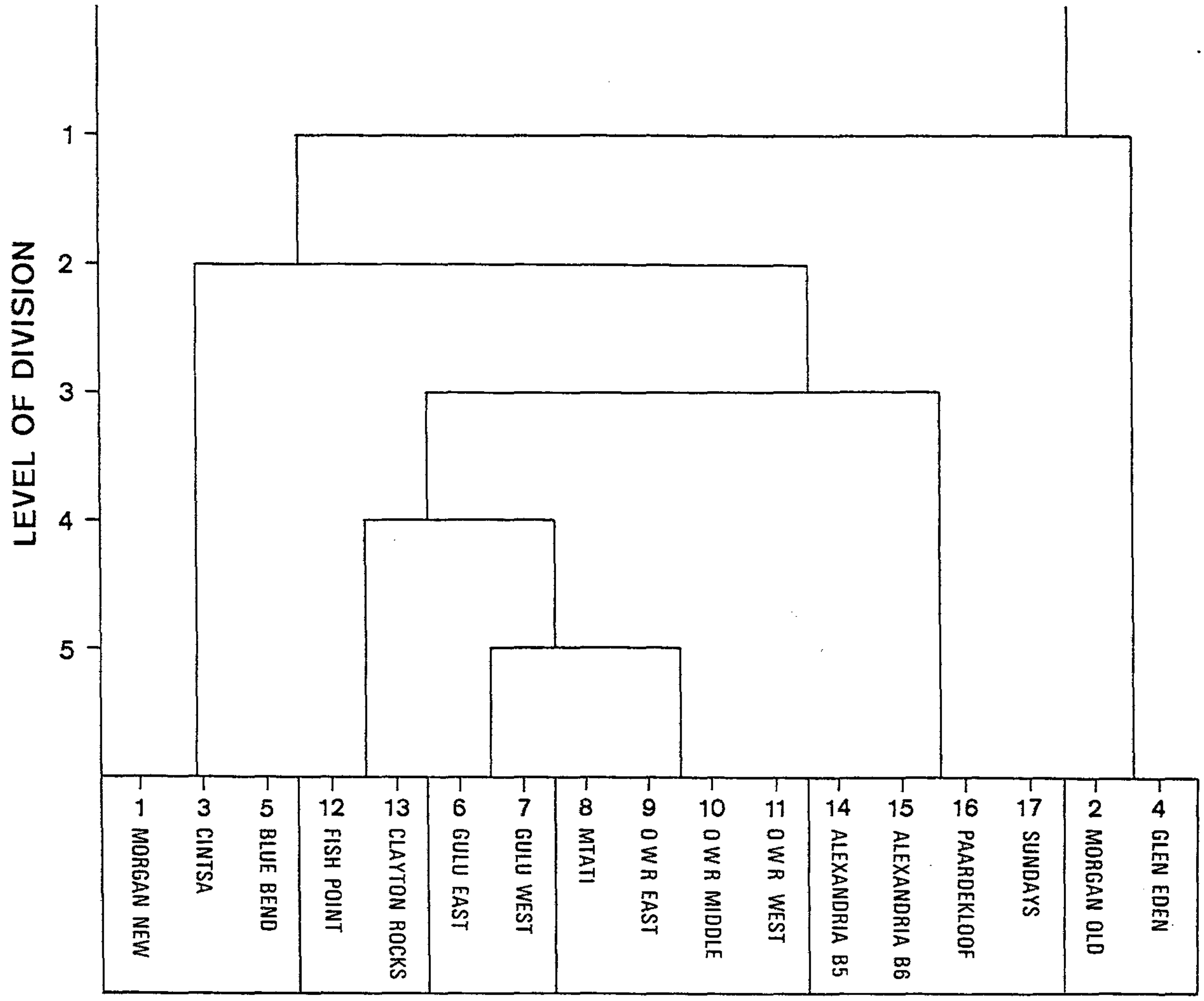


Figure 8.5 Dendrogram showing the classification of the 17 stabilization sites, based on floristic composition.

Level 4 separated Clayton Rocks and Fish Point from the remaining sites. Species richness and total mean cover are high, but total mean density is relatively low (Table 8.3). These two sites share a number of common species, but the importance value of species usually common in other sites , such as *Carpobrotus edulis* and *Passerina rigida* is low. The final two groups were separated at the fifth level of division. The Gulu sites have a predominance of *Casuarina equisetifolia* and *Senecio litorosus*, both uncommon in most other areas. Species richness, diversity and density values are similar for these groups, but the Old Woman's River and Mtati sites have a lower total mean cover and are dominated by *Ehrharta villosa*.

It is important to note that most of the groups defined by TWINSPAN consist of sites found in similar localities, rather than scattered along the coastline. This observation was more clear when the sites were ordinated using DECORANA (Fig. 8.6), where it appeared that axis 1 corresponded to the position of sites along the coastline rather than other factors, such as age, percentage cover or size. Most of the sites north-east of East London are found to the right on axis 1, but appear to be more scattered than those to the left. This may indicate a greater variability between these sites, which range from those dominated by woody or forests species (Glen Eden & Morgan Bay Old) to those dominated by pioneer species (Blue Bend & Morgan Bay New).

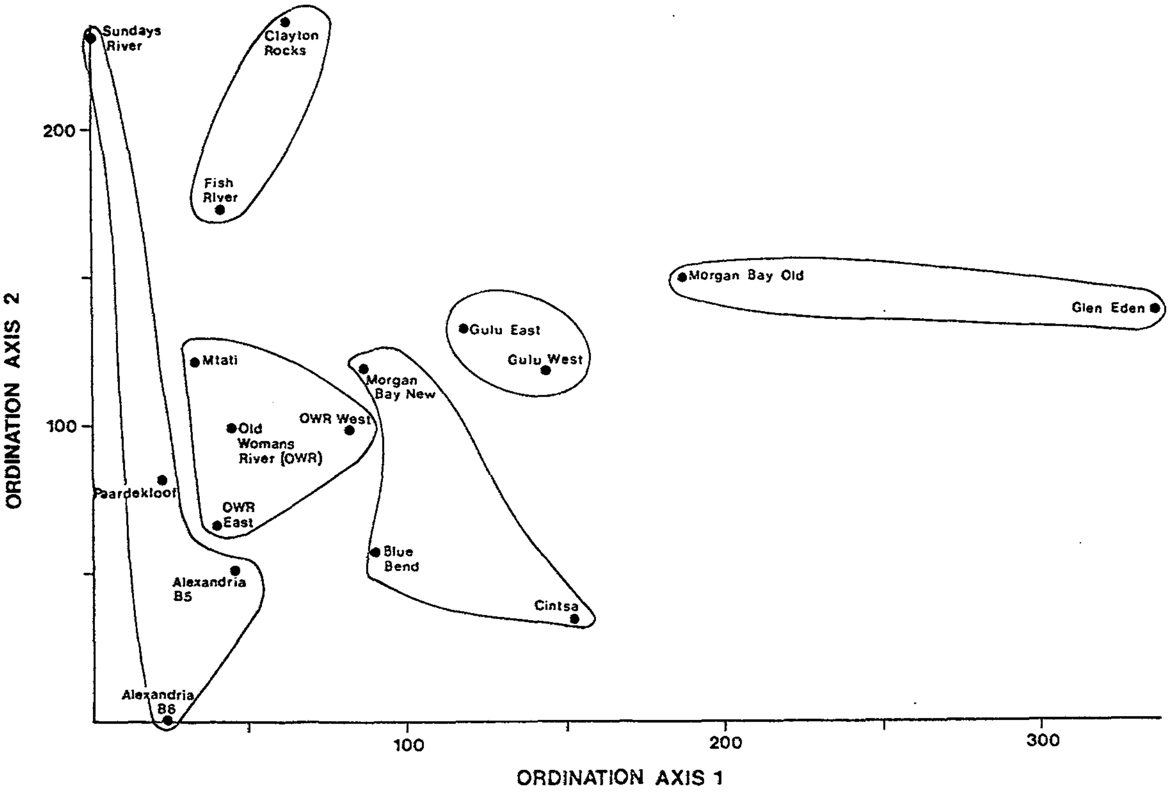


Figure 8.6 Ordination of the 17 stabilization sites using DECORANA, showing sites grouped on the basis of the TWINSPAN classification (Figure 8.5).

However, west of the Keiskamma River, sites are more closely grouped along axis 1 (Fig. 8.6), despite the fact that they are spread over a greater length of coastline (Fig. 8.1). It therefore appears that, although differences in species composition accounts for much of the variability along axis 1, these differences are not related to the natural distribution of the indigenous dune vegetation, as noted in Chapter One. Rather, it is more dependent on the types of species which were planted at the various sites. This is supported by the greater difference noted along axis 2 for sites in the Alexandria and Bathurst region, which is related to species composition. The Clayton Rocks and Sunday's River sites both contain typical dune slack species, whereas Alexandria B5 and B6 and Old Woman's River East contain species more typical of the larger stabilization areas (*Ehrharta villosa* & *Silene primuliflora*), despite the fact that they are geographically distinct (Fig. 8.1).

This anthropogenic effect complicates the data, thereby making interpretation more complex, particularly since records at each site are not very detailed (Table 8.2). Other factors which may affect the position of sites in the ordination include total percentage cover and diversity, as both factors appear to increase slightly from left to right, but these changes are not very marked. Unfortunately, the gradients controlling axes 1 and 2 are too complex to elucidate, due to the variation in species used in the stabilization processes. This is compounded by the complexity of the natural dune vegetation in this region, as discussed in Chapter One.

The ordination of the species groups defined by TWINSPAN is also not very clear (Fig. 8.7). However, there appears to be a gradient along axis 1, with less common species usually associated with thickets or well wooded areas on the right. Groups of common forbs and pioneer species are found on the left, and shrubs occur between these groups and the thicket species (Fig. 8.7). The large group on the extreme left consists of a mixture of shrubs, less common forbs and mesic species usually associated with dune slacks. Axis 1 suggests a vague successional gradient from left to right, of species usually associated with the early stages of succession, to those found in thicket communities, as noted in Chapters Two and Four. A further point worth noting is that both *Casuarina equisetifolia* and *Senecio litorosus* are outliers which do not fall into any group. These two species are usually closely associated, as the latter is one of the only indigenous plants capable of growing in the copious leaf litter of *Casuarina* trees, for example at Gulu East and West (Table 8.3). Consequently, this close association has resulted in these species being isolated from other species groups. The variation along axis 1 and 2 may also be related to the range of habitats, or in this study, the number of stabilization sites in which particular species occur. Species found outside the bold line of Figure 8.7 are restricted to a few stabilization sites, whereas species found within the bold line are widespread and more commonly used for dune stabilization.

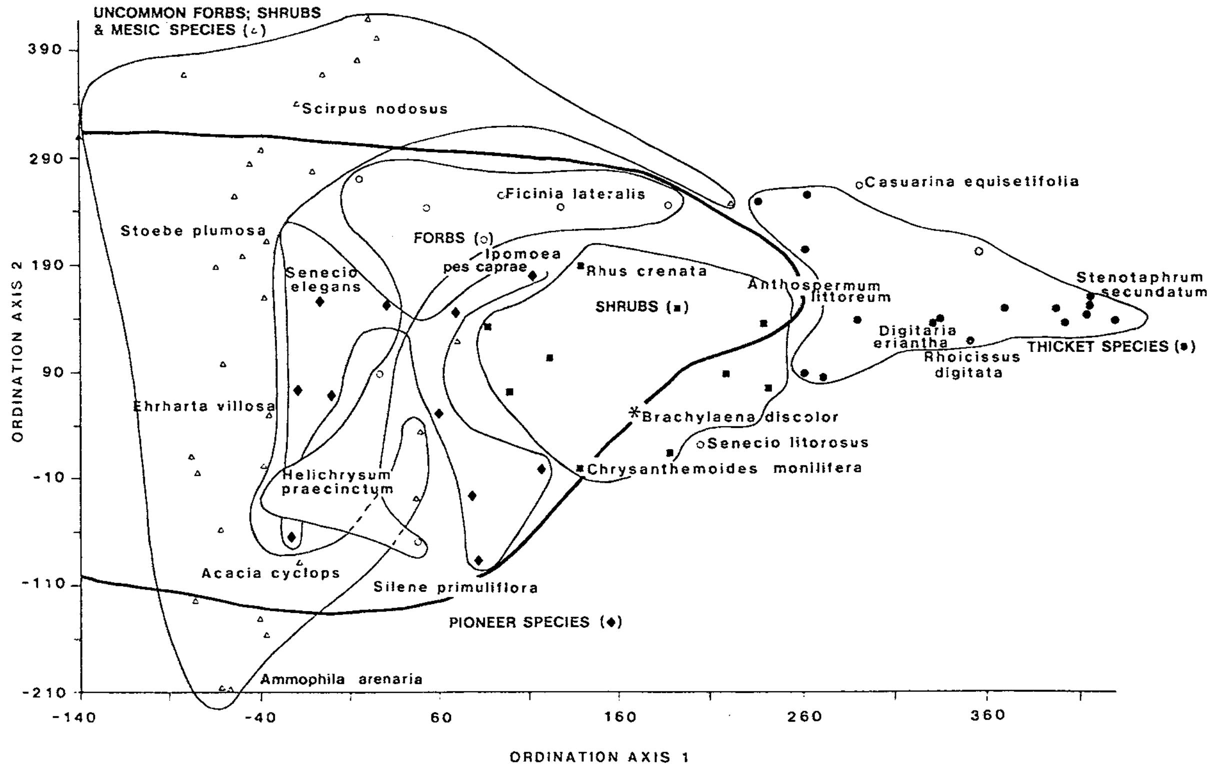


Figure 8.7 Ordination of the species recorded in all stabilization sites, using DECORANA. Species are also grouped on the basis of the TWINSPAN classification. Species within the bold line are those more commonly used for dune stabilization.

This is shown more clearly in Table 8.4, which summarises the importance values of all species in 12 sites. Those common to most sites correspond to the groups found within the bold line of Figure 8.7, and are clearly the most suitable species to use for dune stabilization along this stretch of the coastline.

DISCUSSION

TEMPORARY STABILIZATION OF THE DUNE SURFACE

The historical development of the techniques used for dune stabilization in South Africa have already been discussed (Chapter 7). The basic principle of temporarily stabilizing the sand by packing it with brushwood or some other medium before planting or seeding, has been used successfully in many parts of the world, and the Sellery *et al.* (1983) study highlighted the importance of this stage in the stabilization process.

In South Africa, the area to be stabilized is covered with brushwood, at a density of about 650 m^3/ha, as field trials have revealed this to be a most successful technique (Stehle 1981). Marram grass is seldom used today to create an artifical dune litorale, whereas in Denmark (Skarregaard 1989), the Netherlands (Adriani & Terwindt 1974), parts of the USA (Jagschitz & Bell 1966) and New Zealand (Wendelken 1974) it is extensively used and often planted over the entire area to be stabilized. Its usefulness as a sand binder has been studied in detail by, *inter alia*, van der Putten *et al.* (1988), Adriani & Terwindt (1974) and Maun (1984). Areas planted with marram become invaded by other indigenous species, as the marram dies when sand stabilizes (Hewitt 1970). This may be the result of its intolerance to harmful soil bacteria (van der Putten *et al.* 1988), or soil fungi and nematodes, the latter becoming pathenogenic in stable sands (van der Putten & Troelstra 1990). It is quite possible that a similar situation exists with *Ehrharta villosa*, which grows well in mobile sands protected from salt laden winds, but becomes depauperate when sands begin to stabilize. Its dominance at many sites (Table 8.3) may therefore indicate that sands are still mobile enough for it to survive. The autecology of this species is the subject of more detailed studies, which do not form part of this thesis (Lubke, R.A. and others, in progress).

Many other techniques to temporarily stabilize the sand surface, besides the use of brushwood and Marram grass, exist. In Sicily (Le Roux 1976) and Iraq (Dougrameji & Kaul 1972) *Phragmites* reeds are placed in rows or blocks as wind breaks. In the west Sahara, 2.5 tons of fuel oil is sprayed per hectare, and windbreaks constructed at intervals. This unusual technique has proved successful, with natural vegetation establishing in the stabilized areas (Alvarez de Benito & le Roux 1976). The suitability of artificial liquid sprays as stabilizers was tested by Stanley & Watt (1990) in Australia, who showed that brush matting was superior in all tests. It also appears to be better than hay or grass mulch, as the highest seedling survival was recorded in brushwood packed areas, since the seedlings germinating in hay outcompeted the *Acacia* spp. used in this study (Craig 1985). Grass mulch is also subject to erosion and movement in strong winds, often collecting in dune hollows. In higher rainfall areas it is possible to temporarily stabilize the sand by sowing a cover crop of annual species which rapidly germinate, but die before they outcompete the perenial species which are slower to germinate (Camp & Weisser 1991).

The primary objective of temporarily stabilizing the sand surface is to arrest the flow of sand for a period long enough to allow seedlings or plants to become established. The density of brushwood packing is dependant on the amount of sand movement, which is affected by the strength of the prevailing winds and rainfall. In many cases it is only necessary to create windbreaks, which may be constructed using *Phragmites* reed, snow fences (Jagschitz & Bell 1966), rows of *Ammophila arenaria* (Ranwell & Boar 1986), brushwood (Stehle 1981), slab-wood waste (Wendelken 1974) slat fences (Davis 1975), Nylon shadecloth (Chapter 7) or any other suitable material. The area may also be packed in a checkerboard pattern with cuttings of woody species, but clearly the technique employed in South Africa is succesful and in line with those suggested by Skidmore (1986) for controlling wind erosion. Furthermore, the brushwood protects the young seedlings from wind erosion and desiccation, and provides nutrients as the wood decomposes. Although grass mulch is more effective in providing nutrients, it is less effective in protecting seedlings and stabilizing the surface (Craig 1985; Lubke, R.A. unpublished data). Nevertheless, brushwood is difficult and labour intensive to obtain, and hence costly, as well as being flammable and considered by some as unsightly (Stanley & Watt 1990)

FACTORS INFLUENCING SPECIES SELECTION AND ESTABLISHMENT

Since the policy of the Directorate of Forestry is to use only indigenous species (Cobby 1988), it is important to consider what factors may influence the selection and establishment of species in stabilization areas. The packing of brushwood creates a virtual flow boundry retarding flow between the sand surface and the top of the brushwood canopy, thus sheltering the seedlings in much the same way as an array of plants behave (Willets 1989). A net accretion of sand occurs if plant cover is greater than 15% (Middleton & Schimpf 1986). Thus, it is crucial to successful stabilization that a permanent vegetation cover be established, so that as sand is arrested plant growth continues, as plants play an important role in this process (Hesp 1989).

To achieve a good cover, Jagschitz & Bell (1966) found that broadcast seeding was less effective than transplanting mature clumps of grass. They provided details on how to plant beachgrass (predominantly *Ammophila* spp.) at Rhode Island. Restall (1964) and Wendelken (1974) reported on the development of a mechanical planter used for large scale planting of *Ammophila arenaria* to temporarily stabilize the dunes at Woodhill in New Zealand, before planting *Pinus* spp.

However, the planting of grass species such as marram will not provide a permanent plant cover, and it is therefore important to establish a diversity of species, particularly woody plants, so that a functional, self perpetuating ecosystem may be created. The importance of this concept in the field of restoration ecology has been stressed by Ewell (1990) and Bradshaw (1990). Similar ideals should also be striven for in the stabilization of dunes within sensitive and dynamic coastal systems. The more current research has been aimed at determining suitable species for sand binding (for example Jagschitz & Bell 1966; Adriani & Terwindt 1974; Maun 1984; Craig 1985; Ranwell & Boar 1986), rather than at the establishment of self-perpetuating ecosystems. This is mainly because the primary aim of dune building is to provide a soft engineering approach to the protection of beaches from factors such as storm damage and erosion (Mendelssohn *et al.* 1991); or to repair damage caused by the ever increasing recreational pressure placed on coastal systems (*inter alia* Davis 1975; Tinley 1985; Ranwell & Boar 1986). Nevertheless, since the aesthetic appeal of coastal areas has important economic benefits, stabilized areas should eventually be appealing and harmonious. This is the common objective of the Australia mining industry (Anon 1987b), and should also be the objective of coastal planners and managers. More research is therefore needed on ways of establishing a diverse flora, rather than simply binding the sand. It is also undesirable to use introduced plants on foredunes, as when present in large numbers the morphology of the foredune is changed and other coastal processes may be affected (Heyligers 1985).

Davis (1975) suggests dividing areas into zones on the basis of the natural vegetation, and then establishing suitable species in these zones. Floret *et al.* (1990) suggest that for larger areas factors such as climate, sand type and the substratum underlying the sand should also be considered. Sellery *et al.* (1983) investigated the establishment of vegetation in various zones, which had not been temporarily stabilized, using container grown plants. They found that the roots could not integrate into the moving sand and that windburn of foilage occured after two weeks. The technique was therefore unsuitable, but Dougrameji & Kaul (1972) suggested using "planting bricks" prepared from a mixture of sand, clay and manure, thus preventing plants becoming root bound and providing nutrients as the manure rots. This has been done successfully in Mississippi, where *Panicum amarum* was found to root readily in peat pellets (Eleuterius & Caldwell 1987). However, the use of fertilizer may reduce species diversity, as sand dune habitats are naturally low in nitrogen and phosphorus. Nevertheless, in the Netherlands, fertilizer (N80) improved the vegetative growth of sand dune species, with nitrogen being most important (Adriani & Terwindt 1974). The choice of fertilizer and application rate is critical as at high nitrogen levels, phosphorus may limit plant growth (Dougherty *et al.* 1990). Furthermore, fertilizer prevents Marram grass from producing flowers (Adriani & Terwindt 1974) and this failure to regenerate means that communities may not achieve sustainability (Ewel 1990). Lubke & Avis (1986b) showed that fertilizer lowered the number and variety of dune seedlings, possibly because it may be toxic at these early stages. Species establishment is also known to be limited by sand burial (Tyndall *et al.* 1986; Maun & Lapierre 1986) and erosion (Sellery *et al.* 1983). Clearly, methods to improve the success of establishing plants need to be sought.

Forster (1979) has shown that microbial aggregates were more important at stabilizing sand than either roots or debri on the edge of a foredune. Within the foredune, roots and associated micro-organisms were more important, but in the absence of roots, bacteria and their associated polysacharides played a major role in aggregating and stabilizing the sand prior to colonization by higher plants. Soil microfloral populations are known to respond to vegetation and physical dune characteristics (Rose 1988), and Logan *et al.* (1989) showed that 36 out of 41 dune species had vesicular-arbuscular mycorrhizal (VAM) fungi, which may assist in sandbinding. Dune soils are low in nutrients, subject to leaching and have poor water-holding capacities, making VAM important to plant survival as they release nutrients associated with cementing agents (Rose 1988). For this reason, mycorrhizal plants may be more successful in mobile sands. This is significant with respect to dune stabilization, as the application of fertilizer results in high phosphate levels (Dougherty *et al.* 1990), which tend to suppress mycorrhizal infection (Logan *et al.* 1989). Thus, it may be more worthwhile to innoculate sand binding species with VAM rather than adding inorganic fertilizers, as innoculation has been shown to increase the dry weight of dune grasses (Nicolson & Johnstone 1979 in Puppi & Riess 1987). Furthermore, Koské and Halvorson (1981) showed that VAM may be of considerable importance to the success of any sand dune stabilization programme, and the selection of suitable species should consider the mycorrhizal status of the plants and identify the native endophytes. More recently, Sylvia (1989) showed that the growth of sea oats *(Uniola paniculata)* on Florida beaches was greatly enhanced when seeds were innoculated with VAM. He concluded that innoculated sea oats were better adapted for growth in beach sand. This is possibly due to its improved ability to take up nutrients, a property especially valuable for plant growth in nutrient-poor dune soils (Koské & Polson 1984).

A further factor influencing species selection and establishment is the need to identify the soil forming processes, which is necessary if we wish to understand the prerequisites for the development of a certain vegetation community at a certain position in the landscape (Mücher 1990). More importantly, species common in the surrounding area should be selected as they will blend in with the local landscape and be more adapted to prevailing climatic and environmental factors. It is also important to know the species preferred habitat, and the dominant pathway of succession, which has now been elucidated for this area of coastline (see Chapters 2 & 4). Many of these factors were used to select suitable species for dune stabilization along the Eastern Cape coastline by Stehle (1981) and Lubke & Avis (1986a). However, most of this selection was done on an ad hoc basis (Table 8.2), and no experimental studies have been undertaken to determine which species are most successful, and the factors responsible for this success.

SUITABILITY OF INDIGENOUS SPECIES USED IN SOUTH AFRICA

A comparison of the natural distribution and abundance of indigenous dune flora (Chapter 1) with those most abundant in stabilization sites should provide clues as to which species are most suitable. Figure 1.4 (see pg 34) shows that the more common foredune or pioneer species with wide distributions are *Sporobolus virginicus* and *Scaevola plumieri*, but they have not been used extensively in dune stabilization. The pioneer species of stabilization sites are not very common on foredunes (Table 8.4) and this is probably because species such as *Carpobrotus edulis* and *Silene primuliflora* are easy to propogate by means of cuttings or seeding. Others, such as *Rhyncosia carribea* and *Cynanchum natalitium* are creepers which rapidly spread over the brushwood. The latter is a fairly widespread species common along forest margins (see Fig. 1.4, pg 24). *Zaluzianskya maritima* and *Anthospernum littoreum* probably also invade the temporarily stabilized area by seed, which should be sown in the early stages of the stabilization programme to bind the sand further.

Of the grasses *Ehrharta villosa* is a most suitable species for dune stabilization, and its distribution in stabilization sites (Table 8.4) corresponds to its natural distribution (Fig. 1.4). *Stipagrostis zeyheri* is common in stabilization sites towards the west, and occurs naturally in bushclumps and coastal grasslands (see Chapters 1 & 4). *Pentaschistis heptamera* was fairly common in sites around the Fish River (Table 8.4) despite being noted infrequently in most habitats (see Appendix 1.1). Both these species should therefore be used more frequently.

Species found in dune slacks and widely distributed along the coast (see Fig. 1.4) were common in most stabilization sites, with herbs such as *Helichrysum praecinctum* and *Senecio litorosus*, and the sedge *Ficinia lateralis*, dominating a number of sites (Table 8.4). Most of these species were not planted or seeded and have invaded the areas naturally, being able to do so due to the presence of an adequate seed bank. Clearly, the seeding or planting of the above species, as well as a number of the other *Helichrysum* spp., will increase the initial cover. This will facilitate invasion by secondary species into the more stable environment. The more typical slack species, such as *Scirpus nodosus*, should only be established if dune slacks occur in the area to be stabilized.

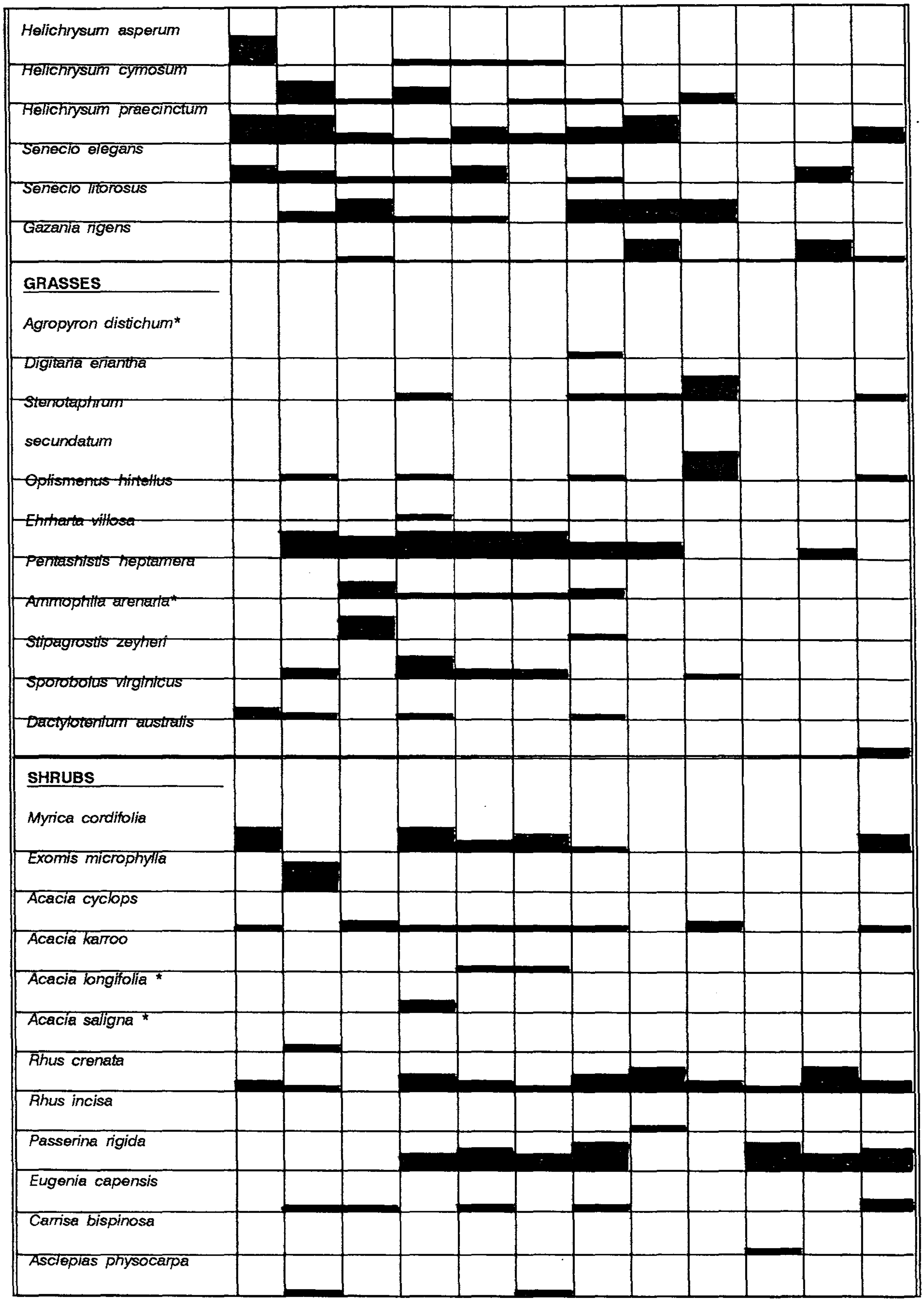
Myrica cordifolia, Rhus crenata, Stoebe plumosa, Metalasia muricata and *Chrysanthemoides monilifera* are all woody species which have been used extensively with a large degree of success (Table 8.4). The former and *S. plumosa* are naturally more common west of East London (Fig. 1.4, Chapter 1) and have become well established in stabilization sites in these areas. The other three species, as well as *Brachylaena discolor* and *Eugenia capensis* also seem suitable, although the latter two have a more subtropical distribution (Fig. 1.4). *Passerina rigida* is also suitable, but despite having a widespread distribution, it has only been used east of Fish Point (Table 8.4). It is wise to establish these species early in the stabilization programme, as natural succession towards Dune Thicket progresses along a similar pathway, and these species were the first woody shrubs to invade the dune slack at Kleinemonde (see Figs. 2.6 & 2.9, pgs 79 & 86). The planting of these species at an early stage is in line with the suggestion that the natural process of succession should be copied (Davis 1975; Stehle 1981; Sellery *et al.* 1983; Avis 1986). This is feasible as the main mechanism of succession follows the facilitation pathway (*vide* Connell & Slatyer 1977; Chapters 3 & 4) and much of this "facilitation" has already taken place as the sand has been temporarily stabilized by brushwood packing and fences. Although the soil properties do not seem to have altered (Table 8.3), the reduction in sand movement, and protection from sand abrasion and salt spray is adequate to allow these secondary species (many of which are key species in succession along this coast - Chapter 4) to survive. However, thicket and forest species can only survive in the older sites

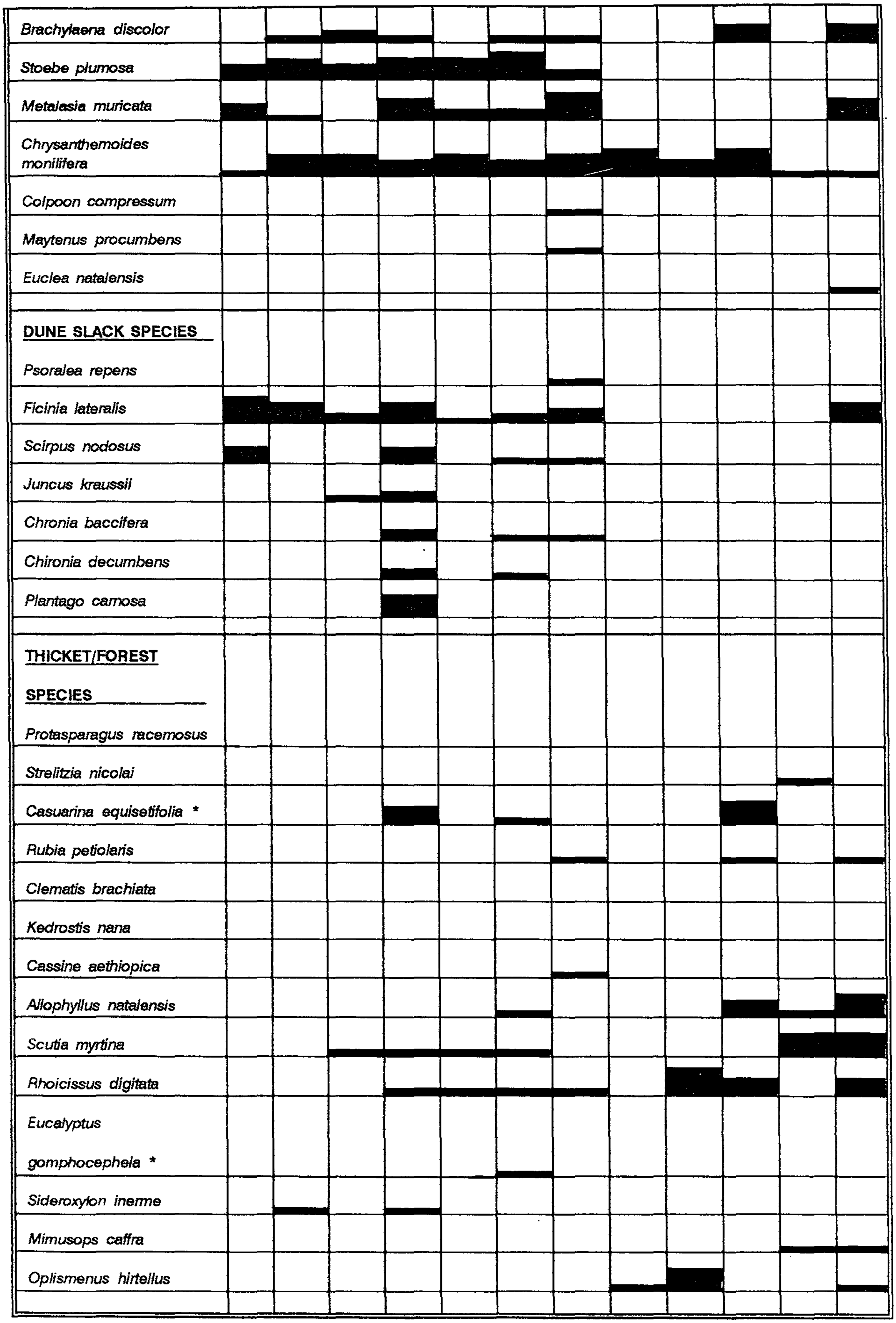
(Table 8.4), except for alien species which are able to colonize available niches at the expense of the indigenous flora (see Chapter 7 & Avis 1985).

Table 8.4 The importance values of all species recorded in 12 stabilization sites (Averages have been taken for the Gulu, Old Womans River and Alexandria B5 & B6 sites. The asterix (*) indicates alien species) Importance values have been summarised into the following 5 classes:

>40	20-39	10-19	5-9	<5
█	▆	▄	▃	▁

PIONEER SPECIES	Sunday's River Mouth	Paardekloof	Alexandria	Clayton / Fish	Old Woman's River	Mtati	Gulu	Blue Bend	Glen Eden	Cintsa	Morgan's Bay New	Morgan's Bay Old
Mariscus congestus				▁	▁	▁	▁				▆	▁
Gladiolus gueinzii								▆				
Tetragonia decumbens				▁	▁					▃		
Carpobrotus edulis		▁		▁	▆	▁	▁	█	▁		▆	▄
Mesembryanthemum atonis									▃			
Silene primuliflora	█	▆		▃	▄	▄	▁	▆			▆	▁
Crassula nudicaulus								▁				
Rhyncosia carribaea		▁		▁	▁	▁		▁				
Tephrosia capensis	█											
Geranium incanum		▁										
Ricinus communis		▁										
Phylica litoralis		▁		▁								
Heteroptilis suffructicosa					▄	▁		▄		▁	▁	
Cynanchum natalitium		▁		▁	▃	▁	▁	▆	▃	█	▆	▁
Sarcostemma viminale				▁								
Ipomoea pes caprae				▁	▁	▁	▄			▄	▄	
Solanum americanum		▁										
Zaluzianskya maritima		▁		▁	▃	▃	▁		▃			▁
Polycarena cuneifolia		▁				▁						▁
Hebenstretia cordata												▄
Justicia capensis					▁							▃
Anthospemum littoreum					▁	▁	▁		▄			▆
Scaevola plumieri					▁		▁				▁	
Felicia echinata		▁	▁	▁	▁	▁						
Conyza pinnatifida	▃			▁								


Helichrysum asperum
Helichrysum cymosum
Helichrysum praecinctum
Senecio elegans
Senecio litorosus
Gazania rigens
GRASSES
Agropyron distichum*
Digitaria eriantha
Stenotaphrum secundatum
Oplismenus hirtellus
Ehrharta villosa
Pentashistis heptamera
Ammophila arenaria*
Stipagrostis zeyheri
Sporobolus virginicus
Dactylotenium australis
SHRUBS
Myrica cordifolia
Exomis microphylla
Acacia cyclops
Acacia karroo
Acacia longifolia *
Acacia saligna *
Rhus crenata
Rhus incisa
Passerina rigida
Eugenia capensis
Carrisa bispinosa
Asclepias physocarpa


Brachylaena discolor
Stoebe plumosa
Metalasia muricata
Chrysanthemoides monilifera
Colpoon compressum
Maytenus procumbens
Euclea natalensis
DUNE SLACK SPECIES
Psoralea repens
Ficinia lateralis
Scirpus nodosus
Juncus kraussii
Chronia baccifera
Chironia decumbens
Plantago carnosa
THICKET/FOREST SPECIES
Protasparagus racemosus
Strelitzia nicolai
Casuarina equisetifolia *
Rubia petiolaris
Clematis brachiata
Kedrostis nana
Cassine aethiopica
Allophyllus natalensis
Scutia myrtina
Rhoicissus digitata
Eucalyptus gomphocephela *
Sideroxylon inerme
Mimusops caffra
Oplismenus hirtellus

The use of a variety of indigenous species for dune stabilization has been successful in most cases, as evidenced by long term studies of a stabilization site at Kleinemonde (Lubke 1983 & unpublished). However, ongoing maintenance is often necessary to prevent the areas being inundated with sand, and it is important to limit pedestrian and vehicle use within stabilized areas, as the young, vegetative shoots are very vulnerable to damage from trampling (Pizzey 1975; Chapter 6). The process is, however, slow when compared to higher rainfall areas such as Natal (Camp & Weisser 1991; Lubke *et al.* 1992). Sand movement remains a problem even when a good cover of vegetation has been achieved, and Masson (1990) found a strong correlation between sand activity and vegetation cover (r = 0.82) in a stabilized foredune in South Africa. Sand movement is therefore an important factor in determining plant communities in stabilized areas, and although Masson & McLachlan (1990) consider a 5 year old stabilized dune to be a functional ecosystem, they state that it is still impoverished and vulnerable.

APPROPRIATENESS OF DUNE STABILIZATION

One needs to consider whether dune stabilization is a necessary and suitable management tool, as many problems arise from its use. Some have been discussed in the previous chapter, and clearly the high cost of the operation means that one must ensure that what is under threat is valuable enough to protect. Jungerius & van der Meulen (1985) feel that it is not always desirable to stabilize mobile sands as they are part of a natural landscape, and the process alters aeolian processes and is costly. As stated in the introduction, many areas surveyed in this study may not have been stabilized had case studies, involving a cost-benefit analysis, feasibility study and risk assessment been undertaken. These aspects should be considered, as Doody (1989) has reported that afforestation of dunes at Tentsmuir Fife, United Kingdom, as well as being costly and slow, has also lead to the invasion of birch onto species rich dune slacks. Carter (1980b) has shown that the stabilization of steep foredunes slows down sediment movement by a factor of around eight. However, due to the erosion mechanism of vegetated slopes more sand is eventually lost from the stabilized dune, and Carter suggests that dune slopes on exposed coasts probably remain more stable as loose sand. Patches of vegetation in large dunefields, such as the Kalahari desert, result in deflation basins which lead to parabolic blowout dunes (Erikson *et al.* 1989), and the creation of deflation basins downwind of stabilization areas in large dunefields may be a further consequence of dune stabilization. At Brodie Island on Cape Hatteras National Seashore, USA, dune building and afforestation, together with a number of other factors resulted in the invasion of marshes by woody species and resultant loss of wetland habitats (Firth 1987).

The above examples highlight some of the problems which may be associated with dune stabilization, but the technique has also been very beneficial in many cases. The best example is that cited by Skarregaard (1989), where damage and serious economic losses were reported in Denmark as early as the 16th century due to drifting sands from coastal dunes. In an attempt to prevent drift sand formation, a Royal Decree was passed in 1539, which prohibited the removal of vegetation. This was a major cause of sand drift, as was the case on the Cape Flats (Chapter 7). The sands were only brought under control in 1792, after

50 years of work in developing the correct procedures for stabilization. A similar situation was reported by Wendelken (1974) in New Zealand, where European settlers destabilized large areas due to bush clearing and grazing. These drifting sands were first stabilized in 1903, and large scale afforestation is now practised. Serious socio-economic problems have also resulted in the need for dune stabilization in Iraq (Dougrameji & Kaul 1972), and threats to human habitation in Central Somalia were solved by revegetating a large dune with species such as *Prosopis juliflora* (Zollner 1986).

CONCLUSIONS

Many of the large scale dune stabilization programmes on the Eastern Cape coast have the primary objective of preventing sand movement which threatens human well being. Often, therefore, the use of alien vegetation has been promoted both here and overseas (Dougrameji & Kaul 1974; Zollner 1986) as the use of indigenous species to restore functional ecosystems may, understandibly, be an unaffordable luxury. Nevertheless, potentially invasive species should not be used due to the threats they pose to adjoining ecosystems (see Chapter 7). Along the coast, however, once the need for a stabilization programme has been determined, the creation of functional, aesthetic ecosystems should be the primary objective of such programmes. This is important as the intrinsic and economic value of these systems lies therein. This study has shown that indigenous vegetation can be used successfully in such programmes on our coastline, but the process is costly, time consuming and slow, often necessitating detailed studies to be undertaken prior to the initiation of a stabilization programme.

CONCLUSIONS

The two main objectives of this thesis were to investigate the dynamics of dune vegetation in the Eastern Cape and elucidate pathways of succession; and to assess the resilience of dune vegetation to recreational pressure, and its suitability for dune stabilization. It was asserted that ecological knowledge of this nature was required to effectively manage these dune systems. This final chapter draws together the information presented in the thesis, and assesses the contributions made to plant ecology and implications for coastal zone management.

My results confirm that the diverse vegetation in the Eastern Cape reported by many researchers is also reflected in the vegetation of coastal dunes. A total of seven distinct communities were recognised, and their species composition was affected by the chorological complexity of the region. Cape taxa were more common in the west, and Tongoland/Pondoland taxa in the east. An increase in woodiness was also noted from west to east, due to both the influence of Tongoland/Pondoland species and the increase in rainfall. Of the four woody communities, Dune Scrub was found further west, where it was eventually replaced by Woody Fynbos, and Bushclumps were generally restricted to the wider dunefield in the west. Dune Thicket dominated the narrower dune cordon in the east. Three types of foredunes were recognised, and four types of Dune Slacks, which were generally more diverse and luxuriant than the other communities of the mobile dunes. However, the low and erratic rainfall, coupled with strong winds are responsible for the paucity of vegetation and maintenance of mobile dune systems along this stretch of coastline.

At a local scale, an increase in community complexity, species diversity and physiognomy from Dune Slack to Dune Thicket was always observed, and it was determined that at this scale climate exerts a strong influence on the establishment and growth of plants on mobile dunes. Wind and rainfall are particularly important, as the latter directly effects plant growth, and indirectly affects sand movement, which was found to be a major limiting factor due to strong and persistent winds along this coastline. At Kleinemonde, a temporal study of a dune slack revealed at least two main pathways of succession. Under dry conditions foredunes are colonized by woody shrubs such as *Passerina rigida*, but the succession will not progress much further. Under wetter conditions the dune slacks are invaded by woody species more typical of Dune Scrub, and if climate is favourable species of the Dune Thicket will invade. It was possible to divide the key species in this successional process into four main groups, namely: dune and slack pioneers; dune slack colonizers; sand dune colonizers; and dune scrub species. Salt spray and edaphic factors were of secondary importance in the complete successional sequence, but within the Dune Slack soil moisture was the most important edaphic factor affecting species composition. Further studies supported these conclusions, and revealed that communities could be linked along a gradient of increasing complexity (higher species diversity, larger plants, structural development); and changes in species composition could also be independantly linked to changes in edaphic properties, such as decreasing pH and increasing organic matter content. These changes were directional, autogenic and community based, and dune slacks played an important role in initiating the successional sequence.

Studies at Kleinemonde revealed that autogenic processes were very important in the successional sequence, and that the harsh climate prevented the development of a climax thicket community. A study was therefore undertaken at Mtunzini, on the Natal north coast, where a stretch of prograding coastline exposed to a high rainfall presented a fine example of a primary succession, which had not been previously studied in any detail. This succession was found to be predictable, linear and directional, and to follow a single pathway initially which became multiple in later stages. It was definitely driven by autogenic processes, and changes in species composition could be independantly linked to changes in edaphic properties, such as an increase in organic matter and exchangeable bases and decrease in pH. The Facilitation Model of Connell & Slatyer (1977) was the main mechanism of change along the chronosequence, which appeared to be community-based. However, more detailed studies on the demographic and ecophysiological causes of turnover, and the population biology of key species is required to generate models of succession at Mtunzini and Kleinemonde (*sensu* Picket *et al.* 1987). The data presented in this thesis does, however, suggest that on eroding or static coastlines, such as the Eastern Cape, foredunes play an indirect role in the autogenic changes. They reduce sand movement and intercept salt spray, thus creating more suitable and protected habitats in the moist slacks behind them, which are then invaded by mesic species. On prograding coastlines facilitation is more direct, since less tolerant species are able to invade once a new foredune has developed seaward of the previous one, thereby protecting it. A greater number of pathways of succession probably exist at Kleinemonde, in response to the less favourable climate, and this information needs to be considered if the dune manager wishes to manipulate the system by means of processes such as dune stabilization, or expose it to impacts arising from recreational use.

Although the recreational use of three urban beaches surveyed revealed that the current levels of usage did not exceed their physical, perceptual and ecological carrying capacity, current trends suggested that utilization levels will increase due to socio-political changes and increases in population numbers. A questionnaire survey revealed that useful information could be obtained on the adequacy of various facilities and perceptual carrying capacities, as well as the beach users opinion of areas of ecological importance, such as indigenous vegetation. From this survey it was found that the more natural beaches should not be developed commercially, since their natural appeal was considered important. Conversely, on the less natural Eastern Beach, developments such as restaurants and cafés would be an advantage, thus partitioning the resource base of East London's beaches into a number of use zones. This approach would help to solve one of the main problems of coastal management, namely whether to increase access to sensitive areas or to preserve them. This is very important since the vegetation of the natural areas considered attractive by the beach user, and important for ecological stability, was found to be very sensitive to human trampling.

Detailed studies on the susceptibility of dune vegetation to trampling and vehicle effects revealed a very low resilience to these impacts, with Dune Scrub species being least resistant. Vehicles were more disruptive, and dune vegetation has no carrying capacity for ORV's and a very low carrying capacity for human trampling. Because of the slow rates of recovery, definitive management policies that maintain an area in the desired condition, whilst allowing maximum use, need to be developed. Stricter control of vehicle use on beaches is needed, and areas should be zoned according to their level of use, so that the natural carrying capacity of high use zones can be increased if possible, or preventative measures taken if not possible. However, it is critical that the utilization levels do not disrupt ecological processes, as this may lead to erosion and the need for remedial measures such as dune stabilization.

Although dune stabilization has been used to manage or disrupt drift sands for one and a half centuries, it was only in the last two decades that indigenous species were used. The use of alien species, which are usually highly invasive, has led to serious problems. These include a reduction in the ecological integrity and aesthetic appeal of coastal systems, and a threat to the diverse indigenous vegetation. The use of indigenous vegetation for dune stabilization should therefore be encouraged, and it has proved successful. However, the process is costly, time consuming and slow, so it would be advisable to follow the process of natural plant succession as closely as possible. Further work is also needed to look at other ways of expediting the process, such as the use of vesicular-arbuscular mycorrhizal fungi to innoculate indigenous species determined from this study as suitable for dune stabilization. The long term objective should be the creation of functional, aesthetic ecosystems, since the intrinsic and economic value of dune systems lies therein. However, the need for a manipulative process such as dune stabilization is often questionable, and detailed studies need to be undertaken prior to its initiation. Problems arise not only from the use of alien species, but also due to the disruption of ecological processes important in mobile dunefields.

It is hoped that the results of the studies described in this thesis will make a valuable contribution to our current understanding of the process of community change in mobile dunefields. An understanding of these processes is very important if one wishes to effectively manage the dune landscape. From the results presented here it is evident that the factors controlling plant succession are complex and inter-related, but play an important role in contributing to the stability of these systems. Although the dune landscape is malleable and dynamic, the plant communities found on mobile dunes were shown to be sensitive to environmental perturbations, particularly human impacts such as trampling. The results of this thesis have therefore provided information useful to coastal management agencies, since little data was previously available locally on the resilience and susceptibility of coastal dune communities to human disturbance. Finally, this thesis has focused attention on the importance of considering ecological processes when managing the coastal dune environment.

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