The Vegetation and Restoration Potential of the Arid Coastal Belt Between Port Nolloth and Alexander Bay, Namaqualand, South Africa.

by

Philip George Desmet

Thesis submitted in fulfilment for the degree Master of Science, University of Cape Town, South Africa.

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SUMMARY

This thesis introduces the environment and the vegetation of the Namaqualand coastal belt between Port Nolloth and Alexander Bay. Aspects of the abiotic environment are discussed and related to patterns and processes observed in the vegetation of the study area. The restoration of the natural vegetation impacted by diamond mining activities is discussed.

The study area, located within the winter rainfall area of the Namib Desert, is one of four global fog deserts. The area is characterised by a near ubiquitous covering of Recent to Tertiary amorphous dunes of marine origin. The dunes can be divided into two broad categories: Recent, mobile white dunes, and Tertiary to Late Quaternary, semi-mobile red dunes. The red dune soils are considered arenosols, underlain by dorbank and calcrete hardpans, whereas the white dunes generally lack this structure, unless they are superimposed on an older dune series. The dune landscape is interrupted by outcrops of bedrock, such as river canyons (Holgat River); inselbergs (Buchu Twins); and koppies. Gravel plains and rocky outcrops cover much of the area on the south bank of the Orange River, as far south as Cape Voltas. The low rainfall (<70 mm) is offset by frequent fog and dew. Summers are dominated by high energy, southerly winds and winters by gentle land-sea breezes interrupted by occasional, warm-easterly "berg" winds.

A complete bio-inventory of higher plants of the study area was undertaken. Patterns of diversity and endemism were analysed in relation to plant growth form and habitat. 300 plant species were collected in the study area representing 40 families, with 28% being endemic to the coastal region. The flora is dominated by the Asteraceae (53 species), Mesembryanthemaceae (47), Crassulaceae (28), Poaceae (17) and Aizoaceae (15). Endemic species are over-represented in the Mesembryanthemaceae (60% endemic) and Crassulaceae (44%), and under represented in the Asteraceae (8%), Poaceae (0%) and Aizoaceae (0%). Rocky outcrops have the highest species:area ratio (3.77). They are characterised by their own distinct flora as well as representing a significant proportion (46%) of the species from the surrounding dune landscape. Endemic species are concentrated on these, as well as on the gravel plain habitats. Dune habitats are the most widespread. However, they are characterised by a widespread, generalist flora with low species:area ratio (0.81), few endemics, and share an expected number of species with other habitat types (21%). An endemic species in the

southern Namib can be characterised as being a dwarf leaf succulent in the Mesembryanthemaceae which is most likely to be encountered on a rocky outcrop.

A Twinspan classification and Detrended Correspondence Analysis ordination of the dune vegetation was undertaken. Based on the classification and bio-inventory data, 16 plant communities (associations) for the entire study area were defined and described. Plant associations are distributed primarily according to habitat type (dune, rocky outcrop and gravel plain). Twelve recognisable plant associations occur in dune habitats. Associations in this habitat are distributed primarily in relation to substrata type and position in the dune landscape (DCA axis 1) which can be expressed in terms of soil physical properties, such as texture. This gradient in soil properties is a function of wind activity on the sorting and distribution of sand in the landscape. There is a latitudinal gradient related to biogeographical boundary between the Namaqualand and southern Namib floristic domains (DCA axis 2). DCA axis 3 is related to dune age as expressed in the change in soil properties as one moves from the coast inland, a geological gradient.

The effect of a fossorial rodent, Brant's Whistling Rat (*Parotomys brantsii*), on the re-colonisation by plants of old mining overburden dumps was investigated. An artefact of opencast diamond mining operations is the creation of large overburden dumps where the soil profile down to bedrock (up to 20 m) is inverted. These soils are characterised by high pH, electrical conductivity (EC) and sodicity. Natural revegetation of these soils is slow, if at all. On dumps where these fossorial rodents have created burrow networks, some revegetation has occurred. The hypothesis that plant re-colonisation of these overburden dumps is facilitated by the creation of patches of soil that are ameliorated in some way as a result of the rodent's burrowing activities, was tested. Amelioration of these soils by rodents occurs through the addition of organic matter, soil microbes and plant propagules. Nearest neighbour analysis of burrow-plant and random point-plant pairs on overburden dumps showed that rodent burrows are positively associated with the occurrence of plants. The excavation and mixing of dump soils by rodents significantly raised the pH, lowered the EC and a five fold increase in microbial activity between rodent-free and rodent burrow mound soils was observed. Fossorial rodents create small patches (50x50cm) of increased microbial activity in an otherwise near-sterile edaphic environment. When rodent activity on these sites has ceased, these patches form the focus for plant colonisation of overburden dumps. This research highlights the potentially keystone role that the soil microbial community plays in the structure and functioning of arid rangelands.

An ecological approach to the restoration of diamond mining damage is presented and discussed. This discussion highlights the need to introduce a restoration program that implicitly integrates ecological patterns and processes into future restoration programs. The effects of fossorial rodent activities highlights the role that soil biological processes play in the structure and functioning of this arid ecosystem. This is supported by current thinking in arid rangeland ecology. The role of abiotic factors, such as precipitation and wind, in the restoration process are discussed. It is stressed that restoration is an exercise in applied ecology, not agronomy nor engineering. A framework for sustainable, ecological restoration planning and implementation in the context of our present understanding of this arid system, is provided.

ACKNOWLEDGEMENTS

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Special thanks is extended to all those people who have contributed to this project in some form or another: Wendy Paisley and the students and staff at the IPC; Shirley Cowling; the staff of the Bolus, Compton and Stellenbosch Herbaria, especially Jo Beyers, for plant identifications and taxonomic guidance; Mike Burns (EMATEK); Fred Ellis (University of Stellenbosch); Steve Hammer (Mesa Botanical Garden); Graham Williamson; Ernst van Jaarsveld (Kirstenbosch); Peter Bruyns; Cornelia Klak; Maike Gerbaulet; Mike Struk; William Bond (UCT Botany); Willie Stock (UCT Botany); and, the academic and support staff of the UCT Botany Department. I am deeply indebted to all of them for their contributions.

Finally, I would like to thank the FRD and IPC for funding this project.

Chapter 1 General Introduction.

The original aim of this project was to investigate the restoration potential of vegetation damaged by diamond mining activities between Port Nolloth and Alexander Bay on the west coast of South Africa. Early on, however, it was realised that the paucity of ecological data on the vegetation of this area would be a stumbling block to achieving this aim. Consequently, the focus of this study changed from looking directly at the restoration, essentially an applied ecological study, to a descriptive study examining aspects of the vegetation of the study area. Thus the key questions asked in this study were:

1. What is the vegetation of the study area?
2. How can one restore this vegetation?

This thesis is the product of two and a half years of investigation and thought on the environment and vegetation of this north-west corner of South Africa. The thesis is structured so as to provide the reader with a comprehensive understanding of the vegetation of the area, beginning with an introduction to the abiotic environment, geology and climate, and progressing towards an analysis of the flora, such that one is left with an understanding of what is there, how it is structured and why it is structured in this way. This information is integrated into an analysis of the problem facing restoration attempts on this coast and how one can go about successfully tackling the restoration process.

The thesis is long. I found this unavoidable. My desire to provide a comprehensive background to the abiotic environment of the area adds significantly to the volume of this thesis. This, I believe, was an important exercise as it will provide the reader with an understanding of the desert environment of the southern Namib, its history, and what the patterns or processes are that influence the distribution of plants in the landscape. This background is vital when interpreting the results from later chapters dealing with the vegetation and restoration. When approaching the vegetation aspects of this study, I did not simply want to present a phytosociological study of the vegetation. My goal was to place the analysis of the vegetation within a context of the desert environment in which it occurs. This will provide the reader with a more functional understanding of the vegetative patterns observed in the landscape. As becomes apparent in the chapter dealing with restoration, such an understanding will underlie any successful restoration work conducted in the area.

Chapter 2 discusses the abiotic environment of the study area, providing the reader with a background to the environment of the area. It reads a bit like a text book and I apologise for this. The following chapters build upon this framework to provide successively more detailed layers of information on the biotic environment. Chapter 3 looks at the patterns of plant diversity and endemism at a landscape level. Chapter 4 increases the resolution of the preceding chapter by examining community level patterns. This is a phytosociological study which develops our understanding of how plants are distributed in the landscape and why. Chapter 5 increases the resolution still further, and deals with ecological pattern and process within a single plant community. Here, the effects of a fossorial rodent provide some interesting insights into the ecology of this system. When I first decided to investigate the activities of these rodents, it was more out of curiosity and a side project to the main objectives. The results, however, contribute significantly to our ecological understanding of the system.

The penultimate chapter, Chapter 6, attempts to integrate the understanding of the abiotic and biotic environments developed in the preceding chapters with current trends in restoration and arid rangeland ecology, to provide a framework for future restoration work in this system. The task facing the mining community on the west coast, with regard to restoration of diamond mining damage, is formidable. Some important insights into the problem are made in this thesis. Mine managers and restoration ecologists need to build upon the results of this thesis. By integrating the philosophy and ideas presented in this thesis into a comprehensive experimental trail restoration program, proper mining and restoration protocols can be developed and applied that are appropriate both ecologically, and in the context of the arid west coast environment.

It is possible that much of the damage caused by diamond mining to the environment of the west coast could be avoided or minimised if appropriate methods or counter measures are employed. Similarly, the effort that has gone into looking at rehabilitation has, for all intents and purposes, been "barking up the wrong tree". I hope that this thesis will go some way to changing peoples perceptions about the environment of the west coast; the vegetation, and how special it is; and how one should approach its' restoration.

Chapter 2 Characterisation of the Abiotic Environment of the Coastal Belt between Port Nolloth and Alexander Bay.

This chapter provides a description of the abiotic environment of the coast between Alexander Bay and the Port Nolloth on the west coast of South Africa. The chapter covers a wide spectrum of topics that ultimately relate to the nature of the vegetation and the biotic processes that underlie the structure and functioning of this desert system. Topics include a general description of the study area, the geology and geological processes, pedological processes and the climate. The objective of this chapter is to provide the reader with a comprehensive overview of these processes as they contribute much to our understanding of the underlying abiotic processes that drive this system.

1 Location of the study site.

The study site is located on the west coast of South Africa and covers a narrow band approximately 10 km wide along the coast between Port Nolloth (29° 15' S, 16° 53' E) in the south, and the town of Alexander Bay (28° 36' S, 16° 29' E) in the north, a distance of 80 km (Fig. 2.1). The study site covers an area of approximately 750 km^2.

2 A general description of the landscape.

The study site falls within the southern zone of the Namib Desert, one of five west coast deserts in the world lying within subtropical latitudes (Ward *et al* 1983). For the most part, the coastal belt is a featureless, softly undulating dune-covered expanse referred to as the Sandveld (le Roux and Schelpe 1988). Halfway between Alexander Bay and Port Nolloth the Sandveld is bisected by the canyon of the Holgat River. The Buchu Twins (162 m), a pair of coastal inselbergs 30 km south of Alexander Bay, are the only major topographic relief along this stretch of coast. To the north of the inselbergs, the dunes are gradually reduced to a thin veneer of sand, to form a rudimentary pebble pavement or gravel plain on the southern bank of the Orange River.

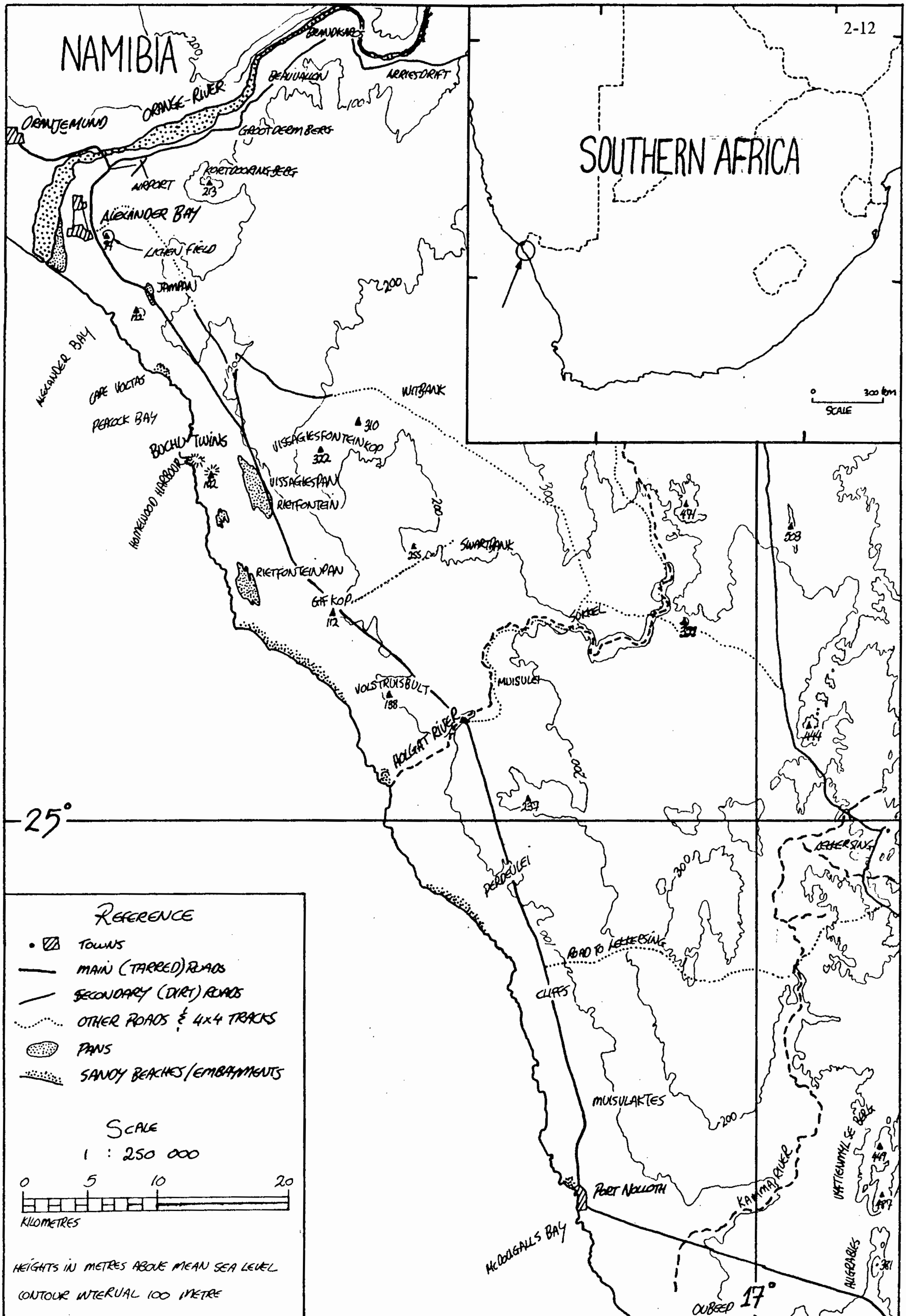
NAMIBIA
SOUTHERN AFRICA
ORANJEMUND
ORANGE-RIVER
BRANDKAROS
BEAUVALLON
ARRIESDRIFT
GROOTDERM BERG
KORTDOORING BERG
AIRPORT
ALEXANDER BAY
LICHEN FIELD
JAMAN
ALEXANDER BAY
CAPE VOLTAS
PEACOCK BAY
BOCHU TWINS
HOLGAT RIVER
WITBANK
SWARTBANK
RIETFONTEINPAN
GIF KOP
VOLSTRUISBULT
MUISULEI
SOKKEL
PERDEVLEI
ROAD TO LEKKERSING
LEKKERSING
CLIFFS
MUISULAKTES
PORT NOLLOTH
KAMMA RIVER
McDOUGALLS BAY
OUBEEP
25°
17°
SCALE
REFERENCE
TOWNS
MAIN (TARRED) ROADS
SECONDARY (DIRT) ROADS
OTHER ROADS & 4x4 TRACKS
PANS
SANDY BEACHES/EMBANKMENTS
SCALE
1 : 250 000
0 5 10 20
KILOMETRES
HEIGHTS IN METRES ABOVE MEAN SEA LEVEL
CONTOUR INTERVAL 100 METRE

Figure 2.1(previous page) A topographical map of the coastal belt between Alexander Bay and Port Nolloth on the west coast of South Africa.

The coast-line lacks any significant embayments or estuaries, except for the estuary of the Orange River. Low lying pans along the coast such as Rietfontein and Perdevlei are evidence of paleo-estuarine systems. Between the Buchu Twins and Alexander Bay there is a series of low rock out-crops, ridges and koppies. South east of the Buchu Twins, lie a group of low granite outcrops which, except for their very tops, are covered with sand and are barely discernible. Prior to the advent of permanent wells, trapped rain run-off from these granite outcrops provided the only source of fresh water for nomadic pasturalists between Alexander Bay and Port Nolloth (De Villiers and Söhnge 1959).

The coastal belt south of the Holgat River consists of gently undulating red dunes and low, dune covered ridges devoid of any significant topographic features. Port Nolloth itself is located on a filled palaeo-estuary and consequently there are a number of saline seeps and pans in the dune landscape around the town. A notable feature of this stretch of coast is the mining activity and a large white, active dune field, Witduine, some 5 km to the east and north-east of Port Nolloth.

3 The geology.

3.1 Regional setting.

The regional geology of the Namaqualand coast consists of Precambrian rock overlain by Cainozoic to recent sediments. The creation of the coastal belt as a physiographic region dates back to the formation of the narrow coastal tract between the South Atlantic Ocean and the Great Escarpment following the break-up of west Gondwana (Africa and South America) some 127 million years (Myr) ago (Partridge and Maud 1987). This development was paralleled by the creation of the Great Escarpment through headward erosion by the ocean, enhanced by epeirogenic[1] uplift of the subcontinent and grading of the coastal tract to the new base level formed by the evolving South Atlantic Ocean (Ward *et al* 1983). This process of pediplanation was augmented by the sediments of the Orange River from the interior of the continent which was experiencing intense erosion of the original Gondwanian surface. In addition, a major marine regression of over 600 m in the Late Cretaceous (70 to 65 Myr BP) affected the continental margin in not only producing unconformities in deposits of the period but more importantly, by exposing the coastal plain. This epoch is referred to as the African cycle of erosion (Partridge and Maud 1987). By the close of the Cretaceous period (65 Myr), the continent had attained its present outline and what we see today as the Namaqualand coastal plain was then the newly formed base level of oceanic erosion or developing continental shelf.

The major rivers draining the interior of the continent had by this time attained their present course (Partridge and Maud 1987). The upper Orange River catchment, however, crossed the Great Escarpment near Loeriesfontein, some 380 km to the south-east, and ran into the sea via the present lower course of the Olifants River, carrying with it diamoniferous gravels. The Knersvlakte is a relic alluvial fan left by this river. The lower Orange system drained an entirely different catchment via its present course across the Great Escarpment. Catchment of the upper Orange/Olifants system was first effected via the Koa Valley following landscape rejuvenation in the Miocene, but the Orange only attained its present course in the Late Pliocene or early Pleistocene after further continental uplift and river capture in the vicinity of Prieska (Partridge and Maud 1987).

The rapid planation of the interior of the southern African subcontinent during the African erosional cycle was brought to a close as a result of moderate tectonic uplift of the subcontinent during the Miocene (ca. 18 Myr). The greatest uplift (300 m) occurred on the east coast. The west coast experienced limited uplift, some 150 m inland of the coast (Partridge and Maud 1987). This period saw the development of a west coast hingeline running from Cape Agulhas through Vredenberg and the Klinghard Mountains (Tankard 1976). West of this hingeline the coastal plain of the African surface warped downwards. This

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[1] Epeirogeny: The uplift or depression of continental or sub-continental land masses as a result of widespread adjustments of level. Epeirogenic movements are generally even in character, producing little more than tilting, slight warping, and minor faulting of the rocks. (Whitten and Brooks 1972)

rejuvenation of the interior and coastal areas of the subcontinent resulted in the Post-African I cycle of erosion. This epoch of erosion lasted about 15 to 16 Myr during which time the African pediplain deposits on the coastal plain, and the weathering mantles beneath, were eroded. Rejuvenation in the interior of the continent resulted in the capture sometime during the Late Pliocene (ca. 3 Myr) by the lower Orange of the pre-existing upper Orange-Olifants system which had migrated steadily northwards, via the Koa valley, from its Cretaceous course.

Asymmetrical subcontinental uplift during the Late Pliocene (ca. 2.3 Myr) again rejuvenated the erosional surfaces across southern Africa. This uplift triggered the beginning of the Post African II erosional cycle. Once again the east coast experienced the greatest uplift, best manifested in the deep incision of coastal rivers. Uplift along the west coast, however, was limited to no more than 100 m along much the same axes as during the Miocene (Partridge and Maud 1987). The asymmetrical nature of the uplift resulted in a distinct tilting of the subcontinent to the west. This westward tilting resulted in a realignment of the Orange River to recapture the upper Orange near Prieska. Headward erosion of the river to where it is today, the Augrabies Falls near Upington, represents the nick point between coastal and inland incision of the Post African II cycle. An important artefact of river incision during the Post African II cycle was the creation of raised alluvial terraces along major river courses (Partridge and Maud 1987). The diamond mines of the Richtersveld and Lower Orange River valley bear testament to the presence of placer deposits of diamoniferous gravels within these terraces. Superimposed upon this second phase of uplift are glasio-eustatic[2] changes in ocean level which had a pronounced effect coastline dynamics.

During the Late Pliocene major climatic changes began to manifest themselves in a series of climatic fluctuations which were accompanied by large scale changes in the extent of the earth's ice caps (Partridge and Maud 1987). These are discussed more fully in Section 5.2 of this chapter dealing with the palaeo-climate of the southern Namib. The deepening of these cycles at the beginning of the Middle Pleistocene (1 - 2 Myr) gave rise to the "ice ages". These characterised the remainder of the Pleistocene. Naturally, these changes had a significant impact on the style of sediment accumulation in the interior of the country. Significant also,

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[2] Eustatic: Pertaining to absolute changes in sea level, i.e. to world wide changes and not local changes produced by local movements of the land or sea floor (Whitten and Brooks 1972).

were the impacts of ocean level transgression on the nature of colluvial and aeolian process in coastal areas. Along the west coast, these eustatic fluctuations in ocean level resulted in the formation of sequences of wave cut marine terraces and more extensive sand accumulation on those areas of the coastal plain under the influence of migrating dune fields. Sea level regression during these episodes exposed extensive tracts of unconsolidated sediments on the inner zone of the continental shelf to aeolian mobilisation, leading to dune field formation. This local process of landward sand accumulation is the most important process in terms of understanding the geological structure of the present coastal plain of Namaqualand. The presence of large shallow coastal embayments had a much greater effect on the accumulation of aeolian sediments as opposed to the presence of coastal cliffs.

Superimposed upon the sculpturing of the continental fringe by wave cut terraces and transgressing palaeo-rivers, is that of local tectonic activity. Examination of these platforms reveals little longitudinal correlation between marine terraces, even over short distances (Davies 1973). Since the beginning of the Post African II cycle of erosion, the evolution of the west coast during the Quaternary is characterised by large eustatic oceanic fluctuations and minor local-scale tectonic activity rather than by large-scale continental movement

3.2 Basement geology: Pre-Tertiary geology.

The basement geology of the coastal belt dates from the Pre-Cambrian (600+ Myr) (De Villiers and Söhnge 1959). Any Cretaceous deposits laid down during the African erosional cycle have long since disappeared in subsequent erosional episodes. Basement geology is discussed briefly for the following reason. Apart from providing plants with a different physical environment in which to grow, the soils of the study area are derived principally from aeolian deposits (colluvial soils) and not from weathered basement material. Consequently, basement geology, the weathering or composition thereof, exerts no major edaphic influence on the distribution of plants. The occurrence of inselbergs (koppies) or rock outcrops in the dune landscape does, however, influence the distributions of plant species. This is discussed more fully in the following chapter.

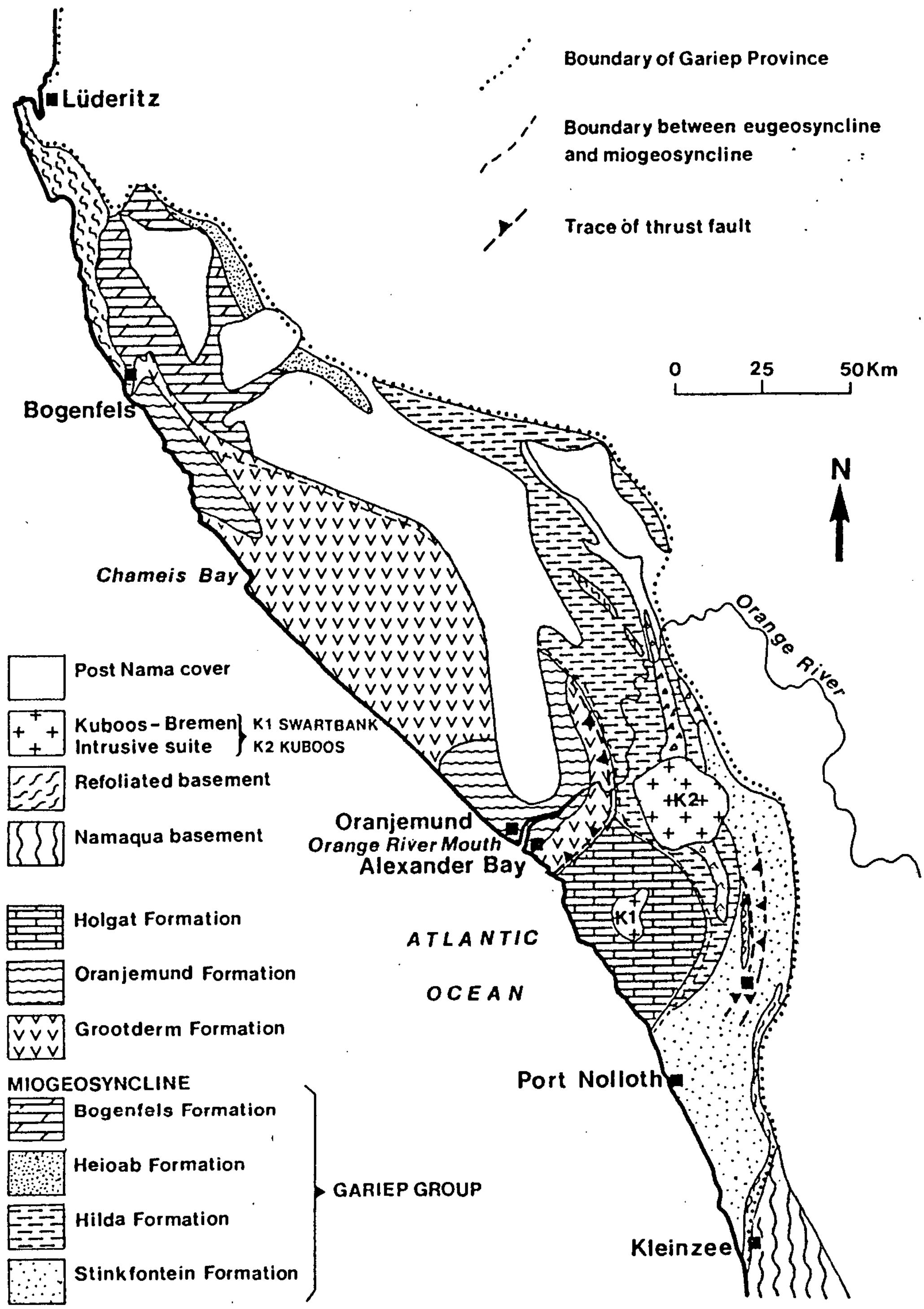

Figure 2.2 Precambrian bedrock geology between Kleinzee and Lüderitz.

Apart from the exposed bedrock along the rocky shore, there are four major outcrops of bedrock in the study area. These areas are the pebble plains and low koppies around Alexander Bay; the Buchu Twins; the granitic intrusions north of Vissagies Pan; and the canyon of the Holgat River. Bedrock throughout the remainder of the study area is overlain by Tertiary to Recent deposits in the form of active to semi-active aeolian sands. Fig. 2.2 is a map of the basement geology of the coastal belt representing the four geologies encountered in the study area.

3.2.1 The Gariep System.

The Gariep System, so called after the Khoekhoen[3] name for the Orange River, consists of highly schistose metavolcanics and sedimentary rocks (schist's) and is divided into four series two of which, the Holgat and Grootderm Series, occur within the study area. It is separated from the quartzitic Stinkfontein Formation to the south and east by a thrust fault buried beneath the dunes.

3.2.1.1 The Holgat Series.

Strata of the Holgat Series, so called because the Holgat River traverses the entire visible length of the succession, underlies most of the coastal plain of the study area. From a line immediately to the north of Cape Voltas to Wurmkop trigonometric beacon in the south, and west of a line between Torkop and Windwaai trigonometric beacons, the series covers an area of approximately 1400 km^2. Besides the canyon of the Holgat River, the series is exposed on the Buchu Twins, Namaquakop and Spitzkop. The Holgat Series consists of parallel strata of quartzites, schists and arkoses (arenaceous rock). Apart from the Buchu Twins inselberg, the Holgat Series appears fairly stable in terms of regional tectonics. There appears to be a gentle fold axis tending to the south east from Cape Voltas through Duikerkop, Gifkop and Volstruisbult, forming the low ridge that runs near parallel to the coast.

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[3] Gariep is the Khoenhoen name for the Orange meaning "river" (Raper 1987).

3.2.1.2 The Grootderm Series.

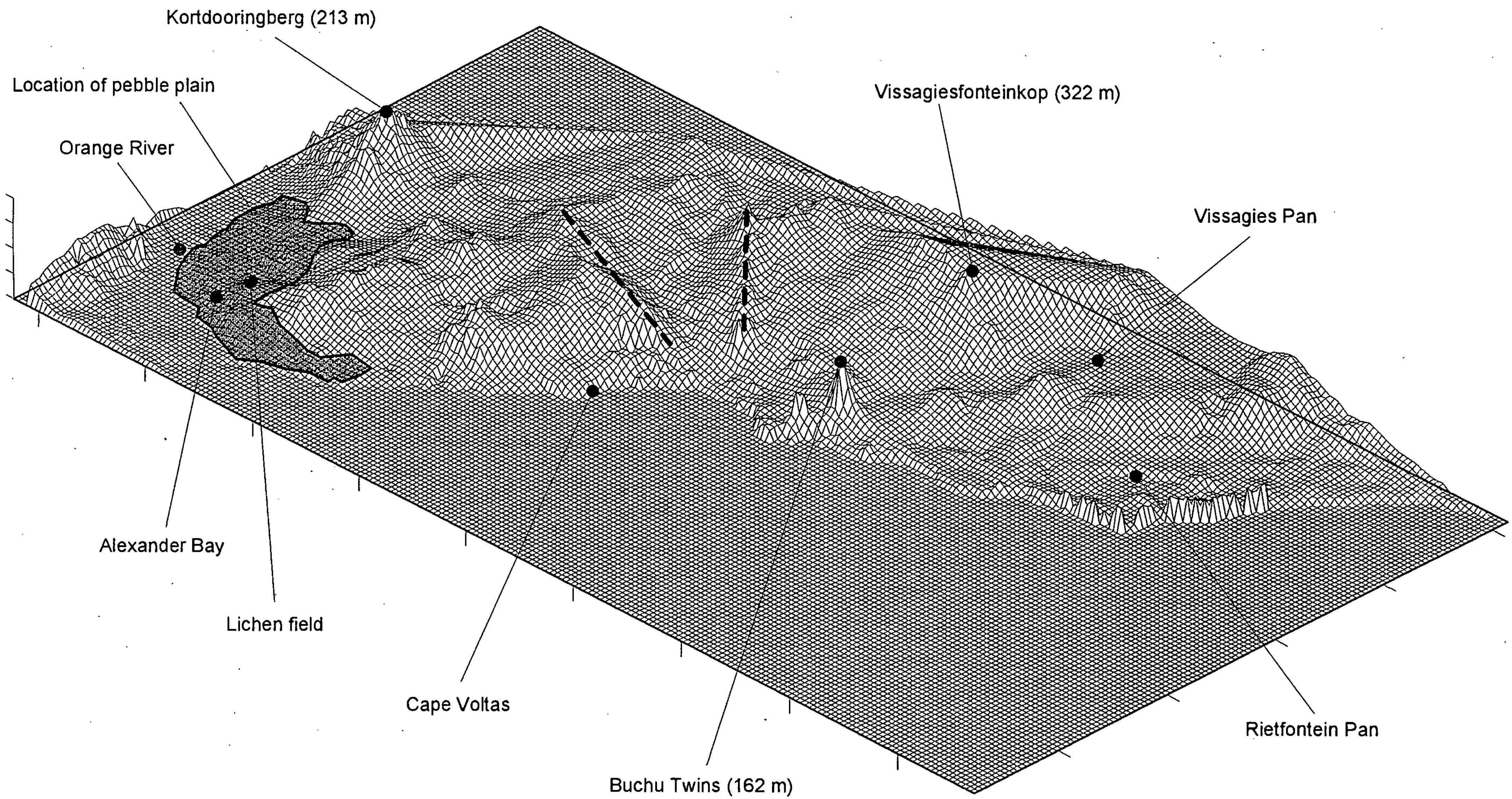
To the north of Cape Voltas, volcanic and sedimentary schists of the Grootderm Series thrust over the Holgat beds to form a conspicuous ridge line extending in a north-easterly direction for about 30 km from Cape Voltas to Arrisdrif (Fig. 2.3). From this ridge to the north, the landscape consists of undulating, low hills and ridges, partly buried by sand, sloping down gradually towards the Orange River.

The existence of this fault is partly responsible for the sand-input shadow limiting the supply of sand to the gravel plains to the north. A combination of (a) high energy southerly winds in vicinity of the mouth of the Orange River; (b) the presence of a physical barrier to sand input from the south; and (c) the absence of sandy coastal embayments to the north of the fault (to supply sand to this area) have effectively starved the plains south of the Orange River mouth of significant sand inputs. Throughout time, this has facilitated the formation of the lichen field and gravel plains and their associated flora, around Alexander Bay.

3.2.2 The Stinkfontein Formation.

To the south of the Holgat series lies the quartzites, conglomerates, grits and sandstones of the Stinkfontein Formation.. For the most part this formation is buried by sand dunes and is exposed only along the rocky shore and in small, isolated rock outcrops in the dunes between Oubeep and Port Nolloth. Cliffs (4m) between Perdevlei and Muisvlakte provide evidence of some minor warping in the bedrock. However, nowhere in the study area is there evidence for major faulting in this series as occurs in the Holgat Series.

Figure 2.3 (overleaf) A surface grid plot of the coastal area immediately to the south of the mouth of the Orange River. The ridge-line created by the thrust fault between the Grootderm and Holgat Series (dashed lines) creates a sand shadow, cutting of aeolian sand inputs to the area immediately south of Alexander Bay. Part of this sand shadow is occupied by the lichen field to the SE of the town.


Kortdooringberg (213 m)
Location of pebble plain
Orange River
Vissagiesfonteinkop (322 m)
Vissagies Pan
Alexander Bay
Lichen field
Cape Voltas
Buchu Twins (162 m)
Rietfontein Pan

3.2.3 The Swartbank Pluton.

The fourth geological formation is the grey gneisic granites of the Kuboos Series (Namaqualand Basement Granites). This igneous intrusion penetrates the Holgat Series east of the Buchu Twins in the area between Rooibank , Witbank and Swartbank and is termed the Swartbank Pluton.

The Swartbank granite, largely buried under the dune sand of the coastal plain, is exposed in about one dozen places over an area of approximately 150 km^2. The southern most occurrence, and the largest outcrop, is at the Swartbank trigonometric beacon. No where are the contacts between the coarse porphytic granite and the schist's of the Holgat Series exposed, however, it is inferred that this granite is of a younger age and intrusive in nature. This igneous intrusion is believed to be a south western branch of the much larger Kuboos Pluton which forms the distinctive Ploeg Berg in the east near Kuboos.

Box 2.1 A note on the Buchuberg.

On the South African Governments' Surveys and Mapping Department 1:250 000 topographical of Alexander Bay (2816), the two inselbergs lying on the coast 30 km south of the town are called Boegoeberg Noord and Boegoeberg Suid. Why the name boegoe or buchu is used is difficult to establish. This term is usually reserved for aromatic members of the Rutaceae (Rutoideae), especially *Agathosma* spp., that are associated with the Cape fynbos region. In this case, however, it may refer to the highly aromatic *Selago robusta* found growing on the slopes of the inselbergs. To the best of my knowledge, William Patterson (1755-1810) was the first to employ the name in his travelogue dated 1779 calling them the "Buchu Twins" (Forbes and Rourke 1980). This was probably a modification of the name "Twee Gebroeder" which appeared on a map of Namaqualand produced by Patterson's travel companion, Colonel R.J. Gordon.

Patterson had this to say about the Twins:

"...as they were situated at a very small distance from each other, and were very similar in their figure and size, we gave them the name of the "Two Brothers" and in this desolate region there was no one who could dispute any denomination by which we chose to distinguish whatever we met with..."

Problems arise when referring to the Twins as there is another Buchuberg in Diamond Area No.1 of Namibia, probably also named after the same plant as it appears to be widespread north of the inselbergs. There is a third Buchuberg on the Orange River, south of Kheis between Prieska and Upington. South of Niewoudtville, there is jet another Boegoeberg. To avoid any problems or misunderstandings when referring to the two inselbergs, throughout this text I employ Patterson's name, Buchu Twins.

I have been told that there are a number of plant species endemic to the Buchu Twins. This story probably originated because the Buchu Twins are the only topographical relief along this entire stretch of coastline. It is quite probable that a rocky "island" isolated from the mainland by a "sea of sand" would contain unique species or subspecific taxa. One of the objectives of this project has been to clarify any preconceptions regarding the flora of these inselbergs.

3.3 Tertiary and Quaternary geology: The coastal shelf.

This section aims to provide a brief synopsis of the history of this coastline from the early Pleistocene to present. The marine terraces are discussed in some detail, not so much because of their influence on present vegetation patterns or processes, but from the point of view that these form the foci of present diamond mining operations along the coast and also the marine fauna deposited on these terraces provide some key insights into the past coastal environment.

The study area forms part of the coastal shelf of the African continent. Since the early Pleistocene, with the minor continental uplift associated with the beginning of the Post African II cycle, the western margin of the coastal shelf has gradually been exposed through a combination of eustatic sea level fluctuation and local tectonic activity (e.g. bedrock warping and continental uplift). It is therefore fitting to begin the description of how much of the current landscape evolved during the Mid to Late Pliocene, some 2 million years ago. A feature of the bedrock of the coastal shelf, and consequently the gross morphology of the landscape, is that it is said to be "antecedent" (Pether 1986). It is considered to have been developed by fluvial incision during the Mid-Tertiary, as well as through marine action. Thus, the present shape of the landscape is not only a functions of marine terrace incision, but also dissection by palaeoriver courses.

As the level of the ocean dropped during the Quaternary, it carved into the bedrock a series of shelves or marine terraces which represent hiatuses in this drop or rise. This phenomenon has been the focus of much research. Many authors have attempted to unravel the altitudinal as well as latitudinal relationship between marine terrace complexes on the west coast (both above and below current sea level) to gain insights into the history and character of the ocean-land interface. The word complex refers not only to the series of marine terraces, but also the complex nature in which they are encountered in the landscape. Not only has ocean level regression and transgression resulted in terraces of younger age superseding older terraces, but also local warping of the coastal geology and uplifting of the African continent resulted in nonconformities in terrace succession both in geological time and on different parts of the coastline, due to local shifts in altitude (Davies 1973). As mentioned earlier, Tankard (1976) ascribes the differential warping and tilting to the presence of a NNW tilt axis or "hinge line" running as a zone of tilting from Cape Agulhas on the south coast through to the Klinghard Mountains in Namibia. This "hinge line" could be represented by the fault running through Duikerkop eluded to in the earlier discussion on Pre-Tertiary geology.

Between Port Nolloth and Alexander Bay, as well as the entire west coast of South Africa, there are four recognised sets of aerial marine transgression complexes (Pether 1986, Tankard 1976, de Villiers and Söhnge 1959, Davies 1973, Carrington and Kensley 1969):

1) The Grobelar Terrace (75 to 90 m above seas level or m.a.s.l.)
2) The Upper Terrace (45 to 50 m.a.s.l.)
3) The Middle or Oyster Terrace (11 to 35 m.a.s.l.)
4) The Lower Terrace (0 to 8 m.a.s.l.)

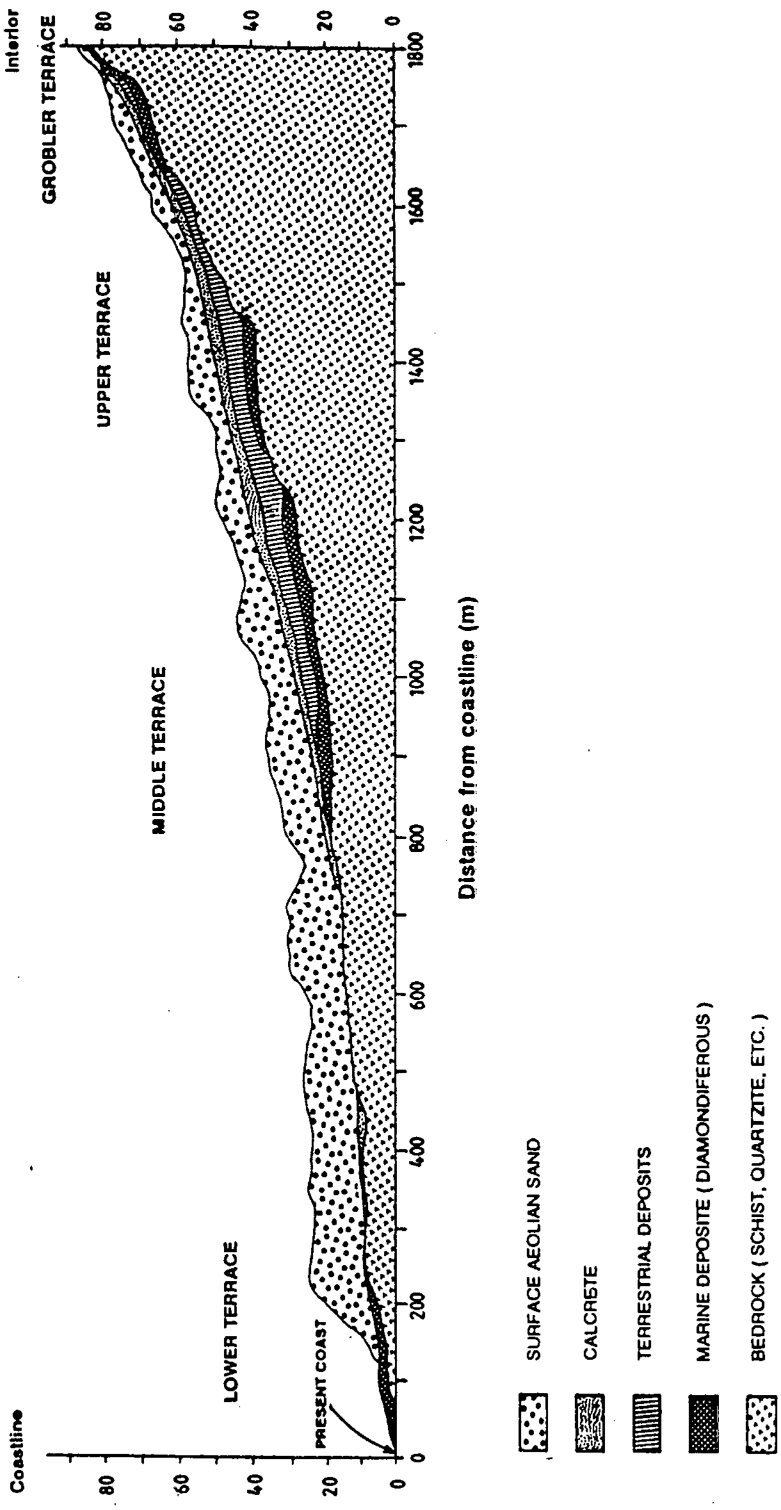


Figure 2.4 A diagrammatic representation of a cross-section through landscape (From Burns 1994).

Before mining operations began in 1926, the marine terraces were exposed at only a few localities, the most extensive being to the west and south west of where Alexander Bay is today, and also around Peacock Bay and the Buchu Twins. Elsewhere though the terraces are buried under anything up to 30m of aeolian Tertiary and Quaternary sand deposits (Fig. 2.4).

The oldest terrace complex extends seawards (west) from 75-90 m.a.s.l. and is called the Grobelar Terrace. Due to extended fluvial erosion, this terrace is not very pronounced, contains minor marine deposits and has a localised distribution along the coast. This terrace dates to the Terminal Pliocene. The Upper Terrace (45 to 50 m.a.s.l.) is overlain by diamond rich marine gravels. The western edge of the terrace is characterised by a low marine cliff with a broad level bench which has an uneven floor bounded in the east by a high sea cliff (ca. 6 meters), with caves and tunnels. It is generally accepted (Pether 1986) that the 90m complex represents an ocean level maximum around the Early to Middle Pliocene and the Upper Terrace complex is inferred to begin with the Late Pliocene.

The Middle Terrace complex is the most extensive of all the terraces, sloping gently from 34 meters to about 11 meters above sea level. This terrace is associated with the presence of a distinct band (25-30 m.a.s.l.) of the warm water mollusc *Crassostrea margaritacea* and is therefore termed the Oyster Terrace (Davies 1973). The presence of this mollusc indicates that either full develop of the cold Benguela Current upwelling along this coast only occurred after the Early Pleistocene (< 2 million years BP) or that the intensity of upwelling fluctuated in relation to the Glacial/Interglacial cycle and the movement of the South Atlantic Anticyclone to create periods of significantly warmer ocean temperatures.

The Lower Terrace is the youngest of the terraces with marine gravels lying very close to the surface covered only by a thin calcrete layer and mobile near shore dunes (see Fig. 6.1) This terrace contains marine gravels deposited during ocean regression during the Terminal Pleistocene (ca. 125 000 BP) and also very recent gravels deposited during the Mid-Holocene high (ca. 5000 BP) (Deacon and Lancaster 1988).

Anomalies in the bedding of marine gravels arise across the succession of terraces where successive layers of marine gravels are separated by layers of terrigenous sands or muds. This has been ascribed by de Villiers and Söhnge (1959) to ocean level regression followed by episodes of transgression. This is a feature to some extent of the ocean regression/transgression cycle associated with the Tertiary.

Recently, radiocarbon dating of marine deposits have helped to unravel an ocean level sequence for the Quaternary (Miller 1990). By combining these data with fossil fauna data (Pether 1986, Tankard 1976, de Villiers and Söhnge 1959, Davies 1973, Carrington and Kensley 1969) it is possible to derive an ocean level curve for the west coast for the last approximately 2 million years. From the Mid-Pliocene maximum at the 90 m.a.s.l. the general trend of the ocean through the Quaternary has been regression to a minimum coinciding with the Last Glacial Maximum some 18000 to 17000 thousand years ago at an altitude of approximately -130 m.a.s.l. (Miller 1990, Deacon and Lancaster 1988). In the quest to locate diamonds associated with buried marine terraces on the ocean floor off the mouth of the Orange River, it has been shown that the succession of aerial marine terraces continues on the ocean floor to the depth of the ocean level at the Last Glacial Maximum (de Decker 1986). From this Late-Pleistocene minimum the ocean level increased to reach a Mid-Holocene high at 2 m.a.s.l., approximately 5000 years ago (Miller 1990, Parkington 1986, Deacon and Lancaster 1988).

An interesting feature identified during the survey of the ocean floor is the presence of channels cut into the bedrock. These channels represent palaeo-drainage lines and are continuous with terrestrial drainage features represented on the coast by the presence of pans and sandy embayments. The largest of these channels is in the region of Rietfontein and Gielie's Bay and it is suggested by Keyser (1972) that this represents the course of the palaeo-Holgat River. From seismic investigations, these channels in the bedrock do not extend beyond 30 m.b.s.l. It is possible that the course of the Holgat River was diverted along its new, more southerly course some time during the Middle to Lower Pleistocene (ca. 100 000 BP, Deacon and Lancaster 1988). Further evidence for the recent adjustment in the course of the Holgat is encountered near Sukkel, east of the main road to Alexander Bay, where the canyon cuts through the well developed dorbank, calcrete and silcrete layers of Tertiary dune deposits.

Box 2.2 Replacement products: calcrete, silcrete and dorbank.

Replacement is a term widely used in geology to describe the process whereby one constituent in a system is progressively substituted by another (Whitten and Brooks 1972). In the context of sand dune pedogenesis, replacement products are the result of soluble components, principally calcium and silica, being eluviated and later crystallised in lower strata of the sand profile. Along the west coast three prominent replacement product are observed - caliche or calcrete, dorbank and silcrete. The physical and chemical properties of these illuviated horizons has an impact on the distribution of plants in the landscape and is of major importance to plants attempting to grow in the post diamond mining landscape. This is discussed further in the chapter on restoration (Chapter 6).

Calcrete exists as a near ubiquitous layer under the loose surface sand of the dune landscape up to the edge of the near shore zone (see Figs. 4.2 and 6.2). Its distribution is interrupted only by palaeo-river courses, estuaries and other coastal areas inundated and reworked during the Holocene ocean level rise. Essentially the process of formation is the result of calcium bicarbonate in the soil solution being precipitated and later crystallised as calcium carbonate in a lower horizon. It is a slow process and rainfall-dependent. In a clay-loam soil, the minimum rainfall limit is about 200-300 mm rain annually. Because water infiltration is much better in sand, it is possible for calcrete to form where annual rainfall is 50-100 mm (F. Ellis pers. comm.). Calcrete is of great significance for plant life as it is impenetrable to roots. In places, aeolian erosion of the sand exposes the calcrete layer, especially on the crests of dune-covered ridges or near the coast where wind action is greatest.

Dorbank is another common replacement product usually found lying above the calcrete layer (see Fig. 6.2). It is one of two hardpan formations found in South Africa, the other being silcrete (Ellis and Lambrechts unpubl.). Dorbanks are related to the duripans of other soil classification systems. They are a hard subsurface horizon, generally with a red or reddish brown colour. They range in thickness from as thin as 30 cm to more than four metres and occur at shallow depths (<50 cm) below the soil surface. They occur extensively on level to slightly sloping land, mainly footslopes, in the semi-arid (mean annual rainfall <250 mm) Karoo where they cover an area of approximately 1.93 million ha, and other semi-arid parts of southern Africa (Ellis and Lambrechts unpubl.). Dorbank is associated with soils developed from unconsolidated parent materials. A typical dorbank soil profile consists of a red coloured, non-calcareous orthic A horizon approximately 30 cm thick, overlying a red apedal B horizon, a weakly structured (red) neocutanic B, or a neocarbonate B. Unconsolidated material underlying the dorbank is generally weakly structured and highly calcareous or gypsic.

The main physico-chemical characteristics of dorbank soil profiles are high sand content (clay<10%); high alkalinity (pH>8.3) in the A and B horizons; less alkaline dorbank layer; sharp decrease in electrical resistance and increase in soluble salts from A to B and dorbank horizons; and high exchangeable sodium percentage (Ellis and Lambrechts unpubl.). Silica is the dominant cementing material. In the Karoo, dorbanks are encountered on well-drained, lightly textured soils developed from transported materials (e.g. aeolianite). The high pH of the A and B horizons increases the solubility and mobility of silica, while the high exchangeable sodium contributes to clay dispersion. Under prevailing low rainfall conditions, the soluble silica will not leach through the profile but rather accumulate in the subsoil. Carbonates being more soluble than silica, will under the same conditions move further down and accumulate in a position below the silica cemented horizon while gypsum will accumulate still deeper (Ellis and Lambrechts unpubl.).

The third type of replacement product encountered on the west coast is silcrete. Silcrete occurs at or near the soil surface and can range in thickness from less than a metre, up to 5 m. In South Africa, silcretes are characteristically associated with Tertiary erosion surfaces and occur as a remnant capping in the landscape, and are therefore of palaeo-environmental significance (Ellis and Lambrechts unpubl.). The conditions under which silcrete was formed are not clear, but their pale colour point to silica accumulation and cementation under hydromorphic, sandy conditions (e.g. palaeo-estuaries and river channels).

Dorbank is a feature of the present arid climate conditions or similar palaeoclimates, with silica accumulation in well drained, unconsolidated materials. Prospecting trenches reveal alternating strata of calcrete and dorbank below the present dune profile down to the marine deposits overlying the bedrock (see Fig. 6.2). This would indicate that as least since the Early

Pliocene the climate along this stretch of the west coasts has not differed significantly from the present.

3.4 Tertiary to Recent deposits.

3.4.1 Salinas and pan deposits.

Pans in the coastal plain consist of two types (de Villiers and Söhnge 1959): (1) those formed by the movement of sand dunes across old drainage lines or simply occurring in elongate depressions between the dunes, and (2) those representing marginal lagoons, termed salinas, formed as the sea receded during the Holocene or earlier. Salinas differ from pans encountered further inland along the coast, in that they represent old lagoons which have their own natural supply of ground water, usually in the form of sea water seepage and not rain runoff, and also local encrustations of gypsum or common salt. Theses type of pans are referred to as salinas (Dardis and Grindley 1988, Whitten and Brooks 1972) or lacustrine deposits if they were formed as inter-dune lakes or pans (Deacon and Lancaster 1988). The largest of these coastal salinas is found at Rietfontein. Salinas are also encountered at Perdevlei; to the south of Port Nolloth at Obeep extending almost to Kleinzee; Vissagies Pan; and Jam Pan. The surface of these pans, where exposed between transgressing terrigenous dune sand, is a salty clay (de Villiers and Söhnge 1959) underlain by a layer of compacted green sand, a relic of the past alkaline-anaerobic marsh environment.

3.4.2 Sand dunes.

There are seven determinants to dune development along the coast (Tinley 1985), (1) wind regime, (2) sand supply, (3) coast trend and configuration of shorelines (degree of exposure and deflection of the effective winds), (4) rainfall regime, (5) plant colonisation, (6) sea (longshore drift and wave action), and (7) river mouth dynamics (change of flow and sand input). The last two mentioned influences are confined mainly to the foredune zone.

A simple wind rose is not indicative of coastal dune movement since wet sand is much heavier to move than dry sand. In addition to being arrested by plant growth, the high incidence of coastal fog, and, nearer to the coast, the copious aerosols of salt spray, act as retarders of sand movement. Understanding dune dynamics requires a knowledge of both local physiography and climate. For example, periods of major sand movement in this system are related not only to seasons of high energy winds but also and high aridity. Understanding the nature and properties of dunes and dune soils is crucial to our understanding of present vegetation patterns and processes. The following section is aimed at covering some of the many aspects of the morphology, properties and dynamics of dunes.

3.4.2.1 Classification and description of dune types.

There are a number of dune types represented within the study area. Below approximately the 90m surface contour one encounters relatively active and young dune systems owing much of their youth to recent Holocene ocean level changes. Above the 90m contour one encounters dunes which are much older, more stable and of simpler form to the younger coastal dunes. The classification of dunes below (Table 2.1) follows Tinley (1985).

A feature of all dune types south of the Orange River is that they are all affected by vegetation. As living organisms, plants are unique as sand traps. Their aerial shoots provide an open, flexible, obstacle to wind-driven sand. The sudden drop in wind velocity and the sifting effect of the open obstacle results in sand and other aeolianites being deposited in and around the plants. Burial by sand stimulates further growth up through the sand and in this way mounds and hummocks are formed and from these, embryonic dunes. These mounds are termed phytogenic mounds, shrub coppice dunes (Lancaster 1989) or phytogenic hillocks (Danin 1991).

Table 2.1 The dune types represented along the coastal belt between Port Nolloth and Alexander Bay.

A. Primary Dune Types (derived directly from beach deposits)

1. Fore or frontal hummock dunes - impeded dunes with vegetation important, orientated parallel to the source beach. Occur along the coast down wind of sandy beaches. Are the highest of dune types represented along this section of coast.

B. Secondary Dune Types.

1. Back shore hummock dunes present between Port Nolloth and Muisvlaktes, at Rietfontein and also the mouth of the Holgat River.
2. Linear transgressive dunes leading out up-wind from back shore hummock dunes systems and are transgressive, usually crossing salinas or older dune sequences. Good examples of these dune types are encountered in the vicinity of Rietfontein pans moving over a series of salinas; the tail end of the Holgat River mouth dunes transgressing older tertiary dunes to the east of the main road at Swartbank; and also immediately to the south of Jam Pan.
3. Amorphous ancient dunes or remnant dunes are eroded vegetated dunes usually encountered above the 50m contour. They are red in colour as opposed to the white to grey younger dune types and are more stable.
4. Lunette dunes associated with small pans are encountered on Vissagiesfonteinsepan.
5. Active unvegetated hummock dunes over Tertiary sands are encountered in one location at Witduine to the north east of Port Nolloth.
6. Vegetated hummock dunes over salinas or pans. The saline nature of the underlying pans results in a more halophytic dune type (Danin 1991).
7. Transgressive sheets over bedrock (e.g. the pebble plains of the lower Orange River valley).

Wind and wave action imposes continuous multidirectional change on sandy foreshores. Strand plant growth fluctuates with erosion and accretion of the foreshore, and the dunes they form entrain further multiple changes. Dune form and dynamics (where they occur below the 10m contour and lie in close proximity to salinas or pans), and plant communities are affected where deflation exposes the characteristic moist saline horizon of the salina. Thus, the form and dynamics of near shore vegetated coastal dunes is regulated by four main features: (a) The coincident occurrence of effective winds with dry or wet conditions; (b) the input of sand via the ocean; (c) the degree of stabilisation by plants; and (c) presence of saline subsoils.

3.4.2.2 Patterns of dune occurrence.

By far the majority of the current land surface of the study area is covered by moderately stable aeolian, superficial sand deposits of Plio-Pleistocene origin. Towards the coast (below the 30m contour) many of the sands are recent Lower-Pleistocene or Holocene. All these sands have been deposited through wind action. Originally of terrestrial origin, having been deposited in the ocean as river sediments, they can now be described as having a predominantly marine origin. Sections through the dunes down to bedrock reveal that aeolian sand deposits have been accumulating on the surface of the coastal plain since its exposure by the receding sea (see Fig. 6.2). Lying on the bedrock and before the commencement of terrigenous deposits in soil profiles, below the Grobelar Terrace, there are marine and raised beach deposits consisting of gravels (well rounded pebbles, cobbles, boulders and the much sought after diamonds) and shells. These deposits are set in a sandy matrix partly cemented by lime and gypsum into a type of marine conglomerate. In soil profiles above the Grobelar Terrace these marine deposits are absent.

Box 2.3 The red colour of sand.

A phenomenon that fascinated me throughout the project was the change in sand colour as one moves away from the coast. The dunes tend to become redder with distance from the coast or with increasing dune age. If one examines these red dune sands under a microscope, the pigments are seen to occur as extremely thin films which form complete coatings on grains and in parts as thick concentrations which lie within dentations on the grains (Walker 1979). Finer grains are more heavily stained with pigment than are larger grains. The pigment characteristically consist of crystals of iron oxide in combination with clay mineral (aluminium silicate) or pure silica platelets(Walker 1979). The origin of this red pigment deserves some attention.

Figure 2.5 Dust plumes generated by a strong "berg wind" in the southern Namib Desert (METEOSAT VIS image 13 June 1979, 13h30, from Preston-Whyte and Tyson 1988).

All the sand dunes along the Namaqualand coastal plain consist of aeolianites of marine origin. Therefore, all these sands were originally white in colour and with age, these have been stained red by iron oxide. It is thought that the most probable origin for these iron oxides is iron bearing clay minerals present in the soil column (Walker 1979). These clay minerals are not present in nearshore dunes. With time, however, they accumulate on the sand surface as fallout during dust storms. One only needs to look at the satellite image taken during such a "berg wind" sandstorm (Fig. 2.5) to appreciate of the quantities of dust deposited on the coastal plain under these conditions. With time, this dust mechanically infiltrates the soil column and as it does so, precipitates its red colour onto the sand particles.

Water in the desert dune environment infiltrates the sand in an oxidising state through the retention of dissolved atmospheric oxygen. The presence of carbonate and gypsum in surficial deposits indicates an alkaline weathering environment. These two factors create ideal conditions for the chemical precipitation of iron oxides. Since these clays are not in equilibrium with meteoric water, upon repeated wetting by surface and interstitial water, they are likely to release iron through a process of chemical hydrolysis in the form of iron oxide. This iron is probably initially present as amorphous ferric hydrate or finely crystalline goethite, both of which convert to hematite upon ageing.

With time and distance of transport, so dune sands in arid deserts gradually become more pigmented. The two opposing processes of abrasion of sand particles, loss of pigment, and accumulation of pigment, when particles are at rest, are constantly at play. These processes affect the various size sand particles differently. Large grains are more easily abraded and so pigment loss is the dominant process whereas small particles experience more accumulation of pigment. In places where the wind sorts sand particles of the same age differentially according to particle size, accumulations of fine particles are a much darker red compared to accumulations of larger particles. Thus, the intensity of reddening is not a reliable measure of dune age.

3.4.2.3 Dune dynamics - sand movement in the landscape.

The Sandveld has for the most part a covering of plants. Sand movement in vegetated dune systems differs significantly form those of unvegetated dune systems such as the Great Sand Erg of the central Namib Desert. While an unprotected surface may be highly erodable, vegetation reduces sand loss by wind in three ways. Firstly, it shelters the soil from the erosive force of the wind by covering a proportion of the surface. Secondly, it reduces the force of the wind near the ground by extracting momentum from the wind at a height above the surface. Thirdly, it traps soil particles in transport, thereby acting as a catchment for sediment (Wolfe and Nickling 1993). Plants act as barriers to the wind simply due to their physical presence in the landscape. Therefore, standing vegetation is still effective in controlling wind erosion, even when dead. The implications of this become apparent when one examines plant community dynamics in arid, sandy systems. A characteristic of most arid systems is that vegetation cover is often non-continuous. Consequently, the soil surface is directly exposed to the force of the wind and such surfaces are susceptible to wind erosion.

As air moves over a rough surface the resultant flow is nearly always turbulent. Vegetation represents a significant obstruction to the flow of air above the ground surface. The resulting velocity profile depends, in part, on surface characteristics including the size, shape and arrangement of the surface elements (Wolfe and Nickling 1993). At a certain height above the surface, the drag effect on wind by vegetation is negligible. The layer of significant shear is usually in the order of a few hundred metres thick. The winds within this layer may be further divided into two regions. The first region is the upper inertial sublayer where flow is sufficiently above the roughness elements (plants), such that the height above the effective surface provides the only length scale necessary to describe its profile. The second region is the roughness sublayer or wake layer which lies inside and just above the roughness elements. In this layer air flow is complicated and the resultant flow profile is dependent on a number of element length scales such as plant height, width and spacing.

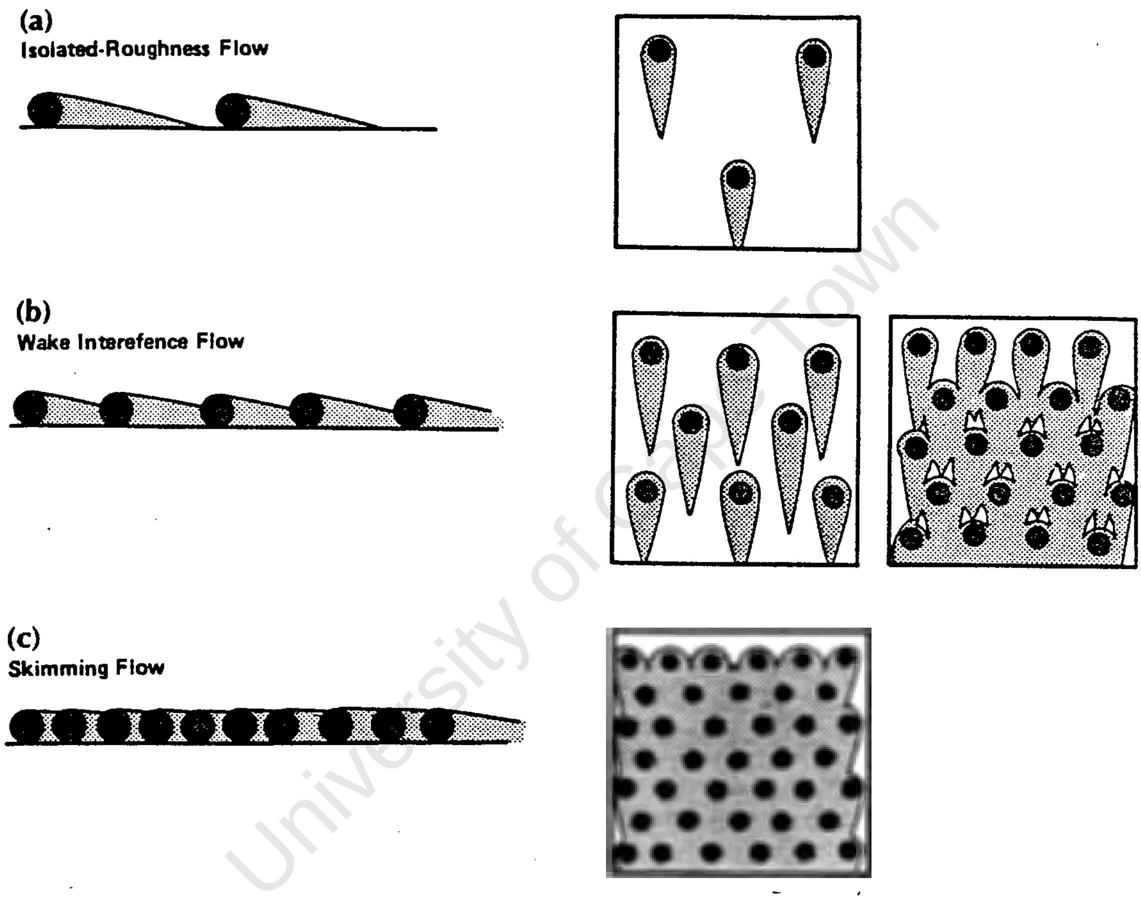


Figure 2.6 The protective role of sparse vegetation in wind erosion. Illustrates theoretical wake development around roughness elements for increasing density. The shaded area around the elements is the wake region. Behind the elements is a region of flow deceleration representing an area of protection provided by the roughness elements. The lights areas represent the region of flow where the inertial layer might be expected to penetrate to the soil surface. With increasing element density (decreasing spacing) the surface protected by the decelerated region increases (from Wolfe and Nickling 1993).

The concept of flow regimes is relevant to the role vegetation plays in protecting intervening surfaces from wind erosion. Vegetation interacts with the mean flow by: extracting momentum from the wind; producing turbulence in the form of wakes behind obstacles; and breaking down large-scale turbulent eddies into smaller scale motion. The flow of air within a layer of vegetation is related to the size, shape, spacing and arrangement of the individual plants. These roughness elements interact to modify the form of the flow above the surface. In the case of a single element the effect is typically, for a wake region to develop downwind of the obstacle in which the wind speed is less than the surrounding region. Within the wake region, eddies are shed by the obstacle causing the flow to separate from the surrounding air mass. To the sides of the obstacle an accelerated region develops as air is forced around the obstacle. Associated spiral vortices generated on either side are termed horseshoe vortices (Wolfe and Nickling 1993). As the number of roughness elements increases, so the flow regime over the surface changes significantly.

The flow that develops over an array of roughness elements which are widely spaced is termed isolated roughness flow (Morris 1955). As depicted in Fig. 2.6, each element acts in isolation with a fully formed wake and separation region. With a decrease in spacing, the wakes formed by the roughness elements do not fully develop before another roughness element is encountered. This is termed wake interference flow. A further decrease in spacing results in wake generation being strongly suppressed by surrounding elements. Stable vortices are created between the elements and the regime is termed skimming flow. Here, the entire surface is within the protected wake region even though there may be a considerable proportion of bare sand. Wind tunnel experiments using elements of similar size and shape established that skimming flow should result at plant covers of 40 % and above (Table 2.2).

Table 2.2 Flow regimes and associated roughness concentrations from flow experiments (from Wolfe and Nickling 1993).

	Roughness element descriptions		
Flow Regimes	Spacing to height ratio (S_p/h)	Per cent cover (C) %	Roughness concentration (L_c)
Isolated roughness flow	>3.5	<16	<0.082
Wake interference flow	3.5-2.25	16-40	0.082-0.198
Skimming flow	<2.25	>40	>0.198

Typically, skimming flow is believed to be associated with vegetation types such as forests or crops where individual plant spacing is close and the canopy essentially closed. In arid systems isolated roughness and wake interference flow would dominate. Within these flow regimes, a significant proportion of the force of the wind may extend to the surface to act as a mechanism for wind erosion. The degree of erosion protection provided by vegetation under each of these forms of flow is still uncertain, as is the more fundamental question of how much vegetation cover is required within each flow regime. A useful parameter used in this context is the roughness concentration.

The actual velocity profile over a vegetated surface depends in part on the size, geometry and arrangement of plants. For solid roughness elements the relevant variables include height, width, shape, spacing and arrangement. For plants, additional variables including porosity and flexibility may have to be considered. A useful measure relating aerodynamic variables to roughness element geometry and spacing is roughness concentration (L_c, Table 2.2), defined as the ratio of the sum of the upwind projected areas of the roughness elements to the floor area:

$$L_c = (nA')/S$$

where n is the number of elements on the surface area, S and A' is the upwind projected area of each element, equivalent to the product of the average element height and diameter. The roughness concentration is a convenient variable which summarises the geometry and spacing of plants (or other roughness elements) in a dimentionless manner. Musick and Gillette (1991) use roughness concentration as a variable to describe sparsely vegetated surfaces. When plant cover is low, the roughness concentration is low (≈0.001) and the roughness length (z_o) approximates that of the surface. Roughness length is related to the height (h) and the roughness concentration of the obstacles:

$$z_o = 0.5hL_{cm}$$

where 0.5 is an approximation of the average drag coefficient of obstacles. As plant cover increases the surface becomes physically rougher and the roughness length increases proportionately to a maximum, L_{cm}. Above this maximum the surface becomes smoother as plant density increases, the elements become mutually sheltering with full wake interference approaching skimming flow. It must be remembered though, when one is dealing with vegetation, plant porosity results in greater flow scatter and consequently at higher roughness concentrations, roughness length decreases more slowly than predicted.

The precise effect of sparse plant cover on the transport of dune sand by wind is a critical factor in understanding the morphology, evolution and global distribution of aeolian dunes. It is also of considerable practical importance in sand stabilisation, rehabilitation and restoration ecology. Buckley (1987) derived a simple equation that quantifies this effect using living plants that approximate natural vegetation. For wind velocities V up to 15 ms^{-1} and plant cover C up to 17 %, the rate of aeolian sand transport, q ($g.cm^{-1}.s^{-1}$), is closely approximated by the equation:

$$q = B(V(1-kC)-V_t)^3$$

where B is Bagnold's constant (Bagnold 1941), V_t is a threshold velocity for sand movement, and k is constant dependent on plant geometry. For typical small erect or spreading herbaceous dune plants, k = 0.018; for small rounded stemless plants k = 0.046.

What Buckley (1987) does highlight is the significant effect sparse vegetation can have on reducing sand movement. For a wind velocity of 10 $m.s^{-1}$, the cut off plant cover were there is no more sand movement (viz. q= 0) is 37 % and for a wind velocity of 15 $m.s^{-1}$ it is 43 %. At a wind velocity of 15 $m.s^{-1}$, a plant cover of roughly 10 % will reduce the rate of sand movement by 50 %. The threshold velocity for bare unvegetated dune sand movement is approximately 3.33 $m.s^{-1}$. For vegetated sand this value increases by $V_t/(1-kC)$, thus for erect or spreading plants with a cover of 17 % this value is, for example, 4.8 $m.s^{-1}$. These calculations were made using dry sorted dune sand. Clearly, wet sand will not behave in at similar manner.

These numbers provide useful insights on where and how much sand is moving in a vegetated dune landscape, simply by looking at the vegetation. By examining the threshold velocity of sand movement one can estimate minimum wind speeds required for sand to be moved in any given dune vegetation type. These insights are also useful for determining minimum requirements for revegetation density and architecture.

One aspect of wind-vegetation interaction not explicitly examined in the literature is that of wind gusts. All the above equations were derived using constant flow or stationary winds. This does not accurately represent the situation encountered in natural systems. Gusts are significant in vegetation where canopy gaps allow gusts to penetrate the to the bottom of the canopy and spread outward. Before we can gain an accurate understanding of the erosive properties of wind it will be necessary to integrate the variable nature of wind into the above equations.

4 The physical, chemical and ecological properties of dune soils.

The nature and properties of dunes in arid and humid climates differ substantially (Tinley 1985). In the following discussion the focus is exclusively on sand dunes occurring in arid climates and, more specifically, those occurring in the southern Namib Desert on the west coast of South Africa. Tinley (1985) provides a more detailed account of littoral dune systems for South Africa as a whole.

4.1 What are dune soils?

To a geologist, marine derived dune soils are referred to as quartzose, shelly, well-sorted sands (Tinley 1985). Coastal dune sands are composed chiefly of lighter quartz minerals of terrestrial origin and calcite from sea shells. Much of the sand comprising the Namaqualand Sandveld has been described as feldspathic sands of terrestrial origin (Scott *et al* 1994). This sand can be placed in two broad categories. Terrestrial sand that has been deposited in a marine environment as river load, and subsequently deposited and reworked on the sea-shore, is the dominant category. Sand reworked through a marine environment has a typically high calcium content and is also well-sorted where fines in the form of clays, and to a lesser degree silts, are either washed out and are not present in recent near-shore dune deposits or are removed by aeolian reworking of the sand. This provides an extremely poor habitat for plant growth because it contains very small quantities of fine-grained particles, organic matter and nutrients

(Danin 1991). Another important feature attributed to the marine environment is that any ferrous oxides present on the grains of quartz when they entered the fluvial environment are washed out in the reducing aqueous environment. Thus, when sand is deposited on the sea shore it is white and devoid of any iron compounds.

The second category of sand comprises sands of terrestrial origin deposited on the banks of rivers, and subsequently reworked without entering the marine environment. These sands do not occur within the study area. Such sand is typically less sorted with a greater range in grain sizes, coarser, and more acid due to the absence of calcium. In Namaqualand, these sands support Sand Plain Fynbos vegetation as opposed to the Strandveld that occupies the marine sands.

In addition to the quartz (silica) and calcite, these sands may also contain a selection of heavy minerals present in the soil when it was first eroded from the water catchment. The distribution of these heavy minerals is very patchy and depends largely on the geology of the catchment of sediment origin. Mining of these heavy mineral deposits on the west coast is already underway. The Namaqua Sands Project at Brand se Baai, is an example, where ilmenite, rutile, zircon and magnetite is mined from surficial deposits of the minerals. Another significant deposit of these minerals lies on the north bank of the Groen River (Namaqua Sands pers. comm.). The prevalence of a low rainfall arid environment means that the minerals remain as surface deposits and are not eluviated through the soil profile. The significance of these minerals, up to 14% of soil volume (Namaqua Sands pers. comm.), on the occurrence and physiology of plants has yet to be understood, although investigations are underway (D. Keys pers. comm.).

With age, the white littoral sands change colour as a result of aerobic weathering of the feldspars and heavy minerals resulting in ferruginization of the dune sands and development of clay minerals (Tinley 1985), and as a result of aeolian inputs of clay particles into the soil profile from off-shore berg winds (see Box 2.3 The red colour of sand). This ageing results in the colour sequences observed as one moves away from the coast or along dune age gradients from white littoral sands through pallid or whitish-grey sands to the orange (yellow brown) to orange-brown sands that characterise much of the Namaqualand Sandveld. In terms of the South African binomial soil classification system (Soil Classification Working Group 1991) this sequence can be categorised by the Beachwood pallid non-red regic and the Henkries red regic sand of the Namib Form through to the fersiallitic dystrophic families of the Hutton Form (Tinley 1985, Scott *et al* 1994).

Despite their singular unifying characteristic of loose quartz sand grains, dune arenosols comprise a large variety of forms and series depending on the particular combinations and sequences of soil forming process to which they have been subjected, and to the intensity and duration of these (Tinley 1985). The predominant process is that of leaching (eluviation) where mobile components of dune soils are moved to lower horizons where they accumulate (illuviation) in the subsoil to form cemented hardpan formations. The two dominating mobile constituents in the dune soils of the west coast are calcium and silica which form calcrete and dorbank hardpans, respectively (see Box 2.2 Replacement products: calcrete, silcrete and dorbank). With the onset of dune stabilisation by vegetation, the deep amorphous dune soil profile of the near-shore zone is transformed into a structured profile characterised by loose surficial sand underlain by impermeable hardbank layers. For plants, the consequence of this impermeable layers is significant as it effectively restricts the available rooting depth. Plant growth on dunes also induce other changes in the substratum by trapping fine-grained particles and adding organic material, thus improving the local edaphic conditions. These changes facilitate the subsequent establishment and growth of other plants (Danin 1991).

4.2 General properties of sand.

Sand particles are loosely packed with intervening air spaces. The result is that they are well aerated and exhibit a seasonal and diurnal temperature change from warm to hot in the day in summer, to cool or cold at night in winter. Due to their open structure, sands are poor conductors of heat. Therefore, temperature drops rapidly from the surface downwards. They are excessively drained (i.e. have low water holding capacity). Sands are thus a dry and droughtly habitat. As there is no surface runoff, sands entrap any and all rain that falls. The deeper soil moisture is protected from evaporation by the loose sand surface through its poor conductance of water.

Due to their structureless profile and porousness, sands are easily leached and thus tend to be acid dystrophic substrata in humid climates. Dune sands of marine origin are typically alkaline due to their generally high calcareous content from finely divided shell fragments. They are therefore dominated by a single macronutrient in the formative and early stable stages prior to modification by leaching and deep weathering processes. Sand dunes on the coastal plain derived directly from rivers without marine influence tend to become acid on leaching. This could be a key variable in explaining the occurrence and distribution of Sandveld fynbos in Namaqualand.

Thus from the plant perspective, living on sand dunes present three major problems: (1) low water holding capacity; (2) high mobility of particles under strong winds; and (3) low nutrient content due to the nearly pure quartz substrate. Other important features of dunes of marine origin include (Tinley 1985):

(1) Since they are wind formed, aeolian winnowing selectively sifts the finer and lighter particles from the heavier. Hence finer sands and light shell fragments compose backdunes as they are carried further inland, and coarser sands occur in the foredunes. Between dune crests and slacks away from the foreshore a similar sorting occurs. Dune crests are a point of sand accumulation and high wind activity. Fines (i.e. clay and silt), if not leached out, are blown away by wind action. Here, the soils are typically deep loose sands. Dune slacks, on the other hand, are eroding or deflating environments where the illuviated sub-soil has been eroded. Therefore, they are generally shallow soils rich in fine eluviated material not yet subject to wind sorting.

2) Littoral sands, particularly within one kilometre of the sea, are subject to repeated deposition of salt from aerosols carried by onshore winds. The stronger the wind the greater the salt load deposited. This is one of the principal features separating coastal dunes from more continental desert dunes (Danin 1991).

3) The weathering potential is kept high all year round by warm moist conditions (high relative humidity and mild to hot temperatures).

4) On the west coast, dunes on the coastal plain receiving more than 30 mm annual rainfall can support ephemeral plant growth (Danin 1991) and greater than 50 mm mean annual rainfall dunes become stabilised by perennial plant growth (Tinley 1985). The stabilisation of dunes allows pedogenesis to proceed resulting in many co-related processes: (a) leaching of carbonated and silicates; (b) the build up of humus in the topsoil and formation of humus stained topsoil (grey sand); (c) loss of calcium may be offset by its high content in rainwater next to the sea, and deep rooted woody plants return calcium in their litter fall; (d) accumulation of plant waxes in the topsoil resulting in the formation of a water repelling, hydrophobic layer; and (e) the development of a hardpan layer and the concomitant restrictions on plant rooting depth.

4.3 The effect of high calcium content in dune sands.

Owing to their sea-shore and water-washed origin, coastal dune sands are alkaline and low in micronutrients. Their high calcium carbonate content further induces deficiencies in the nine elements, including aluminium, cobalt, copper, copper, iron, manganese, zinc and in boron, phosphorous and potassium, either by making them insoluble or inhibiting their availability (Tinley 1985).

High calcium content reduces the toxicity of sodium (also potassium and manganese) where this occurs in excess amounts, enabling plants to tolerate more brack conditions. Low available nitrogen, which is typical at least of the younger dunes, has also been found to increase the tolerance of plants to salt spray. Both features would be advantageous to plants growing on dunes next to the coast.

4.4 The thermal properties of sand.

Sand has thermal properties very different to those of loam or clayey soils. There are two parameters determining the thermal properties of sand: (a) texture and (b) soil moisture (Tsoar 1990). In sands with low or no vegetative cover, texture plays an important role in determining the thermal properties of its environment. Heat is absorbed from solar short-wave radiation and concentrated in the top ≈1 mm of the soil surface. The conduction of heat away from the surface into the cooler underlying sand is known as heat conduction. Thermal conductivity measures the rate at which heat passes through one unit thickness from a warmer area of sand into a cooler one, with one unit of temperature difference between the two. Quartz, the main constituent of sand, is a good insulator and has a low thermal conductivity. However, some 35-40% of sand volume consists of air filled pores which has an even lower thermal conductivity. Thus, the thermal conductivity of sand approximates that of water.

The ratio of the total amount of heat needed to increase the temperature of a unit mass of sand by 1°C to the total amount of heat required to raise the same mass of water at 15°C by 1°C is called the specific heat. Dry sand has a specific heat approximately one quarter that of water. Therefore, water requires a very large input of heat to increase or decrease its temperature relative to air. The result is that dry sand is much more sensitive to thermal changes than wet sand.

The rate at which modification of temperature take place in sand is in direct proportion to its thermal conductivity or its ability to transmit heat, but inversely proportional to its specific heat or the amount of heat required to achieve the modification of temperature (Tsoar 1990). Dune sand exposed to direct solar radiation during daytime transmits the surface heat only very slowly into the ground. This results in a very acute and thin near-surface accumulation of heat. As a consequence, sand temperature reaches maximum and minimum records. Within the first 30 cm of sand, soil temperatures can drop as much as 20°C (Tsoar 1990).

When sand is moist at a depth of 20 - 25 cm, the steep night temperature gradient from a depth of 30 cm up to the surface (maintained at depth and cold at the surface) favours a nocturnal upward flow of subsoil vapour and its distillation into the surface soil, thereby causing subterranean dew. The biological relevance of this source of moisture is in some doubt, however (Noy-Meir 1973).

4.5 Dune sand texture: environment-plant interaction.

The texture of sand is the factor that accounts for the poor vegetation cover and productivity on dunes. It includes low field capacity and a low value for soil moisture availability, as well as a high rate of permeability and leaching. The extreme mobility of loose particles of sand causes them to be easily swept away by wind in a leaping movement termed saltation (Whitten and Brooks 1972). This process is detrimental to plants as grains of sand bombard them causing damage and disease (Tsoar 1990, Danin 1991). This process generally only applies to "fine sand" (0.1-0.25 mm diameter particle size). Medium, coarse and very coarse sand (0.25-2.00 mm diameter) moves by surface creep knocked forward by saltating particles or rolled slowly by the wind. Very fine sand, silt and clay (<0.1 mm diameter) particles have low settling velocities relative to the velocities of the vertical component of turbulent wind flow. Therefore, these particles remain in suspension or quasisuspension in their transport mode and are considered dust (Tsoar 1990). They do not easily accumulate together with the sand unless the latter is covered by vegetation, thus serving as a trap for the suspended lower dust load in the atmosphere.

In addition to the wind sorting of sand particles on dunes through deflation and accretion, the soil profile is enriched by deposits of fines (clay and silt) from the interior (Danin 1991). Fines are trapped by the canopies of plants and deposited. Once the silt and clay content of the top layer reaches 1.5-2%, cyanobacteria may be found (Danin 1991). Their quality increases with time after their first establishment and with increasing amounts of fine grained components in the soil. This initiates a feedback process such that when a threshold fines content in the ground is reached, cyanobacteria establish themselves in the soil and increase sand stability by inducing an aggregation of soil particles (Tsoar 1990). When a surface crust is well developed there is nearly no removal of sand particles by wind (Danin 1991). With time the constituent organisms present in the microbiotic crust increases. They develop into assemblages of various non-vascular plants such as mosses, liverworts, algae, lichens, fungi, bacteria and cyanobacteria (Eldridge and Greene 1994). In addition to their sand stabilising properties, the cyanobacteria present in these microbiotic crusts have the ability to fix nitrogen, thus contributing to the soil nutrient status (Eldridge and Greene 1994). Algae and lichens become an important source of amino nitrogen, oxygen (Tsoar 1990) and organic carbon. Biological soil crusts form an integral part of the dune environment as indicators of sand mobility or land degradation (through human or livestock activities) and through their contribution to the ecosystem structure and functioning. In addition to this, the increase in fines improves the soil water retention capacity and also increases the cation exchange capacity of the soil, thus improving fertility.

The above ecological changes in dune system as a result of plant-environment interaction results in a number of positive feedbacks (Tsoar 1990). The biogenic crust and sand layers are less mobile and can support denser vegetation. This in turn, brings about additional deposition of fines, all of which will eventually lead to plant succession as the properties of the sand substratum are modified. This phenomena of dust settlement promoting dune stabilisation and plant succession is restricted to arid climates. Vegetated dunes in Rice Valley, California contain fines between 4.5 and 6.6%. For Australia, the content is 5% and in the Negev desert this is between 5 and 10% (Tsoar 1990). Fines are, however, absent from the coastal vegetated dunes of The Netherlands because the high rainfall leads to rapid leaching of fines into the subsoil (Tsoar 1990). Mobile dunes are potentially more prone to stabilisation in arid areas than in more humid climates where dust is scarce and leaching high. At the same time vegetated dune systems in arid climates are extremely sensitive to erosion as trampling of the soil crust and removal of plants opens the sand surface to the wind erosion.

Another environment-plant interaction common in dune environments is the creation of phytogenic mounds or phytogenic hillocks (Danin 1991). As sand is deposited around the aerial shoots of plant, mounds begin to develop. Where there is high sand mobility (e.g. the near-shore zone) these mounds may be a few centimetres in diameter or develop into large dunes measuring a couple of meters in diameter and height (Danin 1991). The size of these mounds is potentially an indicator of sand activity, but also the ability of some plant species to persist under constant deposition of sand by the production of new shoots which remain above the soil surface.

4.6 Sand-water regime in dunes.

Coarsely grained sands have relatively large voids in between the grains and this accounts for their low moisture tension. As a result, active dune sand without vegetation has the lowest moisture content at field capacity. Water easily percolates in the sand and the soil moisture availability to plants tends to be relatively very low. The volumetric available water content for sand usable by plants (which is between wilting point and field capacity) is 3-9% (Noy-Meir 1973). Dune sand has approximately 1.28% moisture content at wilting point (Tsoar 1990). The advantage of dune sand in deserts is that a small amount of water input brings sand to above wilting point, while the same amount of rainfall in a loamy soil is still below wilting point. The amount of biomass resulting from 1 mm of rainfall on sandy soils is 2.5 times higher than that produced on fine textured soils (Le Houérou 1986).

On well-graded dune sand consisting of an overall particle size of 0.15 mm, 1 mm of rain penetrates to an average depth of 7 mm, whereas on coarser sand of 0.3 mm, 1 mm of rain achieves an average of 20 mm penetration. Finer soils with better field capacity than sand reduce percolation to much smaller depths. In a loessial soil the same amount of rain penetrates to 5 mm and in clay to only 2 mm. This rate at which water percolates through or permeates sand is known as the hydraulic conductivity of the soil (Tsoar 1990)

Because dune sand offers deeper percolation where moisture is protected from evaporation during dry periods, moisture retention is assured in sand below the upper 30 cm. Hence, desert sand may allow for relatively more vigorous and longer lived mesophytic shrubs than fine grained soils in similar climates. Desiccation of deeper sand layers slows down progressively. In desert sands, the first 5-10 cm of the upper layer are mostly dry within 5-25 days after a significant rainfall event, whereas is takes several weeks for evaporation to dry up the remaining 10-30 cm, and at greater depth there is little direct evaporative loss. Sands can maintain soil moisture above wilting point down to several meters (Tsoar 1990). This favours deep rooted perennial plants as opposed to shallow rooted ephemerals.

Mobile dune soils have little or no vegetation because: (a) the resulting denudation of roots and bombardment by sand particles generally kills plants (Danin 1991); and (b) the loss of soil moisture in mobile sand creates a hyper-arid environment (Tsoar 1990). Sand mobility, not low soil moisture, is the primary limiting factor for vegetation on dunes in both arid and humid climates (Bowers 1982). The better soil moisture properties of sand in arid environments promotes the colonisation of the sand surface by plants. This in turn slows down the rate of sand movement, decreases erosion, reduces the exposure of moisture in the sand to evaporation. The addition of plant organic matter to the soil further benefits the soil moisture regime.

The soil moisture properties of sand of the same particle size distribution can differ as a result of soil organic matter content (Kutiel and Danin 1987). Greater soil organic matter content improves the water holding capacity of dune soils. Plant species diversity and above ground phytomass show a positive correlation with soil moisture content (Kutiel and Danin 1987).

5 Climate of the West Coast between Port Nolloth and Alexander Bay.

5.1 Overview of regional climate.

The study area is located within a region which experiences a relatively cool, dry desert climate. Temperatures are moderated by the cold Benguela Current and low incidence of rainfall are controlled by the South Atlantic Anticyclone, which maintains an almost isothermal atmosphere over the Namaqualand coast (Preston-Whyte and Tyson 1988). The predominantly southerly winds cause the upwelling of the Benguela system which cools and stabilises the near surface air mass and reduces the potential for rainfall occurrence. The climate of the Namib Desert is very much under the influence of the ocean and the cold Benguela Current (Schultze 1965) and can be characterised by extreme aridity on the one hand, and an abundance of fog on the other (Olivier 1995).

Climatic processes are of fundamental importance in determining the structure and functioning of this coastal ecosystem. This section provides a brief overview of the climate and the major climatic indices and variables. This discussion is aimed at creating an understanding of those climatic variables which best explain the regional climate as well as vegetation patterns and processes that are a direct consequence of the climate.

5.2 Palaeoclimates of the southern Namib.

A discussion on the palaeoclimates of the Namib Desert needs to consider the geographical location and shape of the desert when relating available evidence for palaeoclimates in southern Africa to that of the southern Namib Desert. The Namib comprises a narrow track of land, some 2000 km long and mostly less than 200 km wide (Ward *et al* 1983), lying west of the Great Escarpment between the Olifants River in the south and the Carunjamba River in Mocamedes District in southern Angola. Any discussion on the palaeoclimate of the southern Namib or Namaqualand Sandveld needs to consider both the climate scenarios developed for the central Namib Desert and also those relating to the south-western Cape which merges with the Sandveld in the south. Knowledge of the regions palaeoclimates, especially the recent past (ca. 125 000 BP), contributes much to our understanding of observed trends in the distribution of geological features (e.g. sand dunes or calcretes); palaeovegetation relics (e.g. subtropical dune thicket species, *Euclea racemosa*, growing at Koingnaas, 200 km north of the Olifants River well below the 100 mm isohyet; or *Capparis hereroensis*, a northern Namib endemic, growing in the Bitter River dunes (van Jaarsveld 1994)); or the present vegetation matrix.

The causes and age of the aridity in the Namib, and their effects upon the evolution of its endemic biota have been the subject of considerable debate (Van Zinderen Bakker 1975, Tankard and Rogers 1978, Ward *et al* 1983). The available geological evidence indicates a long history of arid climates in the region. The Namib has not experienced climates significantly more humid than semi-arid for any length of time during the last 80 million years (Ward *et al* 1983). Hyper-arid conditions developed from the Late Miocene (7-10 million years ago) onwards (Ward *et al* 1983, Deacon and Lancaster 1988), following the intensification of upwelling by the Benguela Current. Prior to this intensification of the Benguela Current, marine mollusc assemblages reflect significantly warmer ocean temperatures (Ward *et al* 1983). During this period of the Early to Mid-Miocene, the palaeoclimate of the Namib was probably never more than semi-arid and even though rainfall was, at times, considerably higher than at present, "a torrential rainy season and a long dry winter seem to have been the rule" (Ward *et al* 1983). Fossil faunal evidence from sites such as Arrisdrift on the Orange River (Corvinus and Hendey 1978) have been used to suggest widespread savanna conditions throughout the southern Namib during this period. These interpretations do not agree with lithological evidence for the period. In addition, the occurrence of large mammals, including elephant, black rhinoceros, giraffe and lion, still occur well within the current extreme-arid sections of the Skeleton Coast and are associated with riparian habitats such as the Arrisdrift fossil beds (Ward *et al* 1983). Geological evidence from the cross-bedding of palaeo-dunes indicates that throughout the Tertiary, southerly winds predominated. By the onset of the Pliocene, the present semi-arid, winter rainfall climate that characterises the southern Namib today was established (Tankard and Rogers 1978).

Throughout the Quaternary, climatic fluctuations in the central Namib appear to have been of a low amplitude and superimposed upon an arid to hyper-arid mean (Lancaster 1984, Partridge *et al* 1990). The surface survival of end Miocene calcrete palaeosols and lacustrine carbonates suggests that no very humid climates have affected the region in the Late Cainozoic (Deacon and Lancaster 1988). Ward *et al* (1983) argue that the Namib has experienced no climate wetter than semi-arid since the end-Miocene, 5 million years ago.

The palaeoclimate of the central Namib during the Quaternary is characterised by a gradual intensification of arid conditions (Ward *et al* 1983). Pollen samples from deep sea cores taken on the Walvis Ridge show no significant changes throughout undated Pleistocene sequences, which are dominated by Graminaceae, indicating that although there were intervals when the climate was more humid than at present, it was never wet enough to cause major changes in the composition of the vegetation of the central Namib (Deacon and Lancaster 1988). Evidence from fluvial deposits (Lancaster 1984, Ward 1984) and marine sequences (Tankard and Rogers 1978) suggests that there was a progressive increase in aridity throughout the Pleistocene.

Evidence from cave deposits on the southern Cape coast indicate a general cooling in the climate from the Last Interglacial where the fauna, dominated by large mammalian browses similar to what occurred there in historical times, were replaced by migratory herds of grazers.. This shift in the fauna over the period 125 000 to 70 000 BP, was a result of a shift in the vegetation from bush dominated to a more grassy vegetation. The scenario for the west coast appears to be somewhat different though. Evidence from marine mollusc assemblages and evaporite deposits indicate that hot, dry conditions prevailed along this coast during this period (Tankard 1976).

The northward shift in the westerly belt and the frontal systems associated it with the Last Glacial Maximum would have seen a northward migration in the winter rainfall belt of the southern Cape (Van Zinderen Bakker 1976, Tankard and Rogers 1978, Lancaster and Deacon 1988, Partridge *et al* 1990). Thus, the southern Namib experienced a cooler, wetter winter rainfall climate leading up to the Last Glacial Maximum. Evidence from stable carbon isotopes shows that in contrast to the changes observed in the carbon-13 content of bone collagen in Zebra teeth from Melikane Cave in Lesotho, Zebra teeth from Late Pleistocene (ca. 70 000-20 000 BP) and Holocene (7000 BP) units at Apollo 11 Cave excavated on the eastern margin of the southern Namib Desert, show no appreciable difference (Vogel 1983). This suggests that C3 grasses did not spread into southern Namibia during the Late Pleistocene, indicating that this northward migration in the winter rainfall regime did not extend much further north in the Late Pleistocene than it does today.

Presently available dated palaeoclimatic information for the central Namib is confined to the last 32 000 years (Deacon and Lancaster 1988, Partridge *et al* 1990). In the period from prior to 32 000 to 20 000 BP the region appears to have been substantially wetter than today with inter-dune lake and pond deposits in the Namib Sand Sea. River flow was also stronger than present (Ward 1984). A drying trend was present locally after 27 000-26 000 BP. Cool conditions are evident around 23 000 BP. The period spanning the Last Glacial Maximum (20 000-16 000 BP) appears to have been dry in the central Namib. The interval from 16 000 to 12 000 BP sees a renewal of increased moisture availability in the central Namib, continuing until around 11 000 BP. For the Holocene, the climate appears to have been slightly moister than it is today, with a dry interval around 2500 BP.

The large and small mammals, charcoals and pollen records all confirm that the period between 80 000 and about 25 000 BP was distinctly cooler than the present, but not as cold as in the Last Glacial Maximum (Deacon and Lancaster 1988). There is evidence from the charcoal and micromammalian data for moister periods, but the larger mammal fauna shows little variation, being dominated throughout by equids and alcelaphines (Deacon *et al* 1984). The coldest and driest conditions of the last 125 000 years date to the Last Glacial Maximum from 20 000 to about 16 000 BP where temperatures are estimated to be 5°C lower than at present (Deacon and Lancaster 1988). Dry conditions, however, pertain to the southern Cape and appear to differ substantially from recent scenarios developed for the south-western Cape for this period (Cartwright *et al* in press). The vegetation in the southern Cape at the time was again markedly grassier and more open than at present with low species diversity in charcoal, pollen and micromammal records (Deacon and Lancaster 1988). Charcoal and pollen records from the western Cape (Elands Bay Cave) indicate the presence of species characteristic of Afromontane (temperate) rainforest (Cartwright *et al* in press). Despite the fact that the winter rainfall regime on the west coast moved no more than one or two degrees further north during the Last Glacial Maximum, the intensity of this climate no doubt increased in the southern Namib creating conditions substantially wetter than those experienced today. The occurrence of this wetter epoch would explain the presence of anomalies or palaeorelics in the contemporary vegetation of the area such as *Euclea racemosa* which is characteristic of mesic dune thicket vegetation in the south and south-western Cape today.

In the period between the end of the Last Glacial Maximum and the beginning of the Holocene 10 000 years ago, dramatic changes can be seen in the biological data that relate to the relatively sudden rise in global temperatures and the subsequent adjustment of plant and animal communities. This shift is more dramatic in the southern and south-western Cape than elsewhere and was initiated before 14 000 BP. This period was much warmer and wetter in this region than in either earlier or later times (Deacon and Lancaster 1988). The vegetation responded by a shift from grass dominated to a tree and shrub dominated matrix. All data examined from the southern Cape show that the last 10 000 years have been markedly warmer than at any other time during the last 100 000 years, although a marginally cooler interval is suggested in the last 2000 years based on micromammalian and pollen studies (Deacon and Lancaster 1988).

These dramatic shifts in climate and vegetation subsequent to the Last Glacial Maximum in the southern Cape were not reflected in the palaeoclimate nor vegetation of the central Namib (Partridge *et al* 1990). The changes in the climate of the southern Cape, however, must have had an influence on the winter rainfall regions of the southern Namib. The southward shift in the location of the South Atlantic Anticyclone associated with this period (Van Zinderen Bakker 1976, Tankard and Rogers 1978) would have resulted in a drying of the southern Namib environment due to a decrease in the extent or intensity of the winter rainfall regime.

The palaeoclimate of the Namib Desert is characterised by a history of semi-arid to arid conditions, at least for the last 80 million years. For the most part this arid climate appears to have been a summer rainfall, winter drought regime with the shift to a winter rainfall regime with frequent fog associated with the full development of upwelling of the Benguela Current at the close of the Miocene. The overall trend throughout the Quaternary has been one of progressive aridification on which the climatic and eustatic fluctuations of the last approximately two million years have been superimposed. The margins of the desert may have been affected by latitudinal shifts of the climatic belts during glacial/interglacial cycles, but the main arid to hyper-arid core of the desert was probably never eliminated (Ward *et al* 1983).

5.3 A Note on the weather stations.

Climatic statistics quoted in this section come primarily from the Weather Bureau's Annual Reports (WB references). The data from three weather stations are used in this analysis. The first weather station was situated in Alexander Bay town and operated between the years 1931 and 1950 (28°37'S 16°29'E, alt. 12 m), after which the weather station was moved to the town's international airport (28°34'S 16°32'E, alt. 21 m). This station, Alexander Bay WK (Weer Kantoor), was in operation from 1951 till 1984. Today there is no state-run weather station in the area. EMATEK have erected an automatic weather station at the mouth of the Orange River. The third station used here is situated just north of Port Nolloth (29°14'S 16° 52'E, alt. 4 m). It was established in 1920 and is still in operation today.

Measured as a straight line, the distance from these stations to the coast on a SW bearing, is 1 km (Port Nolloth), 3 km (Alexander Bay) and 10.4 km (Alexander Bay WK). Past interpretations of the climatic data from these stations have failed to take note of the these differences in distance from the coast (e.g. Burns 1994). These have resulted in misguided impressions of the coastal climate in terms of latitudinal change and rate and degree of change as one moves away from the coast. This spatial difference must be kept in mind when interpreting the data presented below, especially the fog data.

5.4 Precipitation.

5.4.1 Rain.

The mean total annual rainfall measured at Port Nolloth is 63 mm, 41 mm at Alexander Bay and 46 mm at Alexander Bay WK (Schultze 1965). Rainfall events tend to be distributed between April and August and peak during May, June and July for all stations.(Fig. 2.7). The highest mean monthly rainfall does not exceed 10 mm for all stations. Rainfall decreases from south to north which is reflected in an increase in the unreliability of the rainfall received expressed as co-efficient of variation of average monthly rainfall (Fig. 2.8).

The reliability of the little rain that does fall requires further investigation. The coefficient of variation (CV) for the average monthly rainfall data (Fig. 2.8) demonstrates that only during the winter months (June, July, August) does CV rainfall approach 100%. Rainfall events in summer are highly unpredictable. CV is not necessarily the best method to determine predictability of rainfall as CV is log-linearly and negatively related to rainfall (Fisher 1994). Analysis of time series data for the three weather stations provides an alternative view and demonstrates a similar trend to the CV (Fig. 2.9 and 2.10). There is an indistinct seasonal trend superimposed on a longer term cyclical trend of rainfall increase and decrease (Fig. 2.9). Auto-correlation analysis (Fig. 2.10) of these time series shows that the seasonal auto-correlation in the rainfall data is weak (autocorrelation coefficient <0.2, Fisher 1994) reflecting the poor predictability of the rainfall received from one season to the next.

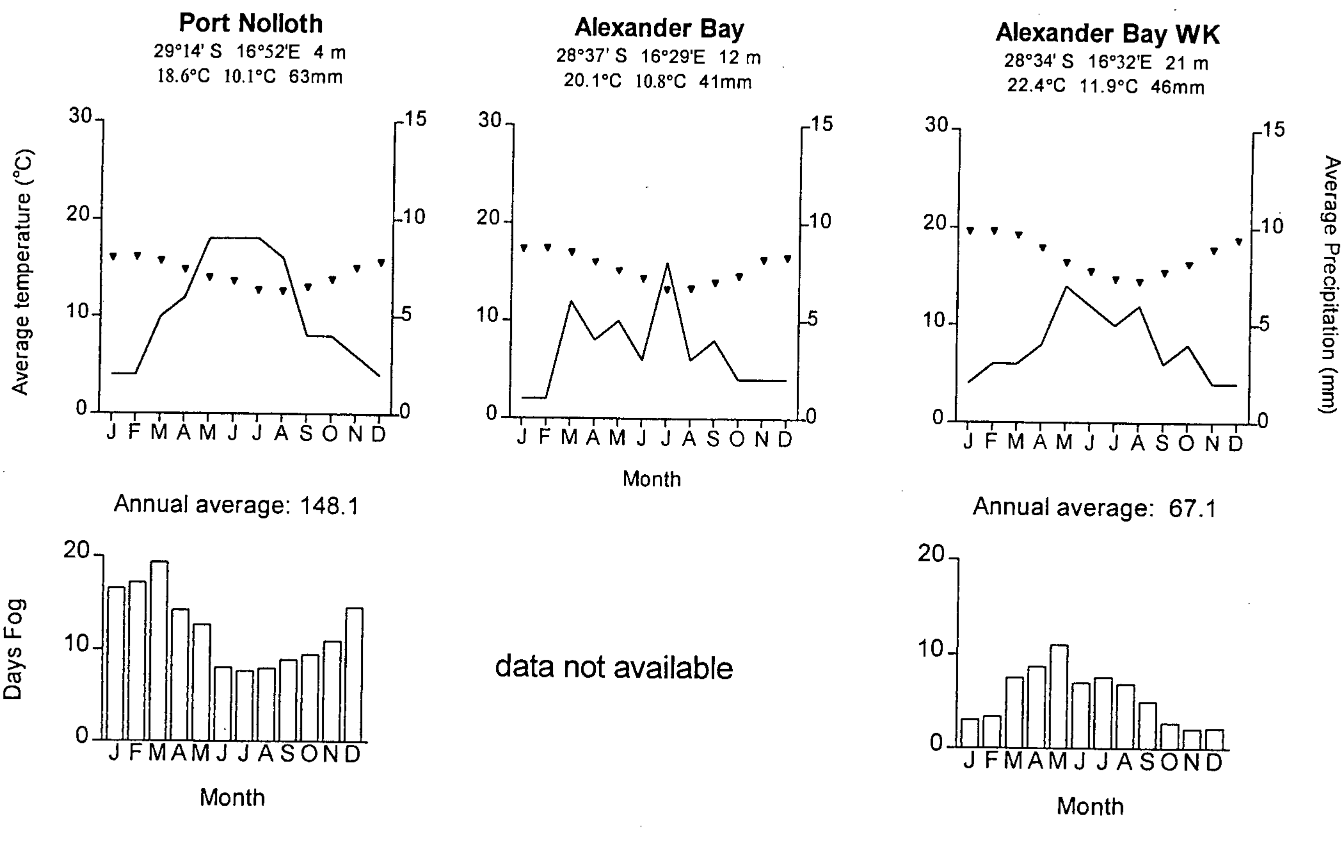


Figure 2.7 Climograms for the 3 weather stations using the scale of temperature = 0.5 rainfall suggested by Fisher 1994.

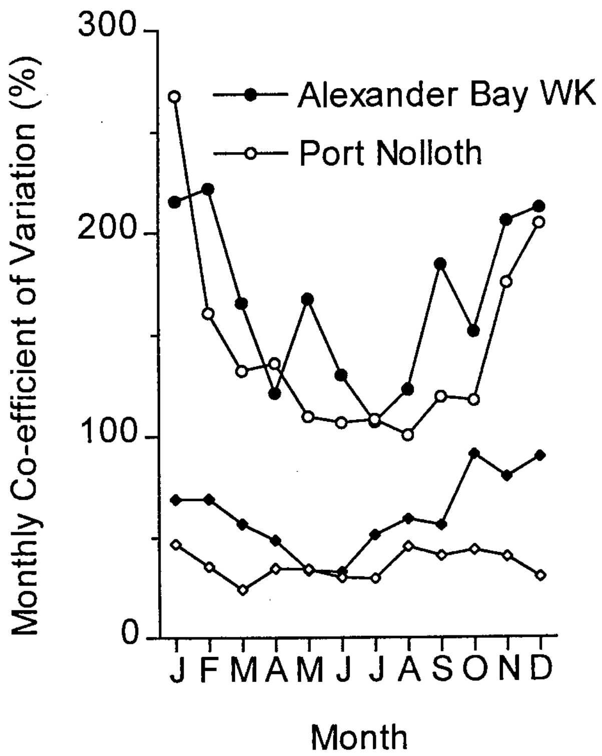


Figure 2.8 Co-efficient of variation of monthly rainfall.

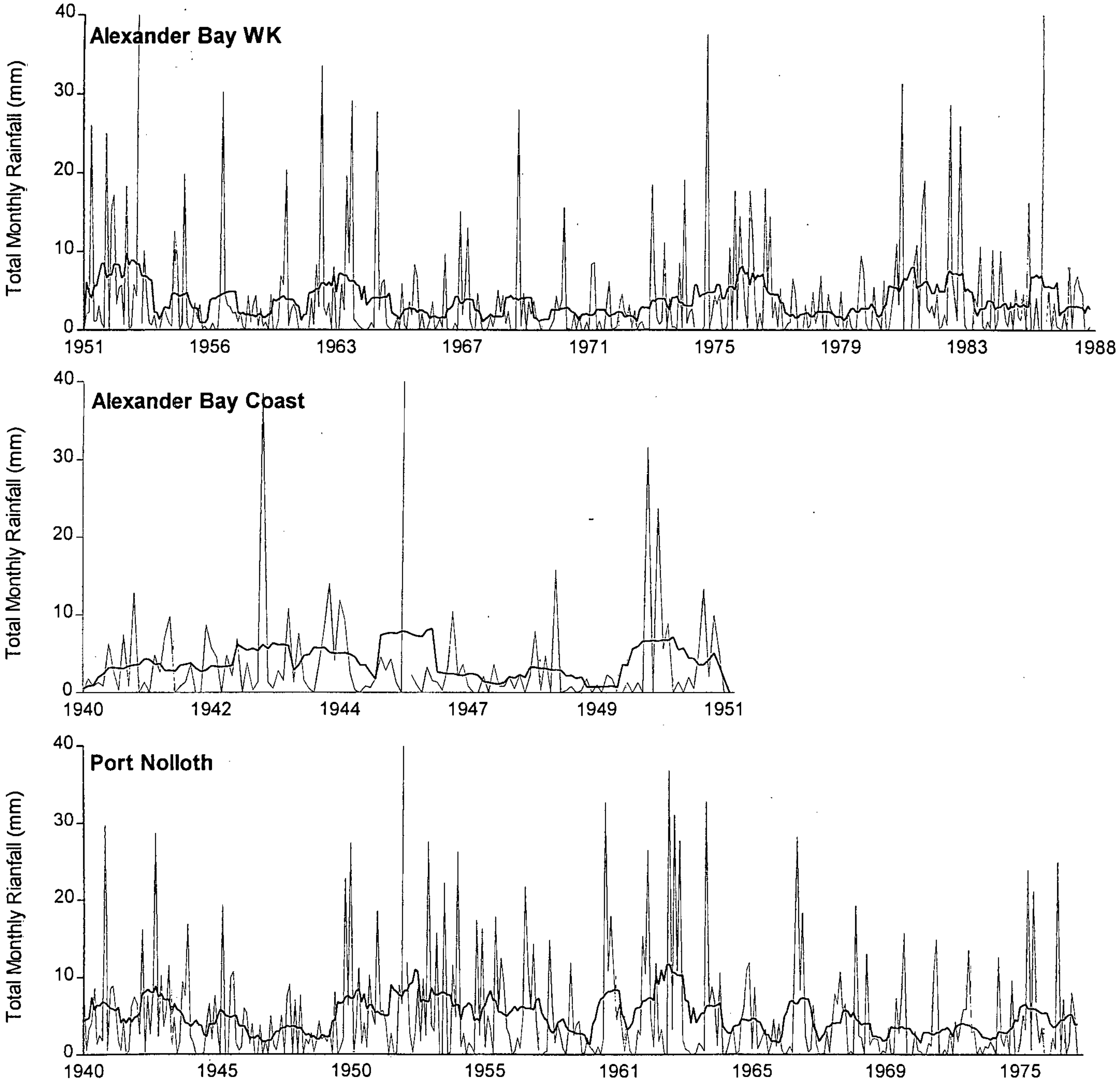


Figure 2.9 Rainfall time series for the 3 stations. The thick solid line is the running mean (5 points either side) and the thin solid line the actual monthly totals.

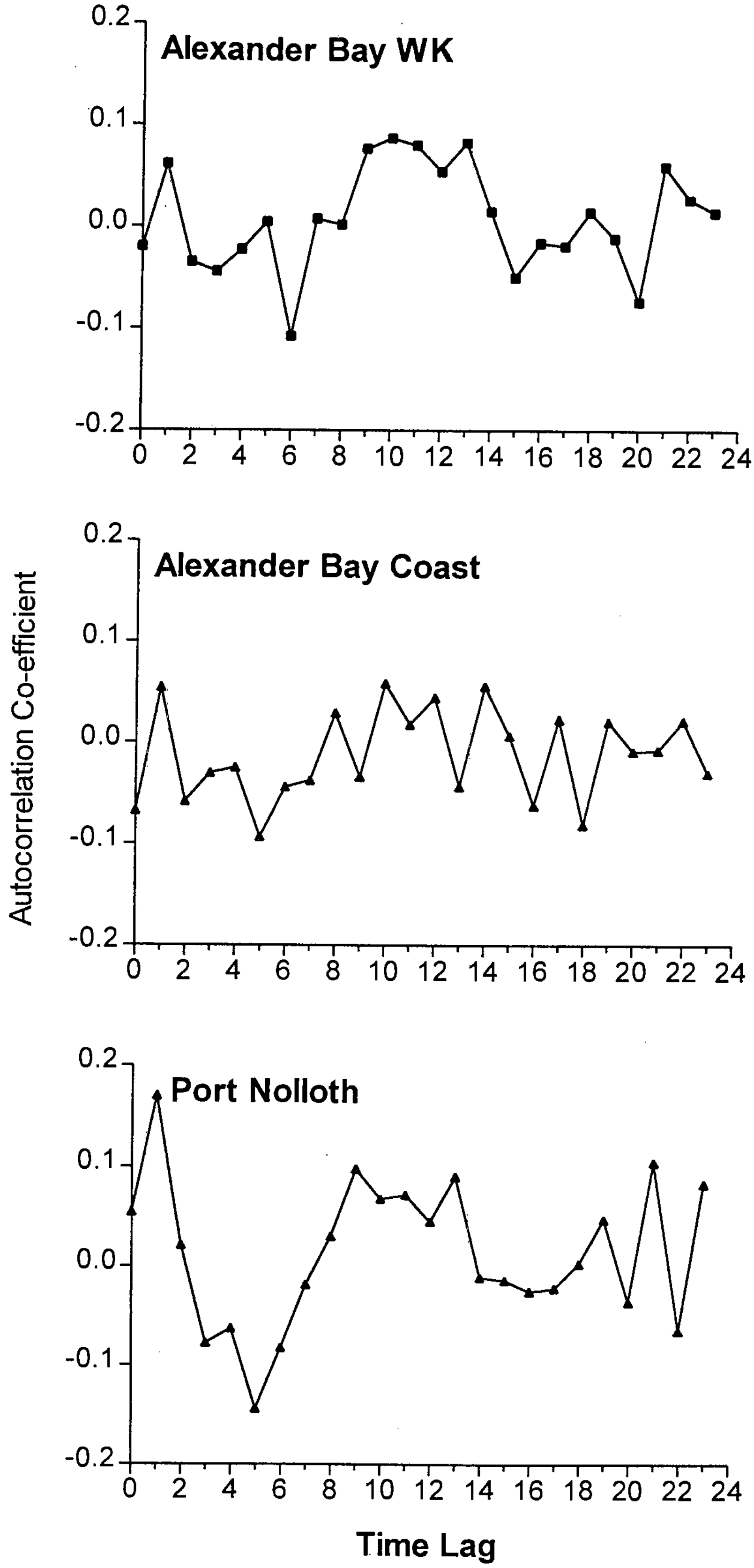


Figure 2.10 Auto-correlation coefficients for monthly rainfall data to 24 lags.

Extreme rainfall events such as thunder-showers, cloud-bursts, snow and hail are rare to non-existent (Tables 2.3, 2.4 and 2.5). Thunder can be heard on less than one day per year at Alexander Bay. At the airport, thunder is heard on average 7 days per year and at Port Nolloth less than 3 days per year (Schultze 1965). The occurrence of thunder is more frequent in the summer months. Occurrence of hail is insignificant having never been recorded at Alexander Bay and a yearly average of 0.1 day per year at Alexander Bay WK and Port Nolloth (Schultze 1965).

Rainfall in the southern Namib Desert on the coast of Namaqualand between Port Nolloth and Alexander Bay is minimal, and for the most part highly unpredictable. Rain that does fall arrives in the winter months and consists of soft, gentle rains. Large rainfall events, > 10 mm, are rare and usually arrives as soft falls over several hours and not in short cloud bursts. However, rainfall variability is such that there is never a year when rain never falls. Thus the occurrence of sever drought (i.e. years with no rainfall) is a very rare phenomenon.

5.4.2 Fog.

Clouds form when air is supersaturated with respect to water or ice (Preston-Whyte and Tyson 1988). One manner in which this can occur is by the mixing of air. Advection fog occurs when warm air with high relative humidity is advected over a cool surface. The temperature differential between air and surface must be sufficiently large to enable the air to reach saturation after a small amount of cooling. Medium velocity winds are also necessary in the advection process since strong winds would cause too much turbulence and vertical mixing to maintain the fog, whereas low wind speeds would provide too little advection and mixing. When air over the Atlantic Ocean moves across the leading edge of the cold Benguela Current flowing northwards along the west coast, temperature is depressed to dew point and fog forms. The coastline constitutes another leading edge with air moving over a hot, arid desert. Inland movement of fog is therefore limited by the arid nature of the new surface conditions and the fog thins and evaporates downwind. By day this process is hastened by surface heating.

Table 2.3 Occurrence of extreme rainfall events at Alexander Bay WK (data from WB 40).

Precipitation Highest on record in (mm):	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
15 mins.	1.4	7.0	5.8	3.0	7.3	5.6	2.8	6.3	1.7	1.3	1.9	3.4
60 mins	3.1	19.7	11.5	3.6	15.5	7.9	5.5	8.3	3.2	1.8	6.0	8.1
24 hours	6.5	28.0	16.5	6.6	39.0	19.5	9.7	21.3	7.4	3.4	19.3	17.1

Table 2.4 Size of rainfall events with average and maximum for selected return time periods for (a) Port Nolloth, (b) Alexander Bay WK and (c) Alexander Bay (data from WB 40).

No. of days with precipitation:		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
(a) Port Nolloth														
0.1 mm	Average	1.6	2.0	2.3	2.5	3.5	3.3	3.6	3.5	2.4	2.6	1.9	1.5	30.7
	Maximum	11	10	11	8	11	9	13	9	9	8	6	6	
1.0 mm	Average	0.5	0.6	0.9	1.1	1.7	1.9	2.1	1.8	1.2	1.2	0.9	0.7	14.6
	Maximum	3	4	3	5	6	5	6	6	5	4	5	4	
10 mm	Average	0.0	0.0	0.0	0.1	0.1	0.1	0.1	0.2	0.0	0.0	0.0	0.0	0.6
(b) Alexander Bay WK														
0.1 mm	Average	1.0	1.3	1.6	2.3	2.7	2.6	2.8	2.9	1.9	2.6	1.5	1.4	24.6
	Maximum	5	5	5	6	11	6	6	7	4	6	7	5	
1.0 mm	Average	0.3	0.6	0.6	1.0	1.4	1.3	1.5	1.4	0.6	0.9	0.4	0.5	10.5
	Maximum	3	3	4	4	7	4	4	5	2	4	3	3	
10 mm	Average	0.0	0.0	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.2
(c) Alexander Bay														
0.1 mm	Average	0.9	0.8	1.1	1.1	2.1	1.7	2.7	1.7	2.2	1.34	1.3	0.9	17.9
	Maximum	4	2	44	3	4	4	7	6	6	5	4	3	
1.0 mm	Average	0.7	0.3	0.6	0.7	1.1	1.1	1.9	0.9	1.2	0.6	0.6	0.5	10.2
	Maximum	1	1	4	3	3	3	6	5	3	2	2	2	
10 mm	Average	0.0	0.0	0.1	0.1	0.1	0.1	0.2	0.1	0.1	0.0	0.0	0.0	0.8

Table 2.5 Highest monthly average rainfall for the three weather stations (data from WB 40).

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Port Nolloth	12	19	29	37	45	48	51	49	27	27	30	27
Alexander Bay	5	12	46	19	16	12	32	20	23	10	13	10
Alexander Bay WK	8	28	39	18	46	28	26	34	26	31	20	18

The predominance of colder coastal ocean surface temperatures during summer, as a result of the seasonal intensification of the mid-Atlantic Ocean high, creates conditions more favourable for fog formation. The dominant flow of air during this period is westerly, thus warm moist air from the mid Atlantic is cooled near the coast and fog forms. As mid summer wind velocities are too high to maintain the integrity of the fog bank, the coast experience fog predominately during spring and autumn, when the wind velocities are lower, but the flow of air is still predominately onshore (Fig. 2.7).

The average total number of days per annum during which fog is recorded at Port Nolloth is 148, or 41 % of the total days. As a result, the sunshine duration averages less than 70 % of the possible total and this has an ameliorating effect on the climate (Burns 1994). Alexander Bay airport experiences, on average, 67.1 days fog a year or 18 % of total days. Fog occurrence at both stations peaks in late summer - autumn. The higher incidence of fog at Port Nolloth is misleading in terms of making generalisations about the occurrence of fog along the coast. These are the only two weather stations to provide fog statistics for this stretch of the coast. The weather station at Port Nolloth is almost on the coast where as Alexander Bay WK is 10.4 km farther inland. The statistics give a reasonable indication of the fog incidence gradient as one moves inland, but these figures should not be used to make reflection about the latitudinal variation in fog incidence. Using Meteosat images, Olivier (1995) estimates the occurrence of fog in the study area to be between 50 and 75 days per annum.

If and how desert plants derive any benefit from fog moisture is unclear. For Swakopmund, with 121 day fog per annum, the amount of water intercepted in 1958 was equivalent to 130 mm of rainfall - more than 7 times the mean annual rainfall (Schultze and McGee 1978). Minimum and maximum annual fog-water totals along a latitudinal transect from Walvis Bay to Gobabeb were 49-158 mm (Rooibank, 20 km inland); 88-271 mm (Swartbank 40 km inland); and 8-48 mm (Gobabeb 60 km inland). The coefficient of variation for fog at the three same stations was 29 %, 29 % and 36 % respectively, whereas that for rainfall was 123 % at Gobabeb and 106 % at Walvis Bay (Pietruszka and Seely 1985). These coefficients for rainfall are similar to those for the rainfall experienced in the study area. Fog is potentially a significant source of water in the desert environment, and also a far more predictable source of moisture than rainfall (Fig. 9) (Pietruszka and Seely 1985).

There is, however, no evidence for direct uptake of fog condensation on leaves by plants (Danin 1991). A notable exception is *Trianthema hereroensis* from the sand erg of the central Namib Desert (Louw and Seely 1982). Von Willert *et al* (1990 and 1992) are of the opinion that any leaf structure capable of absorbing water on the leaves is also a potential route via which water can evaporate. Thus, it would not make sense for plants living in a hyper-arid environment to absorb fog moisture directly from the leaves. A more likely route whereby plants could benefit from fog moisture would be by absorbing condensation on the sand surface (Danin 1991) and stem flow. This route would facilitate the uptake of both fog and dew condensation on the soil surface. Louw and Seely (1982) sprayed tritiated water on the top 1 cm of soil near *Salsola subulicola* and found efficient water absorption by the plant, thus some plants growing in the fog zone of the Namib have well developed superficial root networks (Danin 1991) or efficient mycorrhizal relationship to be able to benefit from alternative moisture sources (see Section 5.4.3 of dew, below).

There is little quantitative understanding of how fog is distributed in the landscape south of the Orange River. Fog has a dramatic ameliorative effect on the coastal desert environment; it is potentially a significant source of moisture for plants; and, it is more predictable in its occurrence. Understanding where, how often and what benefit plants derive from fog could provide vital clues to our understanding of the patterns and processes that underlie the vegetation of the southern Namib.

5.4.3 Dew.

Dew-point temperature is that to which air at a constant pressure and water vapour content must be cooled in order to become saturated and for dew to precipitate (Preston-Whyte and Tyson 1988). In the absence of coastal advection fog, the potential still exists for the formation of heavy dews. Although it is a parameter that is difficult to quantify, moisture derived from dew condensation on plants and the ground is significant and worthy of some investigation.

At night radiative cooling of the air to below dew point temperature causes dew to form on the ground. The extraction of water vapour from the overlying air causes an inversion to form in the water vapour profile. The depth and strength of this inversion is determined by the downward flux of water vapour in a suitable turbulent environment. Thus, the level of turbulence is critical. If it is too low (i.e. calm conditions), dew ceases to form since the ground cannot be replenished by water vapour from above. If the turbulence is too high, mixing inhibits surface radiative cooling to below dew point temperature. The probability of occurrence of heavy dews would be highest when the difference between mean minimum monthly temperature and dew-point temperature is smallest combined with the highest mean monthly relative humidity[4] values and lowest mean monthly night time wind speeds. From Fig. 2.11 it is possible to predict that the highest occurrence of dews is during autumn and spring months. As one moves closer to the coast, so the relative humidity values increase, thus increasing the amount of water condensed during any dew event and, ultimately, the amount of moisture input. Although the coastal air mass is vertically stable owing to the stabilising effect of the cold sea, the proximity to the coast, combined with predominately onshore drift during these periods of near saturated air, will result in the formation of heavy dews.

Annual variation in vapour-pressure adds to our picture of plant available moisture. Examination on the annual trend in vapour-pressure (vp) and the saturation deficit, which is the difference between the vp and the saturation vp (It is sometimes referred to as the "drying power of the air"), show the driest-air months to be during winter, where a nocturnal off-shore wind dominates (see Fig. 2.13). Although rainfall is greatest during winter, the air has its greatest drying power ability (Fig. 2.12). Therefore, for plants, autumn and spring are the best months for growth. The occurrence in winter of dry air, and low incidence of fog and dew would probably results in a bimodal growth or phenological curve for plants living along the coast if rain is not prevalent or regular during the winter months.

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[4] Relative humidity is the ratio of the observed humidity mixing ratio to that which would saturate the air at the same temperature and is expressed as a percentage.

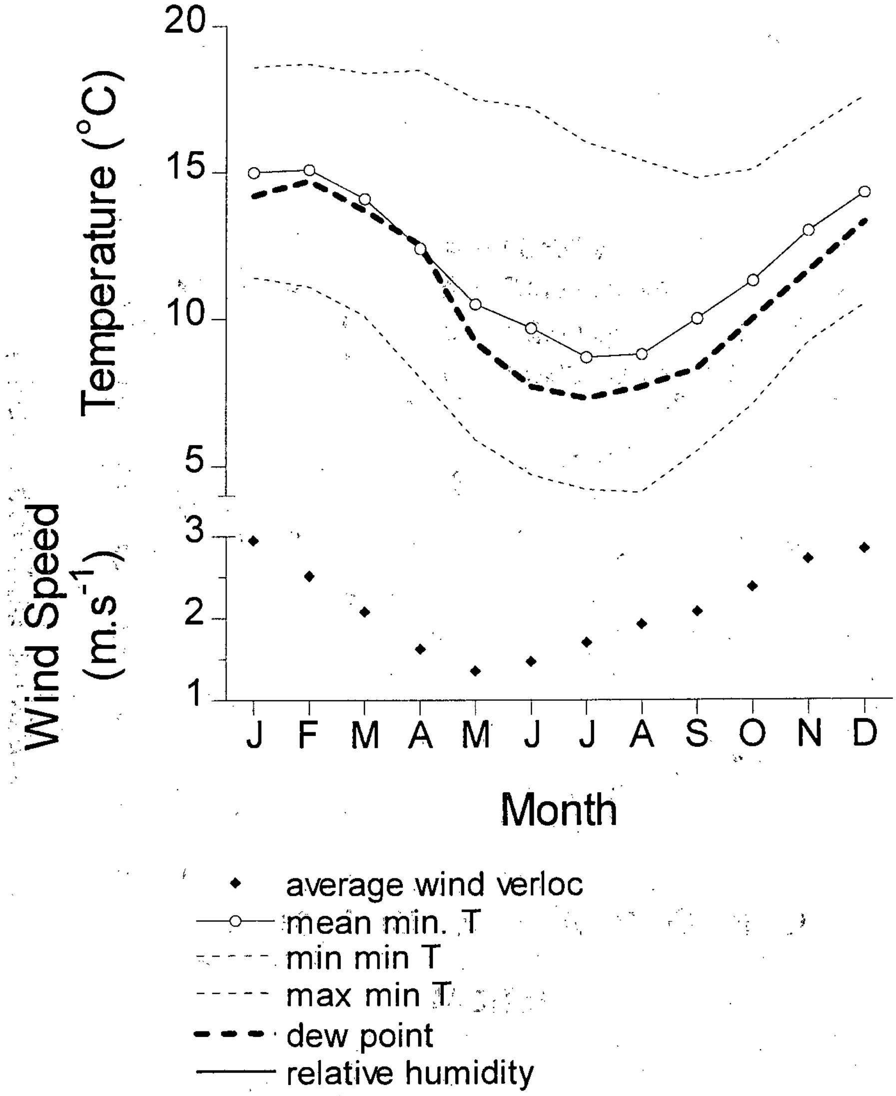


Figure 2.11 The dew potential for various months of the year at Alexander Bay (data from WB 39 and 40).

5.5 Sources of moisture, their predictability and the evolution of plant life forms.

The amount of moisture delivered by fog and its utilisation is uncertain, but fog differs measurably from rain in terms of its predictability. Long-lived perennial plants would only be able to survive in a desert receiving less than 50 mm.yr^{-1} if there was some form of predictability in the moisture regime. Rain is highly variable. Dew is probably a common occurrence but how much water this makes available to plants is unknown. Fog is potentially a substantial water source and its predictability is far greater than that of rainfall. Plants inhabiting the fog zone of the southern Namib Desert should posses a unique suite of ecological characteristics of morphological/physiological features with enable them to utilise these alternative sources of moisture.

5.6 Temperature.

The Atlantic ocean has a significant moderating effect on the coastal temperature regime (Fig. 2.7). Minimum temperatures are particularly stable, i.e. they are not subject to large fluctuations and tend to follow ocean surface temperatures (Table 2.6). The maximum and minimum sea surface temperatures fall approximately two months after the summer and winter solstices, respectively, and so do land temperature minima and maxima (Fig. 2.7). This lag in seasonal temperature and seasons is the norm for oceanic South Africa (Schultze 1965).

Table 2.6 Mean ocean surface temperatures at 32°S 15°E (from Schultze 1965).

JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	Yr
19.4	**20.0**	19.4	18.3	17.8	16.1	15.6	**15.0**	**15.0**	16.1	17.2	18.3	17.4

In contrast, the diurnal temperature maximum can vary considerably and occasionally rises to extremely high values (>30°C) primarily as a result of berg winds. Temperatures above 30°C can be expected to occur at Port Nolloth on approximately 13 days of the year (normally between May and June) and temperatures above 35°C occur under well developed berg wind conditions on approximately 3 days of the year. The section of Alexkor property which is located furthest inland from the coast experiences considerably hotter conditions than at Port Nolloth and Alexander Bay. Temperatures higher than 30°C could occur on up to 80 days of the year at this inland site, while temperatures in excess of 35°C could occur on up to 20 days (Burns 1994).

Within a year there are numerous changes in temperature which can be put into two classes (Schultze 1965):

- Irregular, spasmodic fluctuations varying from a few minutes to a few days.
- Regular periodic fluctuations, namely, (a) the diurnal and (b) the annual variation.

Variation with regard to class 1 is of greatest interest to biologists as these greatly determine the predictability of the environment and consequently the type of plant life histories that can persist (e.g. Von Willert *et al* 1990, Von Willert *et al* 1992). Along this part of the coast, the occurrence of irregular berg winds probably has the strongest destabilising effect on the coastal climate, primarily due to the dramatic and rapid increase in temperature and drying effect of this wind.

Diurnal temperature variation is greatest in winter when nocturnal off-shore air movement is dominant (Table 2.7 and Fig. 2.13). Alexander Bay affords an almost perfect example of land-sea breezes in winter (Schultze 1965). In the morning the wind is a gentle NE, it is nil at noon and maximum, from the SW (diametrically opposed) at 5 p.m. By 10 p.m. the resultant is again nil. During the summer months the diurnal wind regime is incessantly on-shore from the southerly quarter. This varies considerably from the rest of South Africa where the greatest variation is usually encountered in spring (October) (Schultze 1965). This is due to the occurrence of berg winds in the winter months and is experienced by all west coast weather stations.

Table 2.7 Standard deviation of daily mean temperature (°F) for a single date (1st, 6th, 11th, 16th, 21st and 26th) over 10 years (60 values in total) (from Schultze 1965).

Station	Jan	Apr.	Jul.	Oct.
Alexander Bay	2.4	5.7	6.1	3.4

Box 2.4 Berg winds.

Berg winds are important features of coastal climates and are associated with large-scale pre-frontal divergence and dynamic warming of subsiding air moving offshore with anticyclonic curvature (Preston-Whyte and Tyson 1988). The dynamic warming is such that even on the plateau inland of the escarpment positive temperature departures my be experienced. Additional adiabatic warming of the air as it descends from the interior plateau enhances the warming effect. Berg winds may blow for several days or only a few hours. The winds are most common in late winter and early spring. They result in the anomaly of highest maximum temperatures being recorded in winter at many east and west coast stations. Almost all rapid raises in temperature being recorded in winter at coastal stations are the result of berg wind warming. The strong offshore effect of berg winds on the west coast may produce significant dust plumes blowing over the coastal plain, out to sea on the west coast (Fig. 2.4).

Berg winds are usually linked to coastal lows, which together determine much of the characteristic features of coastal and adjacent inland climates. Coastal lows owe their origin to the generation of cyclonic vorticity with eastward or westward movement of air off the high interior plateau, that is large-scale flow having a substantial velocity normal to the coastline. Without the topographic configuration of the plateau, escarpment and coastal littoral, they would not occur. Usually coastal lows are initiated on the west coast and propagate southwards to Cape Town. Thereafter they move eastward and north-eastward around the coast as internal Kelvin waves trapped vertically beneath a strong, low-level subsidence inversion and horizontally on the landward side by the escarpment. All coastal lows produce warm offshore airflow ahead of the system and cool onshore flow behind. The temperatures and wind shift patterns associated with coastal lows resemble those of cold fronts and often may be mistaken as such. The systems are confined to coastal areas, are shallow, decoupled from the wave usually present above the surface layer and seldom produce localised precipitation in excess of mist or fine drizzle.

5.7 Wind.

Wind is the most important controlling variable in determining plant life history strategies, adaptations and distribution along the west coast. The coastal wind regime is determined primarily by the presence of the west coast trough (coastal low) in summer and in winter by the development of a strong anticyclone (continental high) over the interior of the country (Schultze 1965, Preston-Whyte and Tyson 1988). The development of these weather systems is related to the eastward wave of tropical circulation in summer and the westerly frontal wave associated with winter westerly circulation systems, respectively.

High energy southerly quarter winds during the arid summer months determine the direction of sand movement in the Sandveld (Tables 2.8 to 2.10, Figs. 2.14 and 2.16). Strong off-shore winds of short duration in winter are responsible for much aerosol input in the from of fine soil particles into the coastal dune system. The dry summer climate combined with the occurrence of southerly quarter gales dictates the direction of sand movement. This bi-directional co-dominant southerly quarter wind (Fig. 2.14) results in the formation of parallel dune ridges moving in a NNE direction across the landscape. Further inland the winter berg winds are perpendicular to the tempered coastal winds. This tends to mix sand more and results in the formation of a less structure or amorphous dune landscape.

Table 2.8 Percentage gales (wind speed > 13.8 m.s^{-1}) per month for Alexander Bay (data from WB 36).

Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
7.96	5.61	4.46	2.05	0.85	0.46	0.23	1.62	3.63	5.94	7.46	7.0

Table 2.9 45° Sector (s) and percentage frequency (p) of highest wind occurrence (row 1) and least wind occurrence (row 2) for Alexander Bay WK (data from WB 36).

	January		April		July		October		Year	
	s	p	s	p	s	p	s	p	s	p
1	S	60.6	SSW	31.4	ENE	19.1	S	43.5	S	38.0
2	NNE	0.2	N	2.4	N	4.5	NNE	1.0	N	2.3

Table 2.10 Highest recorded hourly wind speed (1) and highest recorded gust (2) in m.s^{-1} for Alexander Bay WK (data from WB 36).

	Jan		Feb		Mar		Apr		May		Jun		Jul		Aug		Sep		Oct		Nov		Dec	
1	S	21	SSE	22	S	21	S	20	S	18	NE	20	S	15	NE	21	SSE	21	S	22	S	24	S	23
2	SSE	30	S	29	SSE	29	S	28	S	28	S	27	NNW	23	NE	30	NW	30	N	34	SSE	31	S	33

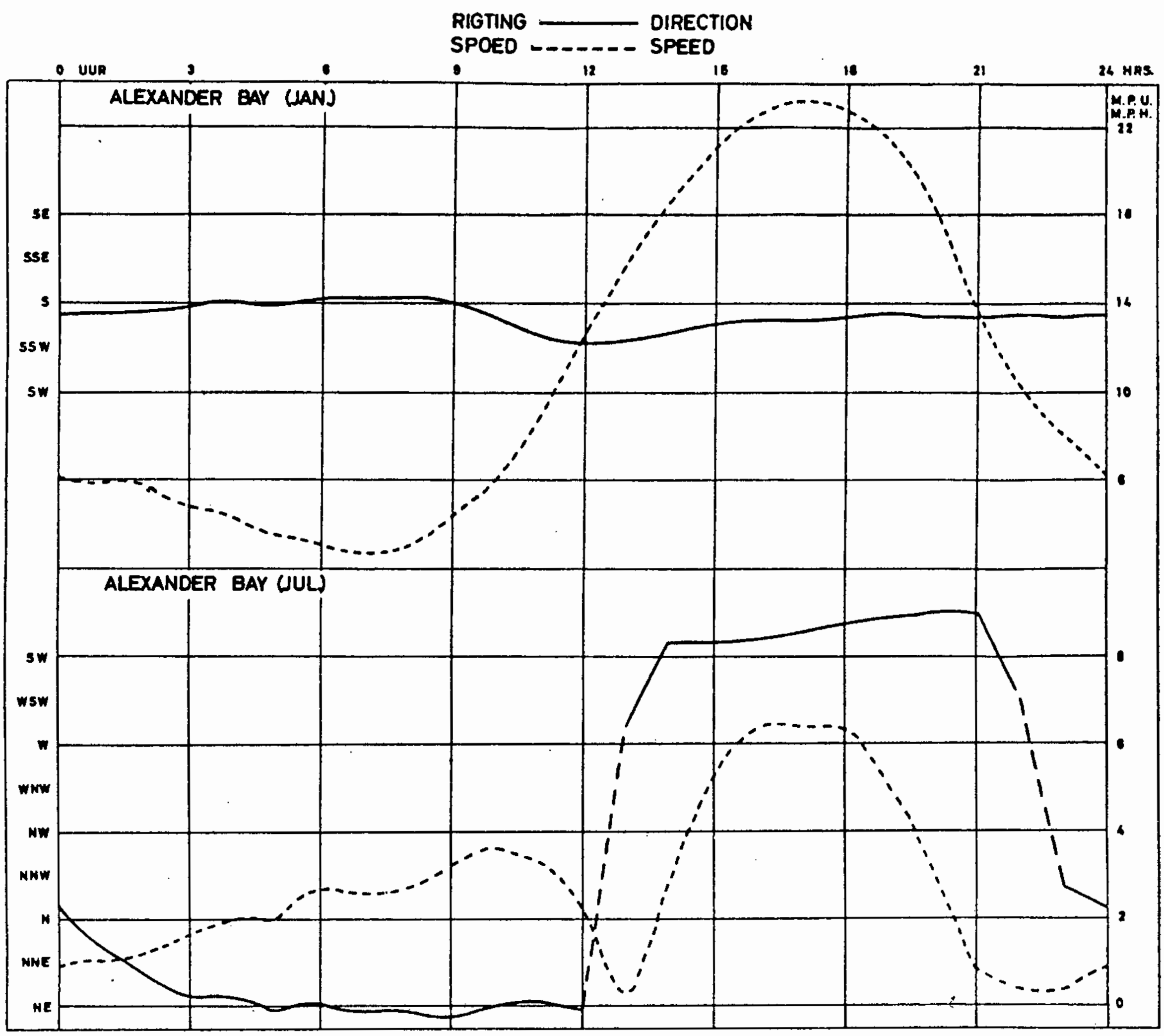


Figure 2.13 The January and July diurnal variation in wind resultants for Alexander Bay (from Schultze 1965).

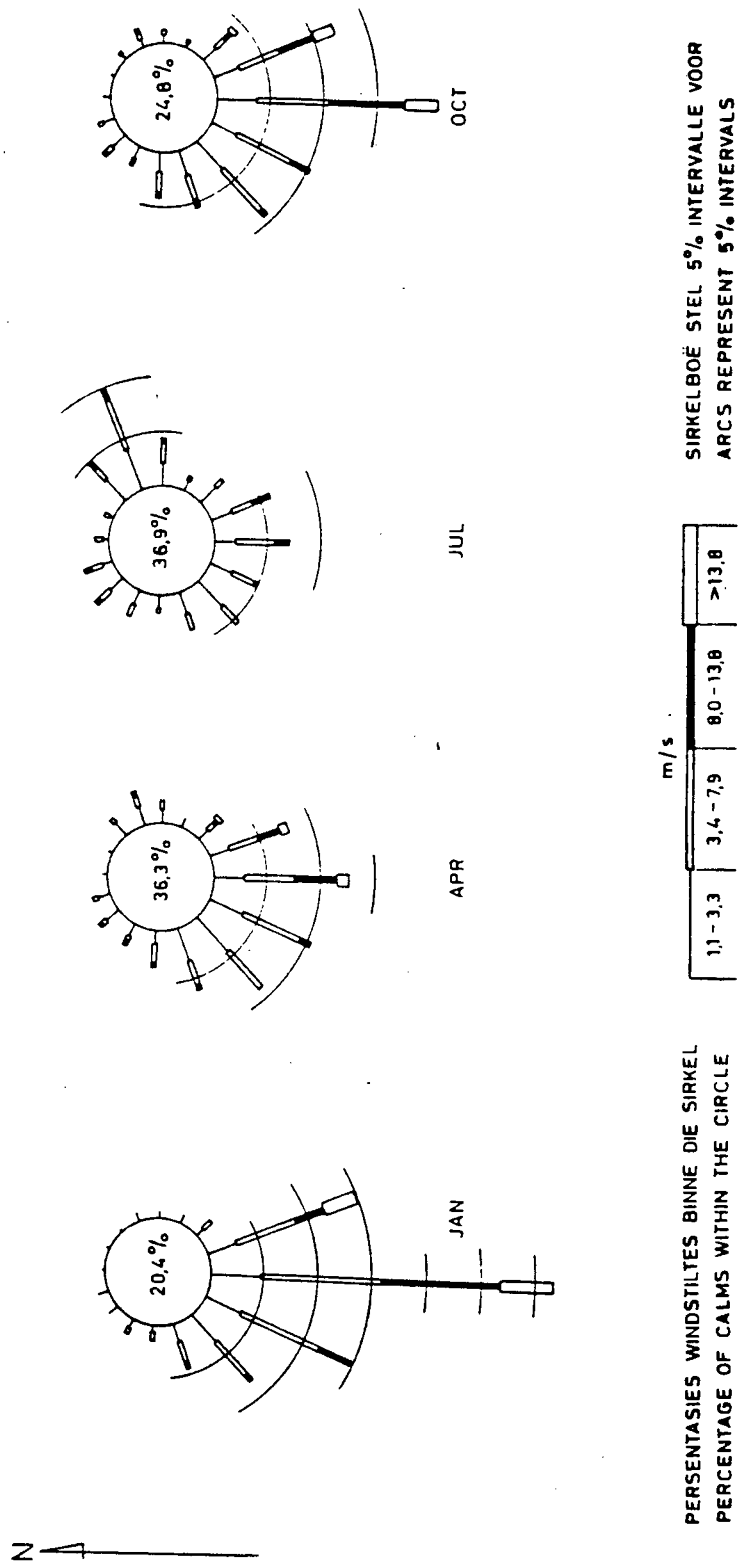


Figure 2.14 Selected wind roses for Alexander Bay WK (from WB 38).

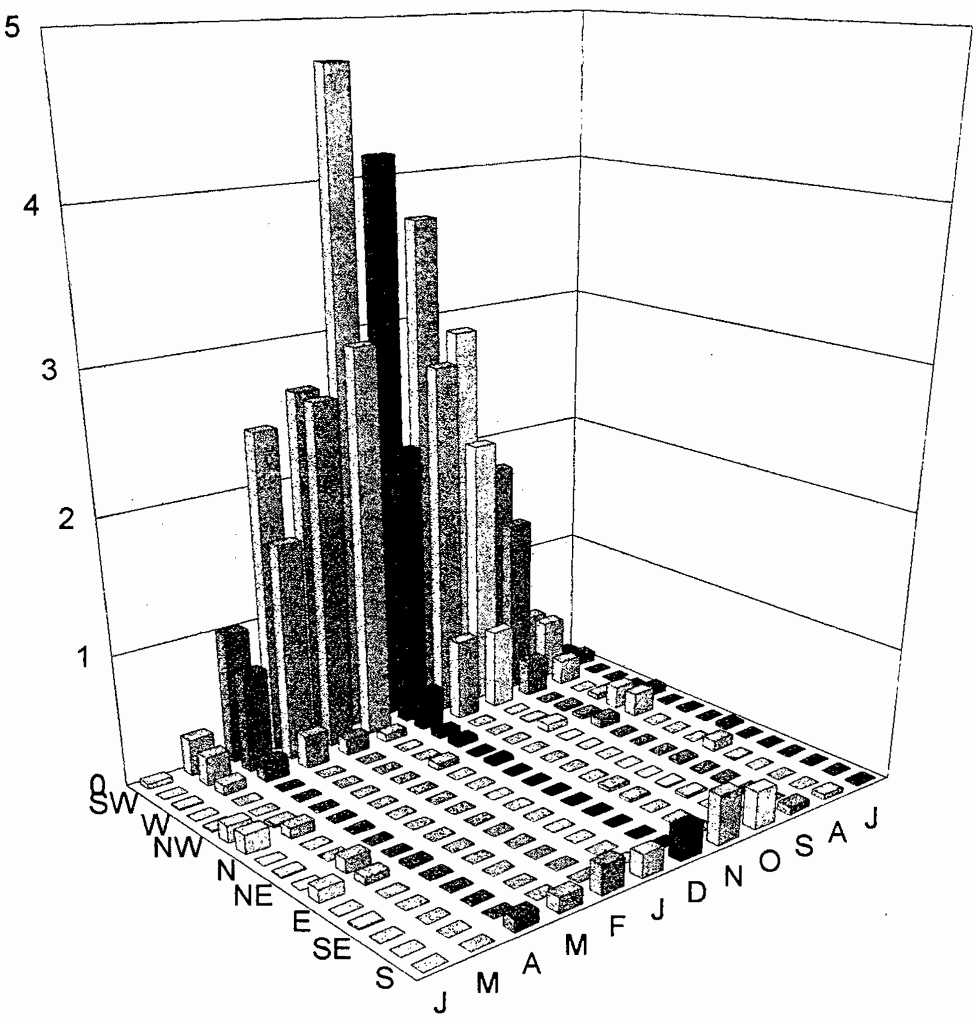


Figure 2.15 A 3-D graphical representation of the direction of and percentage time per month where wind speeds are in excess of 13.8 $m.s^{-1}$ (>50 $km.h^{-1}$ or gale force winds) recorded at Alexander Bay WK (from WB38).

References

Bagnold, R.A. (1941) The Physics of Blown Sand and Desert Dunes. Chapman and Hall, London.

Bowers, J.E. (1982) The plant ecology of inland dunes in western North-America. *Journal of Arid Environments* 5: 199-220.

Buckley, R. (1987) The effect of spares vegetation on the transport of dune sand by wind. *Nature* 325(29): 426-428.

Burns, M. (1994) ALEXKOR Environmental Management Programme Report Vol. 3. Report Number EMAS-C 94, EMATEK, Stellenbosch.

Carrington, A.J. and Kensley, B.F. (1969) Pleistocene molluscs from the Namaqualand coast. *Annals of the South African Museum* 52(9): 189-223.

Cartwright, C.R., Parkington, J.E. and Cowling, R.M. (in press) Fossil wood assemblages from Elands Bay Cave, South Africa: A wetter glacial in the winter rainfall Fynbos Biome? *Palaeogeography, Palaeoclimatology, and Palaeoecology.*

Corvinus, G. and Hendey, Q.B. (1978) A new Miocene vertebrate locality at Arrisdrift in Namibia (South West Africa). *N. Jb. Geol. Palaeot.* 1478: 193-205.

Danin, A. (1991) Plant adaptations in desert dunes. *Journal of Arid Environments* 21: 193-212.

Dardis, G.F and Grindley, J.R. (1988) Coastal geomorphology. in: The Geomorphology of Southern Africa. Moon, B.P. and Dardis, G.F. (eds.) Southern Book Publishers, Johannesburg.

Davies, O. (1973) Pleistocene shorelines in the Western Cape and South-West Africa. *Annals of the Natal Museum* 21(3): 719-765.

De Decker, R.H. (1986) The inner continental shelf off Alexander Bay, Cape west coast: evidence for palaeo-strandlines. in: Tertiary to Recent Coastal Geology. Illenberger, W.K. and Smuts, W.J. (eds.) Institute for Coastal Research Report number 12, University of Port Elisabeth.

de Villiers, J.and Söhnge, P.G. (1959) The Geology of the Richtersveld. Department of Mines Geographical Survey: Memoir 48. The Government Printer, Pretoria

Deacon, J.; Lancaster, N. and Scott, L. (1984) Evidence for Late Quaternary climatic change in southern Africa: summary of the proceedings of the SASQUA workshop held in Johannesburg, September 1983. In: Vogel, J.C. (ed.) Late Cainozoic Palaeoclimates of the Southern Hemisphere. Balkema, Rotterdam.

Deacon, J. and Lancaster, N. (1988) Late Quaternary Palaeoenvironments of Southern Africa. Oxford University Press, Oxford.

Eldridge, D.J. and Greene, R.S.B. (1994) Microbiotic soil crusts: A review of their roles in soil and ecological processes in the rangelands of Australia. *Australian Journal of Soil Research* 32: 389-415.

Ellis, F. and Lambrechts, J.J.N. (unpublished) Dorbank, a reddish brown hardpan of South Africa - a proto-silcrete?

Fisher, M. (1994) Another look at the variability of desert climates using examples from Oman. *Global Ecology and Biogeography Letters* 4: 79-87.

Forbes, V.S and Rourke, J. (1980) Patterson's Cape Travels 1777 to 1779. The Brenthhurst Press, Johannesburg.

Keyser, U. (1972) The occurrence of diamonds along the coast between the Orange River and Port Nolloth Reserve. *Bulletin of the Geological Society of South Africa* 64.

Kutiel, P. and Danin, A. (1987) Annual-species diversity and aboveground phytomass in relation to some soil properties in the sand dunes of the northern Sharon Plains, Israel. *Vegetatio* 70: 45-49.

Lancaster, N. (1984) Aridity in southern Africa: age, origins and expression in landforms and sediments. In Vogel, J.C. (ed.) Late Cainozoic Palaeoclimates of the Southern Hemisphere. AA Balkema, Rotterdam.

Lancaster, N. (1989) The Namib Sand Sea. A.A. Balkema, Rotterdam.

Le Houérou, H.N. (1986) The desert and arid zones of Northern Africa. In: Evenari, E, Noy-Meir, I. and Goodall, D.W. (eds.) Hot Deserts and Arid Shrublands, B. Elsevier, Amsterdam.

le Roux, A. and Schelpe, T. (1988) Namaqualand. South African Wild Flower Guide 1. Botanical Society of S.A., Claremont.

Louw, G.N. and Seely, M.K. (1982) Ecology of Desert Organisms. Longman, London.

Miller, D.E. (1990) A Southern African Late Quaternary sea-level curve. *South African Journal of Science* 86: 456-458.

Morris, H.M. (1955) Flow in rough conduits. *Transactions of the ASAE* 120: 373-98.

Musick, H.B. and Gillette, D.A. (1991) Field evaluation of relationships between a vegetation structural parameter and sheltering against wind erosion. *Land Degradation and Rehabilitation* 2: 87-94

Noy-Meir, I. (1973) Desert ecosystems: Environment and producers. *Annual Review of Ecology and Systematics* 4: 25-51.

Olivier, J. (1995) Spatial distribution of fog in the Namib. *Journal of Arid Environments* 29: 129-138.

Parkington, J. (1986) Landscape and subsistence changes since the Last Glacial Maximum along the western Cape coast. In: Straus, L.G. (ed.) The End of the Palaeolithic in the Old World. BAR International Series 284, Oxford.

Partridge, T.C. and Maud, R.R. (1987) Geomorphic evolution of southern Africa since the Mesozoic. *South African Journal of Geology* 90: 179-208.

Partridge, T.C., Avery, D.M., Botha, G.A., Brink, J.S., Deacon, J., Herbert, R.S., Maud, R.R., Scholtz, A.S., Scott, L., Talma, A.S. and Vogel, J.C. (1990) Late Pleistocene and Holocene climatic changes in Southern Africa. *South African Journal of Science* 86: 302-305.

Pether, J. (1986) The Late Tertiary and Early Quaternary marine deposits of the west coast of the Namaqualand, Cape Province. in: Tertiary to Recent Coastal Geology. Illenberger, W.K. and Smuts, W.J. (eds.) Institute for Coastal Research Report number 12, University of Port Elisabeth.

Pietruszka, R.D. and Seely, M.K. (1985) Predictability of two moisture sources in the Namib Desert. *South African Journal of Science* 81: 682-685.

Preston-Whyte, R.A. and Tyson, P.D. (1988) The Atmosphere and Weather of Southern Africa. Oxford University Press, Cape Town.

Raper, P.E. (1987) Dictionary of Southern African Place Names. Lowry Publishers, Johannesburg.

Schultze, B.R. (ed.) (1965) Climate of South Africa. Part 8. General Survey (WB28). The Government Printer and Weather Bureau, Pretoria.

Schultze, R.E. and McGee, O.S. (1978) Climatic indices and classification in relation to the biogeography of southern Africa. In Werger, M.J.A. (ed.). Biogeography and Ecology of Southern Africa. Dr W. Junk bv. Publishers, The Hague.

Scott, D.F.; Du Toit, B.; Johnston, M.A. and Burns, M.E.R. (1994) The effects of mining on soil properties and the ability of the soil to support vegetation after mining at Kleinzee and Koingnaas, on the west coast of South Africa. Project No. FL 719, Report No. FOR C-, Division of Forest Science and Technology, Pretoria.

Soil Classification Working Group (1991) Soil Classification. A Taxonomic System for South Africa. Memoirs on the Agricultural Natural Resources of South Africa No. 15, Department of Agricultural Development, Pretoria.

Tankard, A.I. (1976) Pleistocene history and coastal morphology of the Ysterfontein-Elands Bay area, Cape Province. *Annals of the South African Museum* 69: 73-119.

Tankard, A.I. and Rogers, J. (1978) Late Cenozoic palaeoenvironments on the west coast of southern Africa. *Journal of Biogeography* 5: 319-37.

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

Tsoar, H. (1990) The ecological background, deterioration and reclamation of desert dune sand. *Agriculture, Ecosystems and Environment* 33: 147-170.

Van Jaarsveld, E. (1994) The Namib Caper, *Capparis hereroensis*. *Veld & Flora,* December: 108-109.

Van Zinderen Bakker, E.M. (1975) Origin and palaeoenvironments of the Namib Desert biome. *Journal of Biogeography* 2: 65-73.

Van Zinderen Bakker, E.M. (1976) The evolution of Late Quaternary palaeoclimates of southern Africa. *Palaeoecology of Africa* 9: 160-202.

Vogel, J.C. (1983) Isotopic evidence for past climates and vegetation of South Africa. *Bothalia* 14: 391-394.

Von Willert, D.J., Eller, B.M., Werger, M.J.A. and Brinkmann, E. (1990) Desert succulents and their life strategies. *Vegetatio* 30: 133-143.

Von Willert, D.J., Eller, B.M., Werger, M.J.A., Brinkmann, E. and Illenfeldt, H-D. (1992) Life Strategies of Succulents in Deserts. Cambridge Studies in Ecology. Cambridge University Press, Cambridge.

Walker, T.R. (1979) Red colour in dune sand. In McKee, E.D. (ed.) A Study of Global Sand Seas. *US Geological Survey Professional Paper* 1052.

Ward, J.D. (1984) A reappraisal of Cenozoic stratiagraphy in the Kuiseb valley of the central Namib Desert. In Vogel, J.C. (ed.) Late Cainozoic Palaeoclimates of the Southern Hemisphere. AA Balkema, Rotterdam.

Ward, J.D., Seely, M.K. and Lancaster, N. (1983) On the antiquity of the Namib. *South African Journal of Science* 79: 175-183.

WB 36 (1974) Climate of South Africa. Part 11. Extreme Values of Rainfall, Temperature and Wind for Selected Return Periods. Weather Bureau Report No. WB 36. Research Division, Weather Bureau, Department of Transport, Pretoria.

WB 38 (1975) Climate of South Africa. Part 12. Surface Winds. Weather Bureau Report No. WB 38. Research Division, Weather Bureau, Department of Transport, Pretoria.

WB 39 (1979) Climate of South Africa. Part 13. Upper-Air Statistics, Wind, Temperature, Geopotential. Weather Bureau Report No. WB 39. Research Division, Weather Bureau, Department of Transport, Pretoria.

WB 40 (1986) Climate of South Africa. Climate Statistics up to 1984. Weather Bureau Report No. WB 40. Weather Bureau, Department of Environmental Affairs, Pretoria.

Whitten, D.G.A. and Brooks, J.R.V. (1972) The Penguin Dictionary of Geology. Penguin Books Ltd. London.

Wolfe, S.A. and Nickling, W.G. (1993) The protective role of sparse vegetation in wind erosion. *Progress in Physical Geography* 17(1): 50-68.

Chapter 3 Phytogeography and Endemism of the Area Between Port Nolloth and Alexander Bay on the West Coast of South Africa.

1 Introduction.

This chapter provides an introduction to the flora and plant life forms of the study area. It also explores of the patterns of species distribution and endemism across the landscape and highlights some interesting trends in these patterns which hold for the study area as well as the rest of Namaqualand. By way of introduction, a description of the regional phytogeography is presented along with some notes the phytogeography of other similar fog deserts elsewhere in the world.

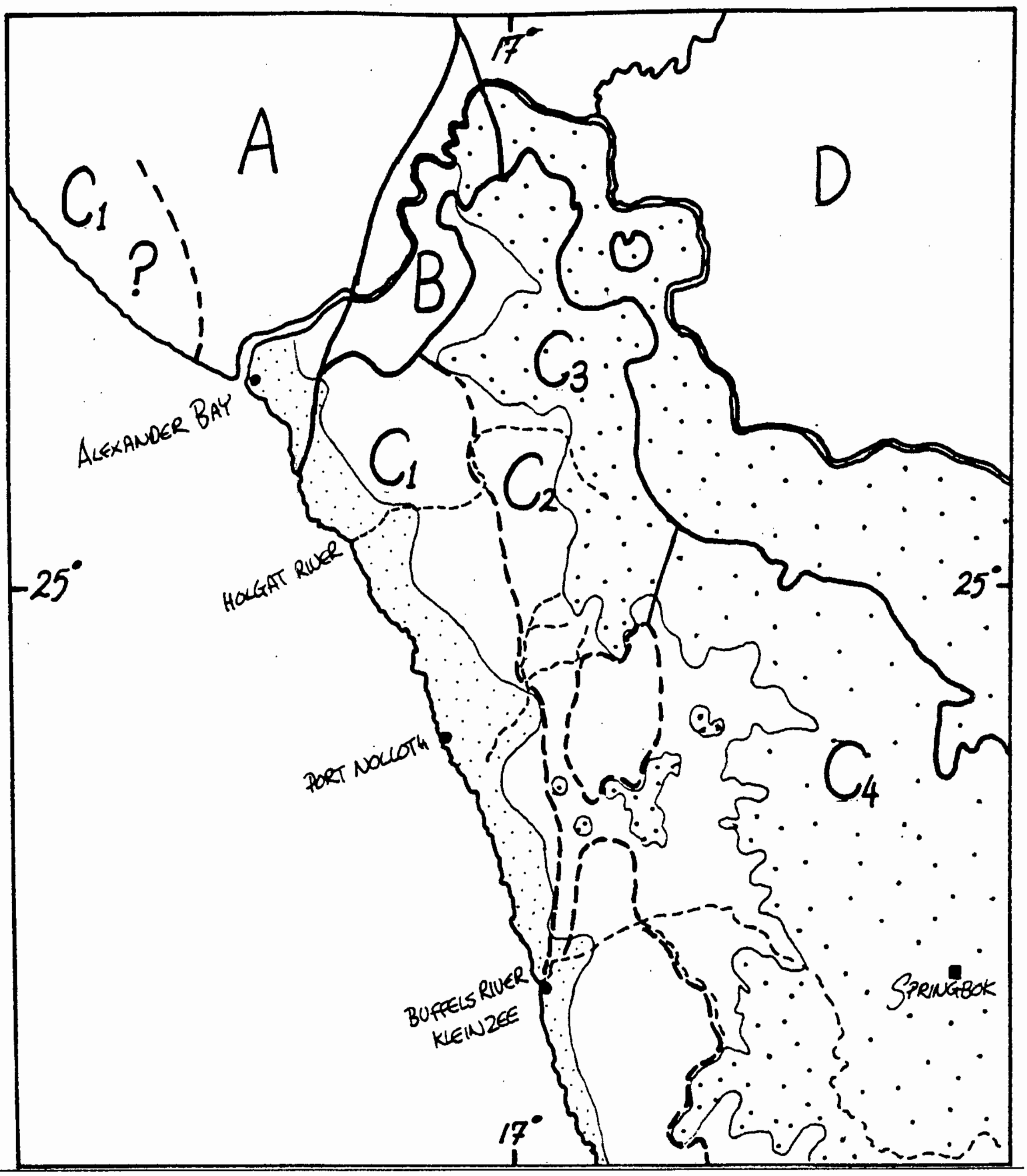
2 Phytgeographical background to the vegetation of the coastal-belt between Port Nolloth and Alexander Bay.

2.1 Regional phytogeography.

There has been much debate on the phytogeography of the region in which the study area falls. It has now been included within the Succulent Karoo Region of the Greater Cape Flora (Jürgens 1991, Cowling and Hilton-Taylor in press). For a semi-arid biome, the Succulent Karoo contains a surprisingly large number of species, in the region of 5000 taxa (angiosperms and ferns, 35% endemic, Hilton-Taylor in press), with a predominance of chamaephytes and geophytes and a scarcity of phanerophytes and graminoids (Milton *et al* in press). The biome is unusual in the high concentration of leaf succulent, low and dwarf shrubs predominantly represented by the Mesembryanthemaceae and Crassulaceae, the regions two largest families (Milton *et al* in press). Within the Succulent Karoo Biome, the coastal belt between Alexander Bay and Port Nolloth straddles two phytochorologically important regions or floral districts: the Succulent Karoo Region in the Diamond Area No. 1 of southern Namibia or the Southern Namib District, previously the winter rainfall area of the Namib Domain (Werger 1978), and the Succulent Karoo of the Namaqualand Sandveld District (Jürgens 1991), previously the north western portion of the Western Cape Domain (Werger 1978). Together these two floral districts can be said to comprise the Namaqualand-Namib Domain of the Succulent Karoo Region (Fig. 3.1).

To the east of these two districts lies the Gariep Centre of endemism. This regionally important centre occupies the mountains between Steinkopf, in the south, and Aus in the North (Hilton-Taylor in press). This centre, in turn, can be subdivided into three locally distinct centres of endemism (Jürgens 1991): the Western Gariep Circle of the southern Namib and lower Orange River valley; the Eastern Gariep and the Western Richtersveld Mountains. The floras of these centres make intrusions into the Namaqualand Sandveld and to the coast along the lower Orange River valley (the Western Gariep flora); down the Holgat Canyon and along the Augrabies Berg to Kleinzee (the Western Richtersveld Mountains flora).

Along the coastal plain, the Namaqualand-Namib Domain shares many of the dominant genera and species, and for the most part the Strandveld vegetation (Acocks Veld Type 55 or Milton *et al* in press VT34), of the Namaqualand Sandveld District. This pattern continues, after a short interlude along the lower Orange River valley, north of the river mouth in Diamond Area No. 1 to Lüderitz Bay (Jürgens 1991, G. Williamson pers. comm.). The narrow band of vegetation running from the coast along the lower Orange River valley constitutes an intrusion of the Western Gariep Centre into the Namaqualand Sandveld district, and is an area of local phytochorological importance. The area contains a number of endemic genera in the Mesembryanthemaceae, e.g. *Dracophilus, Ruschianthemum* and *Juttadintera*. These genera also occur in flora of the Southern Namib District contributing to the high number of endemic species in this district, and distinguishing it as a distinct phytochorological unit from the Namaqualand Sandveld District to the south (Robinson 1978, Jürgens 1991).



Key to map:

Acocks Veld Types

Strandveld of the west coast

Succulent Karoo

Namaqua Broken Veld

A Southern Namib Domain
B Western Gariep Centre of the Southern Namib Domain
C Namaqualand Domain
- 1 Sandveld District
- 2 Lowland Succulent Karoo
- 3 Richtersveld (or Gariep Centre, Hilton-Taylor in press)
- 4 Namaqualand Rocky Hills

D Eastern Gariep Centre of the Namib Subdomain within the Namaqualand Domain.

Figure 3.1 A map illustrating the location of the different phytogeographic zones that are encountered in the study area. Adapted from Jürgens (1991).

The boundary between the Western Gariep Centre and the Namaqualand Sandveld District lies approximately 30 km south of Alexander Bay and runs roughly north-east from the Buchu Twins to the interior. The existence of such a distinct boundary is a result of a combination of geological and environmental factors (see discussion in previous chapter for a more detailed discussion on the origin of the pebble plains). Ecologically, the lower Orange River Valley provides a gateway for both (a) the oceanic influence of fog, salinity and cool moist air and (b) the continental influence in the form of extremely dry hot berg winds and generally hotter conditions during the day due to its lower altitude (Jürgens 1991). This could contribute to the existence and maintenance of the species-rich flora of the Gariep Centre or at least the Western Gariep flora. The existence of a distinct flora in the Western Gariep is a function of a unique environment. Calculated species per genus values for the Southern Namib District (2.9) would indicate that this flora is relatively archaic (Robinson 1978). For the endemic flora of the Western Gariep Centre this value would probably decrease. This relic nature of the flora implies that the environmental forces defining the extant plants and communities of this centre have been relatively stable for a considerable period. Current views on the antiquity of the Namib Desert support the relict nature of this centre. Evolution of arid conditions along the south west coast of southern Africa have been estimated to be between 80 and 127 million years BP (Ward *et al* 1983).

The Namaqualand-Namib flora can be characterised by a strong representation of the families (in order of importance): Aizoaceae (including Mesembryanthemaceae), Asteraceae, Crassulaceae, Scrophulariaceae, Liliaceae, Poaceae (especially the tribe Stipeae), Geraniaceae, Fabaceae, Euphorbiaceae and Iridaceae (Werger 1978, Cowling and Hilton-Taylor in press). The vegetation is dominated by woody chamaephytes with two leaf growth forms dominant: small ericoid or finely dissected, sometimes strongly rolled leaves with hairs; or leaf succulents. Leaf succulence is the predominant form. Stem succulence is uncommon and restricted to a few families mainly the Euphorbiaceae, Geraniaceae and Crassulaceae. Phanerophytes or trees are the exception. The last remnants of Dune Thicket (Low and Rebelo 1996 Veld Type 4, namely *Euclea racemosa*) disappear from the coastal dunes between Kleinzee and Koingnaas. Elsewhere phanerophytes are confined to riparian habitats; semi-mobile dune fields with deep soils; or mountainous habitats within the domain. The phanerophyte component belongs mostly to the families Mimosaceae, Ebenaceae and Anacardiaceae (Werger 1978). There is a high degree of growth form diversity expressed primarily in diversity of succulent leaf forms.

The families Mesembryanthemaceae and Crassulaceae epitomise this radiation together with the genera *Senecio* and *Othonna* in the Asteraceae. In addition to the dominant woody chamaephyte component, there is also a strong annual or therophyte component characterised by the families Asteraceae, Scrophulariaceae and Aizoaceae.

2.2 Plant communities of the Namaqualand coastal plain.

Despite there being some recent work on vegetation classification at the regional to biome scale, there is very little published data on the plant species assemblages or communities within this region. This could be ascribed in part to the deterrent effect on community/descriptive research from the taxonomic maelstrom of the two of the dominant plant families, Mesembryanthemaceae (Hartmann 1991) and succulent Asteraceae (Rowley 1994). Boucher and le Roux (1993) provide a brief analysis of the Namaqualand strand or littoral vegetation and Boucher and le Roux (1989) provide a preliminary description of the Sandveld vegetation between the Olifants and Spoeg Rivers. Jürgens *et al* (in press) presents some data on the plant communities of the Lower Orange River Valley. These are the only published accounts that deal with the plant communities of the Namaqualand coastal plain. Consequently, the following introduction to this area is based largely the classifications of Boucher and le Roux (1989) with the recent additions by Jürgens *et al* (in press).

The vegetation of the Namaqualand coastal plain has been classified into eight broad community types by Boucher and le Roux (1989) (Table 3.1).

Table 3.1 The classification of Namaqualand Sandveld vegetation types between the Olifants and Spoeg Rivers according to Boucher and le Roux (1989).

A Strand communities	
B Strandveld communities	(i) Short Strandveld
	(ii) Medium Strandveld
	(iii) Tall Strandveld
	(iv) White dune Strandveld
C Succulent Karoo	
D Sand Plain Fynbos	
E River and estuarine communities	

The **Strand communities** (Table 3.1) are broadly defined as any coastal vegetation not subject to submersion, but which is under constant maritime influence. These communities comprise elements of VT(veld type)55 and VT57 (Low and Rebelo 1996). North of Kleinzee, these strand communities also include some of the dwarf open succulent shrublands and lichen fields of the Coastal Zone of the Desert Biome (Jürgens *et al* in press), namely the *Zygophyllum clavatum* community, the *Ramalina capensis* sub-community, the *Teloschistes capensis* sub-community, the *Lebeckia multiflora-Cladoraphis cyperoides* sub-community and the *Salsola zeyheri-Cephalophyllum ebracteatum* sub-community.

Within this vegetation, species that are confined to the physiologically dry littoral zone dominate in relation to those of the adjacent inland vegetation types. Boucher and le Roux (1993) define the Strand community zone as being no more that 200 m wide. Plant communities occurring on dunes greater than this distance inland are considered either Strandveld or Sand Plain Fynbos. Namaqualand Strand communities are differentiated from Capensis Strand communities by the presence of *Galenia fruticosa, Hypertelis salsoloides* (= *S. angrae-pequenae*), *Lycium ferocissimum, Psilocaulon dinterii* and *Salsola nollothensis*. *Chrysanthemoides incana, Gazania leiopoda, Lebeckia cinerea, Drosanthemum* sp., *Cladoraphis cyperoides* and *Salsola nollothensis* are often dominant. Generally, these communities can be described as being dominated by dwarf shrubs, mainly less than 0.5 m tall, usually with succulent leaves or stems, and grasses up to 0.75 m tall, lying either on dune beach heads of sandy coastlines or on sand and shingle of rocky coasts.

The Namaqualand Strand communities are divided into northern and southern variants (Boucher and le Roux 1993) with the border between the two being in the region of the Spoeg River. The floristic basis for this distinction is not discussed. One well-recognised and distinct variant of the Namaqualand Strand communities lies between the Buchu Twins and the mouth of the Orange River. The littoral communities along this stretch of coast are dominated by lower Orange River valley endemics (Werger 1978, Jürgens 1991, Boucher and le Roux 1993). This agrees broadly with Boucher and le Roux's' (1993) assertion that phytosociological changes along the littoral reflect inland changes in phytogeography. This intrusion of dwarf succulent chamaephytes terminates on the south bank of the Orange. North of the Orange, the Strand and Strandveld communities resemble the sandy beach and sand plain communities to the south of the Buchu Twins (Jürgens 1991, G. Williamson pers. comm.).

Beyond this 200 m wide littoral zone, the rest of the Namaqualand Sandveld is classified into five vegetation types. The Strandveld, divided into four variants (Table 3.1), is the most widespread of all the vegetation types. This vegetation is characterised by the presence of *Erharta calycina, E. villosa, Protoasparagus capensis, Tetragonia fruticosa* and *Zygophyllum morgsana*. These communities include elements of Strandveld Succulent Karoo (VT55) and Lowland Succulent Karoo (VT57) (Low and Rebelo 1996) and also the communities of the Coastal Zone of Jürgens *et al* (in press).

Short Strandveld occurs on shallow soils and is dominated by low, spreading succulent shrubs (<0.35 m high, <50% cover) such as *Cephalophyllum spongiosum, Galenia fruticosa, Mesembryanthemum barklyii, Othonna longifolia* and *Zygophyllum cordifolium*. **Medium Strandveld** has tall plants (0.5 m, 50-60% cover) and a higher grass component. Typical species include *Arctotis merxmeulleri, Cephalophyllum* sp., *Drosanthemum* sp., *Manochlamys albicans, Ruschia caroli, R. robusta, Tetragonia fruticosa, Vanzylia* sp. and *Zygophyllum morgsana*. *Odyssea paucinervis* is the dominant perennial grass. **Tall Strandveld,** occurring on deep sands is comparatively dense and tall (1-2 m high, 60-75% cover). The dominant shrubs are *Eriocephalus racemosus, Salvia aurea* and *Zygophyllum morgsana*. **White Dune Strandveld** is found on mobile, white Quaternary sands. A succession of communities exists from the recent, active near-shore dunes to the more stable, older dunes further inland. The near-shore is dominated by the grass *Cladoraphis cyperoides, Arctotheca populifolia, Atriplex bolusii, Carpobrotus edulis, Hebenstretia cordata, Lebeckia cinerea* and *Sporobolus virginicus*. Further inland, Dune Thicket species such as *Rhus longispina* and *Euclea racemosa* appear. Also *Salvia aurea, Lycium oxycarpus, Stoeberia utilis, Tetragonia fruticosa, Tylecodon paniculatus, Zygophyllum morgsana* and the geophyte *Trachyandra divaricata* are dominant.

The fifth type of vegetation occurring on the Sandveld of the Namaqualand is **Succulent Karoo** (Table 3.1). This probably refers, in part, to Lowland Succulent Karoo (VT57, Low and Rebelo 1996) or Succulent Karoo of the Namaqualand Coastal Belt (VT31a, Acocks 1988, Milton *et al* in press), and is encountered within the Sandveld on quartz-rich granite outcrops, exposed silcretes and compacted saline slacks between dune crests (Boucher and le

Roux, 1989). Here, a low dwarf succulent-leaved, shrubland, dominated by members of the Mesembryanthemaceae, is found.

Boucher and le Roux (1989) also discuss the occurrence of Sand Plain Fynbos. Possible reasons why one encounters fynbos elements occurring deep within the Succulent Karoo biome, on sand which appears no different from the sand on which Strandveld occurs, are discussed in the previous chapter. What the characteristics of this vegetation in Namaqualand are is unclear. Acocks (1988) does not discuss this distinct fynbos type is any detail (Acocks VT47). Although Low and Rebelo (1996) distinguish west and south coast sand plain fynbos types (VT68), little advancement is made on what actually constitutes Sand Plain Fynbos in Namaqualand.

2.3 The Namaqualand Sandveld: The global perspective.

The Sandveld of Namaqualand and the southern Namib can be referred to as a fog desert where the low winter precipitation is offset by frequent moisture inputs from coastal advective fog and heavy dews. Temperatures are moderated by the dominating, cool maritime on-shore winds. Globally, there are four such deserts: The southern Namib, southern Morocco, the north coast of Chile and central Baja California. These deserts are all located at similar latitudes on the west coasts of continents; experience fog; and, are bounded on either of their latitudinal extremes by mediterranean-climate or subtropical floras.

On the north western coast of North Africa, between the latitudes of 21° and 28° North, lies the Oceanic Sahara (Le Houérou 1986 and 1992). This climatically distinct region of the Sahara desert extends over a strip 25-50 km wide along the Atlantic coast between southern Morocco and Mauritania, an area of approximately 70 000 km^2 (Le Houérou 1992). Here the cold Canary Current brings frequent fog and atmospheric humidity is high. Temperatures are moderated by the cold ocean, ranging between 10 -30° C. Rainfall varies between 25 and 100 mm.

Oceanic Sahara is dominated by what has been termed non-halophilous succulent steppes (Le Houérou 1986) Rates of specific endemism are high amongst plants of both Mediterranean and Palaeotropical affinities. The total flora shows a strong tropical affinity (Le Houérou

1986) and comprises some 450 species of flowering plants (Le Houérou 1992). Here tropical species from the Sahel to the south and Mediterranean Basin to the north penetrate deepest into the Sahara than at any other point. The vegetation is dominated by glypholecine[5], stem-succulent phanerophytes and chamaephytes such as *Euphorbia* spp. and *Caralluma* spp.(Le Houérou and Boulos 1991). Dominant families are the Euphorbiaceae, Asclepiadaceae, Agavaceae, Asphodelaceae, Crassulaceae, succulent Asteraceae, Aizoaceae, Mollunginaceae and Zygophyllaceae. This type vegetation is usually referred to as "Canarian" or "Macaronesian" (Le Houérou 1986, Shmida and Werger 1992).

At the same latitude on the west coast of the South American continent, the northward flowing Humbolt Current brings frequent fog to the coastal desert of Chile and Peru. Rainfall decreases as one moves northwards from 127 mm at La Serena ($29^0 55'$ S) to 2.1 mm at Iquique (21^0 S). This desert is characterised by the presence of a dense, stable, stratus fog bank lying between 300 and 800m. The air here is stabilised by the Pacific High Pressure cell and temperatures are moderated by the ocean. Humidity is high (>80%). As a consequence of the fog distribution and low to non-existent rainfall, vegetation is restricted to the steep sea facing slopes of the coastal escarpment, or Lomas (Rundel *et al* 1991), and the initial portions of the deeply incised river valleys, or "quebradas", that transverse these mountains. The coastal plain below 300m is almost devoid of any vegetation except for cactoid *Copiapoa* spp. and above 900 m, again there is no vegetation. Rainfall is very variable. Drought periods without measurable precipitation may extend as long as six years or more in northern Chile. Moisture for plant growth is derived almost entirely from fog and dew (Rundel *et al* 1991).

As in the Oceanic Sahara, there is dominance of cactoid phanerophytes and chamaephytes from the Euphorbiaceae and Cactaceae, as well as sclerophyllous shrubs. Typical Loma vegetation would consist of a matrix of *Eulychnia iquiquensis*, an arborescent cactus, and *Euphorbia lactiflua*, a large shrubby species, with *Puya boliviensis,* a large terrestrial bromeliad, dominating the lower altitudes of the fog belt; and *Copiapoa cinerea*, a short barrel cactus, and *Eulychnia iquiquensis* dominating the upper limits of the fog belt (Rundel and Mahu 1976). Cover can be as much as 50%. In the south of the Atacama Desert, at similar latitudes to the Namaqualand Sandveld, littoral sand dunes support fairly dense vegetation (15-20% cover,

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[5] Glypholecine - with wavy longitudinal canals or groves (Jackson 1916)

Rundel *et al* 1991), with coastal mattoral species penetrating from the south. However, dunes appear to be an uncommon feature in the landscape. In the Chilean fog desert, the endemic component of the vegetation comprises cactoid succulents, the most notable being *Neochilenia* spp. and *Copiapoa* spp. and the arborescent *Eulychnia iquiquensis*. The region between Charñaral and Antofagasta (27° and 23.5° S) is a centre of pronounced endemism (Rundel *et al* 1991).

The third of the world's fog deserts lies between the same latitudes on the west coast of the Baja California Peninsula of North America. Floristically this desert is related to the much larger, bi-seasonal rainfall, Sonoran Desert, and is generally included in the definition of the desert. However, the occurrence of a number of Baja California endemics and the climate of the peninsula results in it being divided into a number of distinct biogeographic groups differing from the rest of the Sonoran Desert in the Great Basin area of Arizona and northern Mexico. The Vizcaino subdivision of Sonoran Desert-Scrub Biome lies between 30° and 26° 15' North. This is the fog desert of Baja California. It extends from the Pacific coast eastwards to the crest of the drainage divide separating the east and west slopes of the peninsula. Contact on the north is a gradual, merging with Californian coastal sage-scrub and chaparral, on the east with the Lower Colorado River valley and Central Gulf Coast subdivisions of the Sonoran Desert, and on the south with the tropical desert flora of the Magdalena Region of southern Baja California. The physiography of the region is marked by a broad coastal plain rising gradually to the foothills of the peninsula divide, interrupted by low hills in the north and south. Based on rainfall data alone, the Vizcaino region is the most arid of all Sonoran scrub types receiving less than 100 mm annually. The moderating effect of the cold Pacific means that summer temperature are on average 5-6° C lower than continental Sonoran. There is significant moisture input to the system from fog, evident in the rich epiphytic cryptogram flora.

Floristically, the Vizcaino subdivision is distinguished by the dominance of thick fleshy-leaved Agavaceae (*Agave* spp., *Yucca* spp. and *Dudleya* spp.) as well as stem succulent Cactaceae (e.g. *Pachycereus pringlei*, *Ferocactus* spp., *Bergerocactus* spp. and *Opuntia* spp.). Other stem succulent dominants include the characteristic Boojum Tree (*Fouquieria columnaris*), *Idria columnaris*, a succulent up to 20 m tall, *Pachycormus* sp. and many Euphorbiaceae (e.g. *Euphorbia* spp. and *Jatropha* spp.) (Peinado *et al* 1995b). The desert-scrub formations in this region consist of a mixture of these succulent species and other non-succulent sclerophyllous shrubs mainly *Larrea tridentata* and *Ambrosia* spp. (Turner and Brown 1982). Grasses, except for annuals, are almost entirely lacking. Strand vegetation growing on coastal sand dunes differs significantly, structurally, from the coastal succulent scrub of Baja California (Johnson 1977). Coastal dunes are characterised by leaf succulent or canescencent herbs, e.g. *Abronia maritima* and *Sesuvium portulacastrum*, and small, woody chamaephytes, phanerophytes, or rhizomatous grasses, e.g. *Sporobolus virginicus* and *Jouvea pilosa*.

Plant diversity in the Vizcaino fog desert is high when compared to the other south-western American deserts (Peinado *et al* 1995a). This is reflected in the high number of shrubland associations related to the steep aridity gradient experienced as one moves south from the mediterranean climate of southern California and northern Baja California to the tropical-scrub desert of southern Baja (Peinado *et al* 1995a and 1995b, Turner and Brown 1982). The moderated climate of the fog desert allows for chaparral and tropical Sinolian thorn-scrub (Turner and Brown 1982) species to extend much farther along the aridity gradient than would be possible with other desert boundaries. In addition to this trend in species diversity, endemism also increases along the increasing aridity gradient, south into the peninsula. Associated with these trends in diversity is a move away from shrub-dominated to succulent-dominated shrublands (Peinado *et al* 1995a).

Together with the Namaqualand coast, all three of these deserts share the common feature that they support diverse floras, relative to their region as a whole, and are considered centres of endemism within their regional context. All these fog deserts have the following features in common: (a) they exist at the interface between two very different climatic regimes and floras; (b) the moderated climate allows for elements of the floras at both extremes to penetrate very deeply into the desert than would otherwise be the case; (c) fog has a strong moderating effect on the climate, and is a significant source of moisture; (d) they each support unique floras dominated by succulent biotypes; and, (e) they are pronounced centres of regional endemism.

3 Methods.

Details on the study area, the region between Port Nolloth and Alexander Bay, are given in the previous chapter. Plant specimens were collected throughout the study area. Only higher plants were collected. For each specimen, a collection record with location, habitat and habit notes was completed using the collection cards provided by the National Botanical Institute. Plants were identified either by the author, or by the staff at the Bolus (Bol), Stellenbosch (Ste)or Compton (Comp) herbaria. The majority of specimens collected were mounted and placed in a field herbarium. This field herbarium will reside in the Bolus Herbarium in the Botany Department, University of Cape Town, to facilitate easy access to others wishing to identify material from the study area. All collection details were entered into a spreadsheet data base (Quatro Pro DOS). A complete copy of this data base is included on a 1.44 Mb disk in the back of this thesis. Voucher specimens of Mesembryanthemaceae *incertae* were placed in the Bolus herbarium (PGD collection numbers). Other material not used for construction of the field herbarium was given to the Stellenbosch, Compton or Pretoria (Pre) herbaria. Where this is the case, it is indicated in the database. Species names and authors follow Arnold and De Wet (1993). For the Mesembryanthemaceae, nomenclature follows the Bolus Herbarium.

Plant growth forms were classified into seven categories: (1) dwarf leaf succulent; (2) non-dwarf leaf succulent (>0.3 m high); (3) stem succulent; (4) non-succulent shrub; (5) graminoid; (6) annual or forb; and (7) geophyte. All species were classified according to seven broad habitat types: (1) disturbed sites (e.g. road verges); (2) dunes only; (3) dunes and koppies/rock outcrops; (4) dunes and pebble plains; (5) saline habitats; (6) koppies/rock outcrops only; and (7) pebble plains only. A more complete description of species growth form and habitat are available in the collection-record database included with this thesis. All species were classified as either being endemic or non-endemic. A species was considered endemic if its known distribution was restricted to the area between Kleinzee, in the south, Lüderitz, in the north, and the western Richtersveld Mountains, in the east. This region can be considered as the southern Namib coastal fog zone . Chi-squared was used to test the null hypothesis that endemic and non-endemic species are distributed in the same frequency with respect to categories of growth form, habitat and endemism.

4 Results.

300 species from 40 families were recorded for the study area measuring 744 km^2 (Table 3.2), 28 % of them being endemic. A checklist of the flora with respective growth form and habitat codes is presented in Appendix I. The ten largest families in the flora, with the number of species represented and percentage of the family endemic, is presented in Table 3.3. The flora is dominated by the Asteraceae, Mesembryanthemaceae and Crassulaceae. The Mesembryanthemaceae are massively over-represented in terms of their endemic species component (60%, Table 3.3). However, the Asteraceae (8%), Poaceae (0%) and Aizoaceae (0%) are significantly under represented in this respect. Crassulaceae (44%) also shows high levels of endemism, however, this value is not significantly different to that of the flora as a whole, excluding Crassulaceae.

Succulent growth forms dominate the flora of the study area (Table 3.4) both in terms of composition (44%) and also the endemic component (Fig. 3.2a). By comparison, non-succulent shrubs comprise only 19% of the flora. Succulent growth forms are also over represented in terms of their endemic composition, whereas the reverse holds for other growth forms (Fig 3.2a). Within the succulent growth form group, dwarf leaf succulents show very high levels of endemism (Fig. 3.2b). These dwarf leaf succulents are located primarily on rocky substrata (viz. koppies, rocky outcrops and pebble plains) (Fig. 3.2c). Tree or phanerophyte growth forms are entirely absent from the flora. These growth forms are restricted to riparian habitats within the study area (viz. the Orange River Valley). These habitats were not included in this study.

High species density (Table 3.5) and high levels of endemism (Fig. 3.2c) are concentrated on stable substrata, viz. koppies and the pebble plains. Dune habitats occupy the largest proportion of the study area and consequently, the largest number of species (Table 3.5). However, this habitat type has the lowest species:area ratio and endemics are significantly under represented. Koppies, inselbergs and rocky outcrops support the greatest diversity of plants when expressed in terms of species per unit area (Table 3.5). These habitats are rich in endemic species (Fig. 3.2c), unique to these habitats. These habitats also share a significant

Table 3.2 A list of families and number of species represented within the study area.

	Family	Species		Family	Species
1	Asteraceae	53	**22**	Colchicaceae	3
2	Mesembryanthemaceae	47	**23**	Neuradaceae	3
3	Crassulaceae	28	**24**	Sterculiaceae	3
4	Poaceae	17	**25**	Oxalidaceae	2
5	Aizoaceae	15	**26**	Acanthaceae	1
6	Scrophulariaceae	14	**27**	Anacardiaceae	1
7	Geraniaceae	11	**28**	Boraginaceae	1
8	Fabaceae	10	**29**	Campanulaceae	1
9	Euphorbiaceae	9	**30**	Caryophyllaceae	1
10	Selaginaceae	9	**31**	Curcurbitaceae	1
11	Asclepiadaceae	7	**32**	Illecebraceae	1
12	Asparagaceae	7	**33**	Labiatae	1
13	Asphodelaceae	7	**34**	Plumbaginaceae	1
14	Chenopodiaceae	7	**35**	Polygalaceae	1
15	Iridaceae	7	**36**	Portulacaceae	1
16	Hyacinthaceae	6	**37**	Rubiaceae	1
17	Zygophyllaceae	5	**38**	Santalaceae	1
18	Amaryllidaceae.	4	**39**	Tecophilaeaceae	1
19	Solanaceae	4	**40**	Thymelaeaceae	1
20	Apiaceae	3	**41**	unknown	4
21	Brassicaceae	3			

Table 3.3 The ten largest families in the flora with the percentage of each family endemic to the region. Chi-squared tests the null hypothesis that the frequency of endemic species per family is similar to that for the entire flora minus that family (independent sample).

Position	Family	Number of species	% Endemic	χ^2
	Total flora	300	28	
1	Asteraceae	53	8	11.09**
2	Mesembryanthemaceae	47	60	26.10***
3	Crassulaceae	28	44	3.21^{NS}
4	Poaceae	17	0	5.57*
5	Aizoaceae	15	0	4.73*
6	Scrophulariaceae	14	14	0.73^{NS}
7	Geraniaceae	11	45	-
8	Fabaceae	10	30	-
9	Euphorbiaceae	9	33	-
10	Selaginaceae	9	11	-

Significance levels with Yates correction: *** <0.001, ** <0.01, NS not significant, - sample too small for analysis.

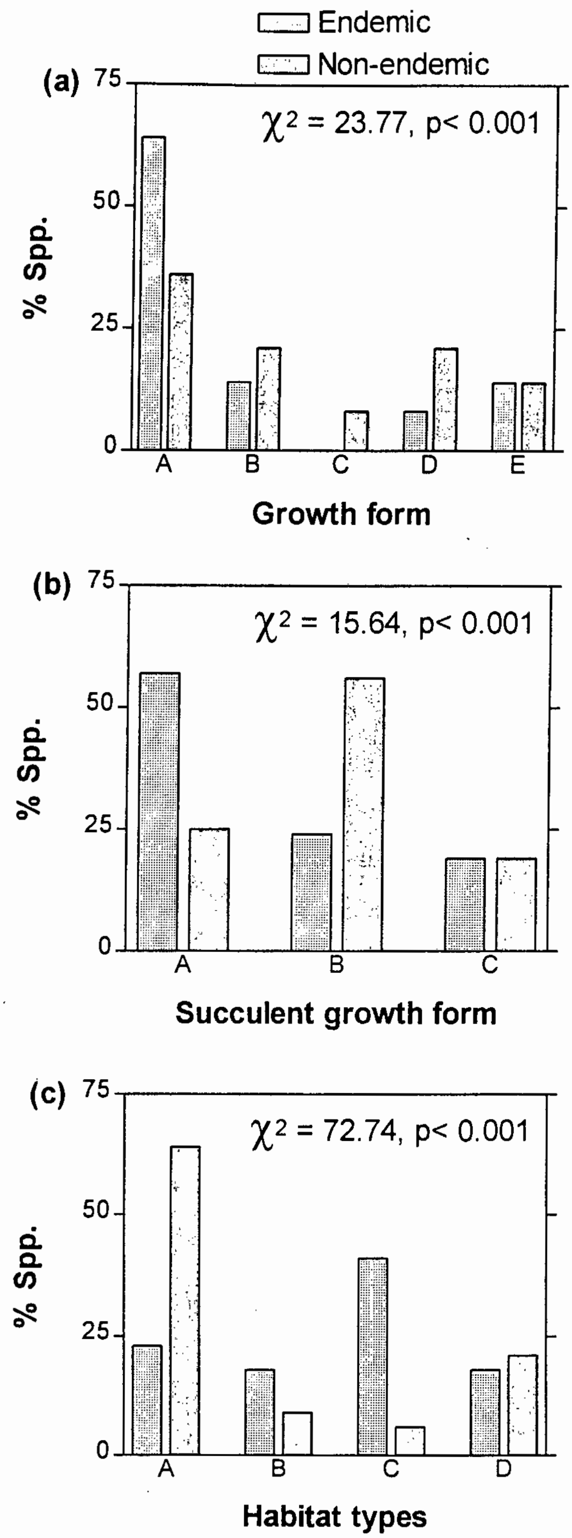


Figure 3.2 Percentage endemism within different growth forms and habitat types expressed as % endemism relative to the entire endemic flora. (a) Growth form vs. endemism, A all succulent growth-forms, B non-succulent shrubs, C graminoids, D forbs and annuals, E geophytes. (b) Within succulent growth forms, A dwarf leaf succulents, B leaf succulents, C stem succulents. (c) Across major habitat types, A dunes, B koppies and inselbergs, C pebble plains, D others (viz. disturbed and halophytic habitats). The Chi-squared tests the null hypothesis that endemics occur in the same frequency as non-endemics across the different categories.

Table 3.4 Distribution of species between different growth form types.

Growth form description	Number of species	% of flora
1. Dwarf leaf succulent	49	17
2. Shrub leaf succulent (non-dwarf)	58	19
3. Stem succulent	25	8
All succulent growth forms	**132**	**44**
4. Non-succulent shrub	58	19
5. Graminoid	17	6
6. Annual/forb	51	17
7. Geophyte	42	14

Table 3.5 The species-area relationship of the three major habitat types. Number of species represents all species restricted to these habitats plus those shared (% shared) with the other major habitat types. Chi-squared tests the null hypothesis that the frequency of species in a specific habitat shared with other habitats is the same for all habitats. Species-area is log species/log area.

Habitat Type	Area (km^2)	Number of Species (%)	χ^2	Spp./Area
1. Dunes	683	198 (21)	5.501 ns	0.81
2. Pebble plains	58	61 (20)	1.067 ns	1.01
3. Koppies & rocky outcrops	3	63 (46)	15.653 ***	3.77
4. Total	744	281 (15)	-	0.85

***: $p<0.0001$, ns: not significant

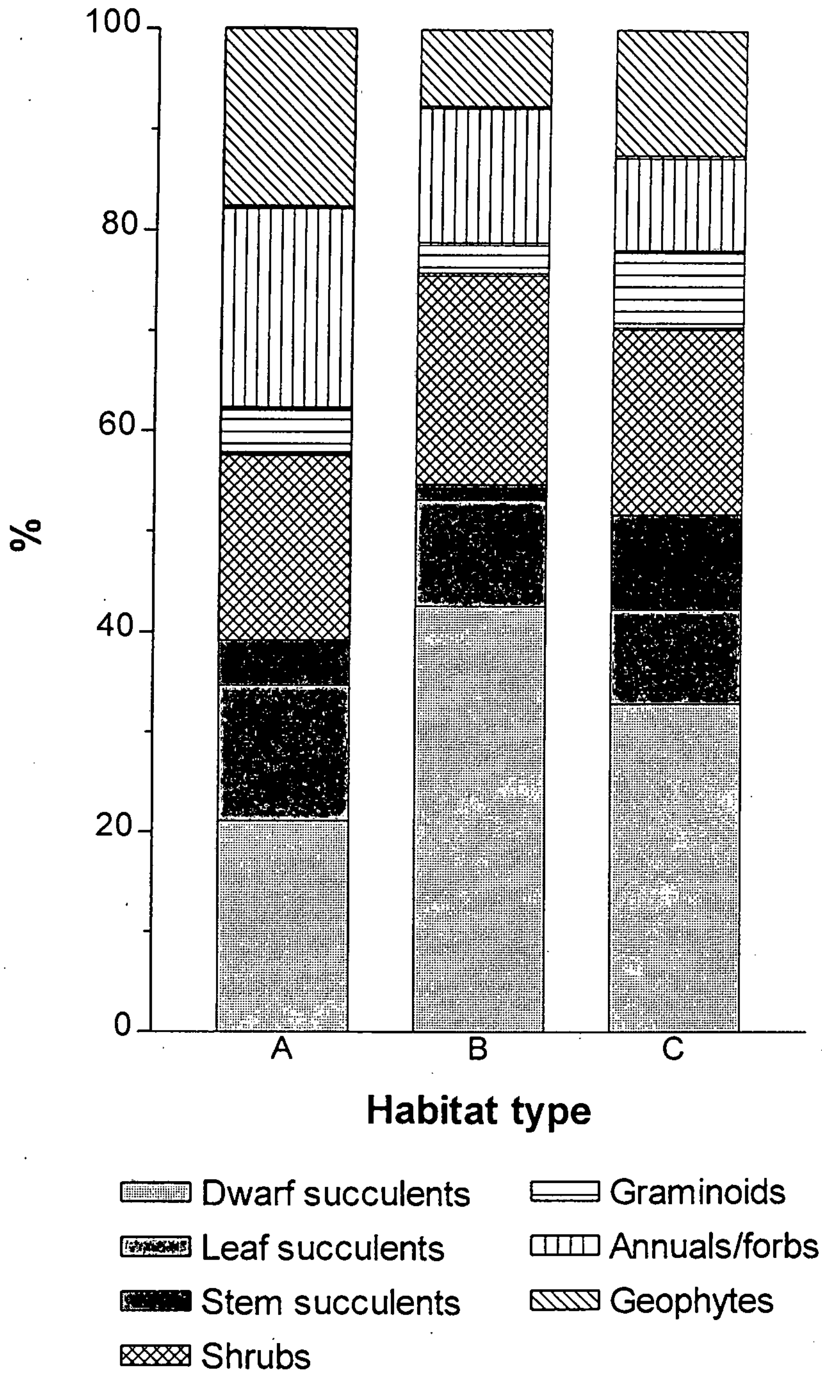


Figure 3.3 Proportional representation of the seven growth form types within the three major habitat types. A dunes; B koppies and rocky outcrops; and C pebble plains.

number of species with the surrounding habitat types (i.e. dunes, Table 3.5), whereas the reverse does not hold for the other habitat types. The pebble plains have disproportionately high numbers of endemic species (Fig. 3.2c), but share an expected proportion of species with the dune flora to the south (Table 3.5).

A comparison of the proportion representation of the seven growth forms within the floras in the three major habitat types (Fig. 3.4), shows that dwarf leaf succulents are concentrated on the rocky substrata. This trend explains the observed patterns in endemism between habitats. All three habitats have similar proportions of non-dwarf leaf succulent and non-succulent shrubs. However, dune habitats have proportionately more annuals, forbs and geophytes. The pebble plains have a high proportion of graminoid species relative to the other two habitat types.

The diversity of vascular plants in the study area is high for a desert area. A comparison of the species-area relationship for the study area with that for other deserts shows that species richness is as high or higher than many other deserts that are orders of magnitude larger in area (Fig. 3.3).

5 Discussion.

5.1 Patterns of plant diversity within the Namaqualand Sandveld.

The flora of the study area is typical of the Namaqualand-Namib Domain. It is dominated by members of the Asteraceae, Mesembryanthemaceae and Crassulaceae. The families represented show a strong affinity with the greater Cape Flora. This supports the currently held view developed by Jürgens (1991) that the flora of the Succulent Karoo Region forms part of a greater Cape Flora rather than part of the Palaeotropical Kingdom. Very few species encountered in the study area occur outside of the greater Cape Floral Region. Species that do are nearly all associated with disturbed or saline habitats.

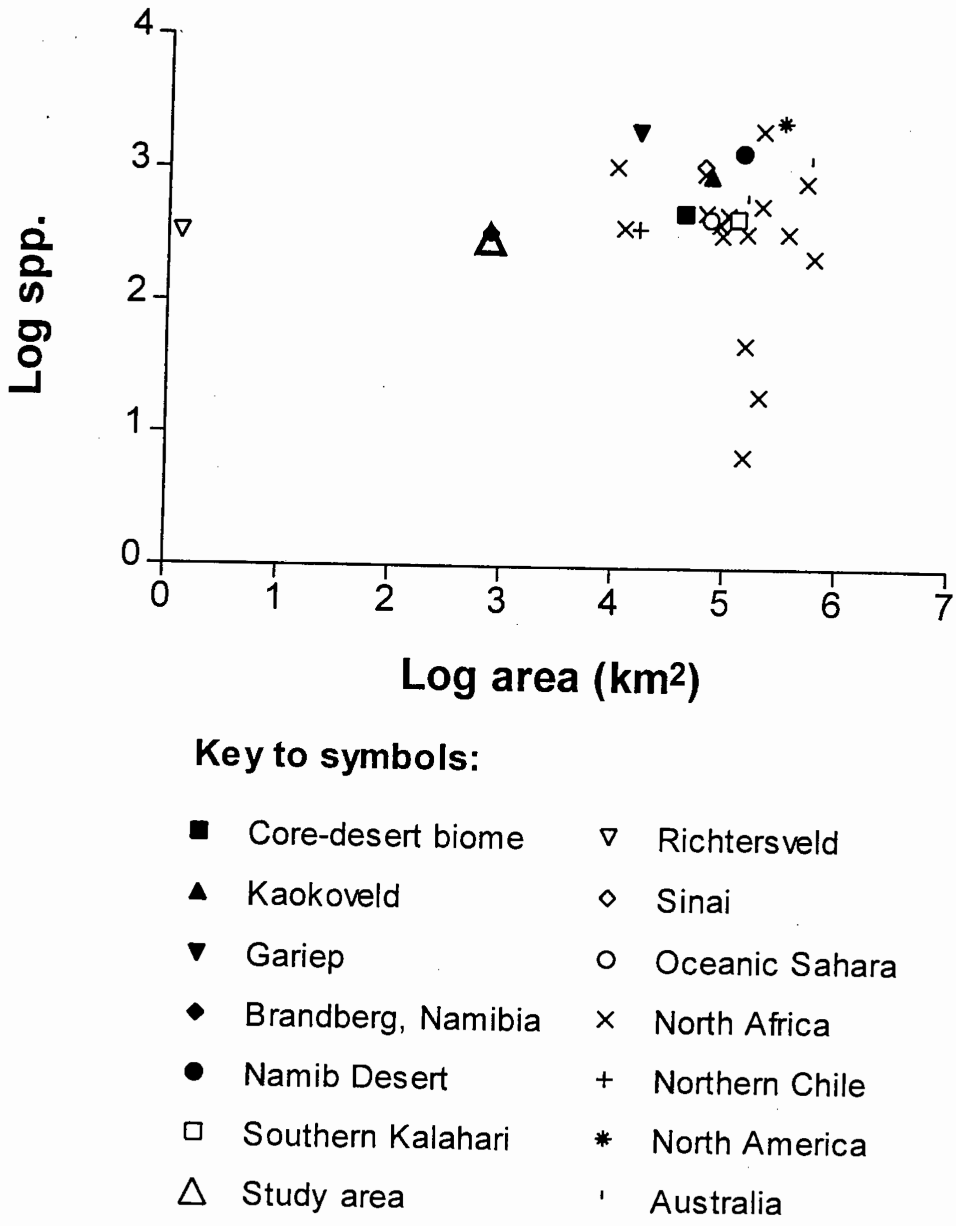


Figure 3.4 The species-area relationship for the study area in comparison to other world deserts. Data from Cowling and Hilton-Taylor (in press).

Species diversity within the study area is high. This is a reflection of plant diversity in the southern Namib Desert as a whole (Cowling and Hilton-Taylor in press). The species diversity of the study area is comparable to that of other world deserts that are orders of magnitude greater in area. The dominance by succulent leaved growth forms is unique for any desert system and clearly sets the southern Namib Desert apart from the other fog deserts. This diversity in the southern Namib is primarily the result of massive radiation amongst largely succulent-leaf lineages, namely the Mesembryanthemaceae, Crassulaceae and Asteraceae (*Senecio* and *Othonna*). The endemic component of the flora, characterised by dwarf leaf succulents in the Mesembryanthemaceae and to a lesser extent, Crassulaceae, epitomises this radiation. The patterns of endemism amongst the major families reflects larger scale patterns of endemism amongst families in the Succulent Karoo Biome (Cowling and Hilton-Taylor 1994, Hilton-Taylor in press). The dominance of leaf succulent growth forms in the flora and the under representation of geophytes, demonstrates strong affinities with the flora of the Gariep Centre of endemism of the western Richtersveld Mountains within the Succulent Karoo Biome as opposed to the Namaqualand Rocky Hills or Vanrhynsdorp centre (Hilton-Taylor in press).

The observed trend in species diversity are not restricted to the study area. This appears to be characteristic of the Gariep Centre of endemism. Nor is it restricted to the Namaqualand fog zone. Compared to other deserts, the four fog deserts all stand out as centres of plant diversity within their respective regional contexts.

Species are not distributed uniformly nor randomly between habitats in the study area. Diversity is concentrated on stable substrata, namely the koppies, inselbergs, rocky outcrops and pebble plains. These habitats comprise substrata and plant niches that are fundamentally different from those of the surrounding dunes (Shmida 1985). Firstly, rocky substrata are more resistant to aeolian and fluvial erosion. Secondly, rocks provide protection against sand abrasion and sun. Thirdly, precipitation received via runoff from rocks increases the amount of water received by plants. Fourthly, skeletal soils on rocky outcrops are edaphically xeric habitats due to shallow rooting depth and poor soil water-holding capacity (Porembski *et al* 1996). Thus, such habitats are stable, protective habitats, but prone to be very moist or water-logged during precipitation events and very droughtly habitats in-between. The strong habitat differences associated with these substrata create steep environmental gradients over very short distances. This would explain the very high observed rates of species turn-over between adjacent substrata (e.g. dunes and koppies).

Rocky habitats in this desert environment would favour dwarf succulent growth types. This is reflected in the results of the analysis of the local flora. This pattern of association between specific substrates and species richness is repeated elsewhere within similar habitats in the Succulent Karoo (e.g. the Knersvlaktes, Struck 1995) and within dwarf succulent genera (e.g. *Conophytum*, Hammer 1993). In general, for the Namaqualand-Namib domain of the Succulent Karoo Region, an endemic species will most likely be restricted to stable, rocky or pebble plain substrates and will probably be a dwarf succulent member of the Mesembryanthemaceae (see also Cowling and Hilton-Taylor in press).

The predictability of alternative sources of precipitation within the southern Namib Desert (fog and dew) and the increased runoff associated with rocky habitats would favour diversification in dwarf succulent growth types which could effectively utilise this predictable, but meagre moisture source. Occasional seasonal droughts fragment populations and increase generation turnover, leading to increased levels of speciation. The high diversity, endemism and species to genus ratios associated with dwarf succulent genera within the southern Namib suggests a recent radiation in these lineages. This could be a result of the geologically recent shift in the climate of the southern Namib Desert associated with the end of the Last Glacial Maximum during the Late Pleistocene from a mesic semi-arid climate, to more xeric, arid climate (Linder *et al* 1992, see section on palaeoclimate in previous chapter for a more detailed discussion). Large-scale fragmentation of populations associated with this drying of the regional climate over the last ca. 14 000 years would favour speciation amongst lineages capable of exploiting the developing climatic conditions.

Within South Africa, pebble plain endemics of the Western Gariep Centre are restricted to the Lower Orange River Valley. None of these endemics are encountered further south on rocky habitats such as the Buchu Twins nor the Holgat River Canyon. For these plants, the special adaptations required for survival on the plains of the Lower Orange River Valley has meant that they have been unable to exploit seemingly similar habitats on nearby "islands" to the south. Species encountered on both the pebble plains and rocky habitats to the south are also encountered in the dunes and are generally widespread, non-endemic species.

5.2 Centres of Endemism.

Recent discussions on the nature and distribution of centres of endemism in the Succulent Karoo Region (Jürgens 1991, Hilton-Taylor in press) have overlooked the existence of a distinct centre of coastal endemism in the southern Namib. In addition to the well recognised Western Gariep Circle of the Gariep Centre, the Namaqualand-Namib Domain is characterised by the existence of a narrow Coastal Centre of plants restricted to rocky outcrops or related substrata adjacent to the coast or within the zone of maritime influence. Excluded from these habitats are near-shore dunes, with their associated halophytic communities (see following chapter). The moderated coastal-desert climate, combined with the high occurrence of fog, result in a climate very different from that experienced even short distances inland (see section on temperature in previous chapter). This view on the existence of a Coastal Zone of endemism is shared with Graham Williamson (pers. comm.). Rocky habitats located near the coast inevitably receive higher aerosol salt inputs, especially in the near-shore zone, than similar habitats further inland. These habitats are probably more saline than their inland counterparts. Thus, there may be an obligate halophytic element in the endemic flora (e.g. *Meyerophytum meyeri* var. *holgatense*).

The epicentre of this coastal zone lies on the pebble plains to the east and south of Alexander Bay. This area stretches from Alexander Bay as far east as Grootderm, where the boundary of the Western Gariep circle lies. The latitudinal limits of this Coastal Centre are probably Lüderitz Bay in Namibia and stretching the length of the southern Namib Desert coast on scattered and isolated rocky "islands" to the coastal cliffs north of the Olifants River mouth. The inland limit of this Coastal Centre is unclear. Floristic criteria for the eastern limit of the zone would exclude similar rocky habitats and mountains on the coastal plain that receive regular fog, e.g. the Holgat River Canyon east of the main road to Alexander Bay; the Klinghard and Buchu Mountains in Namibia; and Fyftien-Myl-Se-Berg and Augrabies Berg inland of Port Nolloth. In addition to the distinct climatic and coastal characteristics of this centre, it is further characterised by a disjunct distribution associated with isolated, suitable habitats along the coast.

A typical character species for the centre would be *Fenestraria rhopalophylla* subsp. *aurantiaca*. The distribution of this species along the coast of the southern Namib Desert, perhaps, better defines the boundaries of the centre, placing the southern boundary of the centre around Kleinzee. Other species associated with the epicentre of this zone at the mouth of the Orange River include *Conophytum saxeatum, Cephalophyllum verrucosa, Brownanthus marlothii, Pelargonium subthorpifolium, P. crassicaulae, Crassula sladenii, Euphorbia stapheliodes* and *E. celata.*. More widespread species occurring off the pebble plains, but similarly restricted to the coastal zone are species such as *Tylecodon decipiens, T. fragilis,* (possibly) *T. bucholtziana, Othonna furcata, Gazania schenkii, Adromischus montium-klinghardtii* and *Meyerophytum meyeri* subsp. *holgatense*. *Wooleya farinosa* is an interesting member as it is restricted to coastal, Pleistocene dunes, dune slacks and shingle beaches between Kleinzee and Hondeklip Bay. Within this Coastal Centre there is subtle latitudinal gradient of species turnover as one moves from the Namaqualand into the Southern Namib Domain. For example, species such as *Tylecodon fragilis* and *Wooleya farinosa* do not occur north of the Orange River and appear to have their centre of distribution to the south of Kleinzee, whereas southern Namib genera such as *Juttadintera, Psammophora* or *Namibia* characterise the northern zone of this centre. This gradient needs to be investigated further.

6 Conclusions.

Broad patterns of plant diversity in the southern Namib can be predicted on the basis of substrata. The flora of the Namaqualand Sandveld is characterised by being widespread with few, localised endemic species. Within this dune system, discrete, isolated enclaves of Richtersveld and Southern Namib flora exist on rocky outcrops and koppies. These habitats, although limited in extent, support a more diverse flora comprising numerous endemic species and rocky habitat specialists, along with a significant subset of the dune species. This combination leads to a very high species:area ratio for these habitats. Within the flora of the southern Namib, the trend amongst the endemic flora is towards dwarf leaf succulent growth forms restricted to rocky habitats. The flora of the southern Namib is also characterised by the presence of a distinct zone of coastal endemics, restricted primarily to rocky substrata.

The observed patterns in plant species diversity in the southern Namib have important implications for conservation strategies aimed at protecting the regions flora. These efforts should concentrate on conserving the vegetation on koppies, inselbergs and other rocky substrata. These habitats show high levels of species diversity; are home to the majority of the endemic flora (dwarf leaf succulents); and have many species in common with non-rocky substrata.

References

Acocks, J.P.H. (1983) Veld types of South Africa. Third edition. *Memoirs of the Botanical Survey of South Africa* 57: 1-146.

Arnold, T.H. and De Wet, B.C. (1993) Plant of southern Africa: names and distribution. *Memoirs of the Botanical Survey of South Africa* 62: 1-825.

Boucher, C.and le Roux, A. (1989) Heavy mineral sand mining project assessment vegetation report. Anglo American Corporation West Coast Heavy Mineral Sands Project Supplementary Report. EEU Report No. 4/90/49. Environmental Evaluation Unit, University of Cape Town, Cape Town.

Boucher, C.and le Roux, A. (1993) Dry coastal ecosystems of the South African coast. In: van der Maarel, E. (ed.) Dry Coastal Ecosystems. Africa, America, Asia and Oceania. Ecosystems of the Worlds 2B. Elsevier, Amsterdam.

Cowling, R.M. and Hilton-Taylor, C. (1994) Patterns of plant diversity and endemism in southern Africa: an overview. In: Huntley, B.J. (ed.) Botanical Diversity in Southern Africa. National Botanical Institute, Pretoria.

Cowling, R.M. and Hilton-Taylor, C. (in press) Plant biogeography, endemism and diversity. In Dean, W.R.J. and Milton, S.J. (eds.) The Karoo. Ecological Patterns and Processes. Cambridge University Press, Cambridge.

Hammer, S.A. (1993) The Genus Conophytum. A Conograph. Succulent Plant Publications, Pretoria.

Hartmann, H. (1991) Mesembryanthema. *Contributions to the Bolus Herbarium* 13: 75-157.

Hilton-Taylor, C. (1994) Western Cape Domain (Succulent Karoo). Republic of South Africa and Namibia. In: Davis, S.D; Heywood, V.H. and Hamilton. A.C. (eds.) Centres of Plant Diversity. A Guide and Strategy for their Conservation. Volume 1: Europe, Africa, south West Asia and the Middle East. IUCN Publications Unit, Cambridge.

Hilton-Taylor, C. (in press) Patterns and characteristics of the flora of the Succulent Karoo Biome, southern Africa. in Van der Maersen, L.J.G. (ed.) Proceedings of the XIVth AETFAT Congress, Wageningen, The Netherlands. Kluwer Academic Publishers, Dordrecht.

Jackson, B.J. (1916) A Glossary of Botanic Terms. Duckworth & Co., London.

Johnson, A.F. (1977) A survey of the strand and dune vegetation along the Pacific and southern gulf coasts of Baja California, Mexico. *Journal of Biogeography* 7: 83-99.

Jürgens, N. (1991) A new approach to the Namib Region. I: Phytogeographic subdivision. *Vegetatio* 97: 21-38.

Jürgens, N; Günster, A; Seely, M.K. and Jacobson, K.M. (in press) Desert. In Cowling, R.M., Richardson, D.M. and Pierce, S.M (eds.) The Vegetation of Southern Africa. Cambridge University Press, Cambridge.

Le Houérou, H.N. (1986) The Desert and Arid Zones of Northern Africa. in Hot Deserts and Arid Shrublands. Evenari, M *et al* (eds.) Elsevier Science Publishers B.V., Amsterdam.

Le Houérou, H.N. (1992) Outline of the biological history of the Sahara. *Journal of Arid Environments* 22: 3-30.

Le Houérou, H.N. and Boulos, L. (1991) Bioclimatic and phytogeographic characteristics of the arid rangelands of northern Africa and the Near East. IVth International Rangeland Congress, Montpellier, France.

Linder, H.P; Meadows, M.E. and Cowling, R.M. (1992) History of the Cape flora. In Cowling, R.M. (ed.) The Ecology of Fynbos. Nutrients, Fire and Diversity. Oxford University Press, Cape Town.

Low, B.A. and Rebelo, A.G. (eds.) (1996) Vegetation of South Africa, Lesotho and Swaziland. Department of Environmental Affairs and Tourism, Pretoria.

Milton, S.J; Yeaton, R.I; Dean, W.R.J. and Vlok, J.H.J. (in press) Succulent Karoo. In Cowling, R.M., Richardson, D.M. and Pierce, S.M (eds.) The Vegetation of Southern Africa. Cambridge University Press, Cambridge.

Peinado, M.; Alcaraz, F.; Aguirre, J.L.; Delgadillo, J.and Aguado, I. (1995a) Shrubland formations and associations in mediterranean-desert transitional zones of north-western Baja California. *Vegetatio* 117: 165-179

Peinado, M.; Alcaraz, F.; Aguirre, J.L. and Delgadillo, J. (1995b) Major plant communities of warm North American deserts. *Journal of Vegetation Science* 6: 79-94.

Porembski, S., Szarzynski, J., Mund, J-P. and Barthlott, W. (1996) Biodiversity and vegetation of small-sized inselbergs in a West African rain forest (Taï, Ivory Coast). *Journal of Biogeography* 23: 47-55.

Robinson, E.R. (1978) Phytogeography of the Namib Desert of South West Africa (Namibia) and its significance to discussions of the age and uniqueness of this desert. In Van Zinder Bakker, E.M. and Coetzee, J.A. (eds.) *Palaeoecology of Africa* 10:, 67-74.

Rowley, G.D. (1994) Succulent Compositae.

Rundel, P.W. and Mahu, M. (1976) Community structure and diversity in a coastal fog desert in northern Chile. *Flora* 165: 493-505.

Rundel, P.W; Dillon, M.O; Palma, B; Mooney, H.A; Gulmon, S.L. and Ehleringer, J.R. (1991) The phytogeography and ecology of the coastal Atacama and Peruvian deserts. *ALISIO* 13: 1-49.

Shmida, A. (1985) Biogeography of the desert flora. In Evenari, M *et al* (eds.) Hot Deserts and Arid Shrublands. Elsevier Science Publishers B.V., Amsterdam.

Shmida, A. and Werger, M.J.A. (1992) Growth form diversity on the Canary Islands. *Vegetatio* 102: 183-199.

Struck, M. (1995) Land of blooming pebbles: flowers and their pollinators in the Knersvlakte. *Aloe* 32: 56-64.

Turner, R.M. and Brown, D.E. (1982) Sonoran Desert-scrub. *Desert Plants* Special Issue 4: 181-221.

Ward, J.D.; Seely, M.K. and Lancaster, N. (1983) On the antiquity of the Namib. *South African Journal of Science* 79: 175-183.

Werger, M.J.A. (1978) The Karoo-Namib Region. In: Biogeography and Ecology of Southern Africa. Werger, M.J.A. (ed.) Dr W. Junk bv Publishers, The Hague.

Appendix I A species list for the coastal area between Port Nolloth and Alexander Bay. **A** Growth form codes: 1 Dwarf leaf succulent; 2 non-dwarf leaf succulent; 3 stem succulent; 4 non-succulent shrub; 5 graminoid; 6 annual or forb; and 7 geophyte. **B** Habitat codes: 1 disturbed; 2 dune; 3 dune & koppie or rocky outcrop; 4 dune & pebble plain; 5 halophyte; 6 koppie or rocky outcrop; and 7 pebble plain.

Families and Species	A	B
Acanthaceae		
Justicia orchioides L.f. subsp. Orchioides	4	7
Aizoaceae		
Galenia collina (Eckl. & Zeyh.)Walp.	6	2
Galenia crystallina (Eckl. & Zeyh.)Fenzl	4	2
Galenia squamulosa (Eckl. & Zeyh.)Fenzl	6	1
Hypertelis angrae-pequenae Friedr.	1	4
Hypertelis salsoloides (Burch.)Adamson var. salsoloides	1	2
Limeum africanum L.	7	2
Pharnaceum confertum (DC.) E&Z var. brachyphytlum Adamson	6	6
Pharnaceum croceum E.Mey. ex Fenzl	6	2
Pharnaceum exiguum Adamson	6	2
Pharnaceum lanatum Bartl.	6	2
Pharnaceum microphyllum L.f.	6	2
Pharnaceum microphyllum var. microphyllum	6	2
Tetragonia fruticosa L.	2	2
Tetragonia microptera Fenzl	1	2
Tetragonia robusta Fenzl	2	2
Amaryllidaceae		
Boophane sp. Herb.	7	2
Gethylis grandiflora L.Bol.	7	2
Haemanthus pubescens L.f. subsp. arenicolus Snijman	7	3
Strumaria bidentata Schinz	7	7
Anacardiaceae		
Rhus undulata Jacq.	4	6
Apiaceae		
Deverra denudata (Viv.) Pfisterer & Podl. subsp. aphylla (Cham. & Schlechtd.) Pfisterer & Podl.	4	1/5
Peucedanum sulcatum Sond.	7	2
Sonderina tenuis (Sond.)H.Wolff	6	2

Asclepiadaceae

Huernia namaquensis Pillans	1	2
Lavrania marlothii (N.E.Br.) Bruyns	1	7
Microloma saggitatum (L.)R.Br	3	2
Quaqua armata (N.E.Br.)Bruyns	1	2
Quaqua inversa (N.E.Br.)Bruyns	1	2
Rhyssolobium dumosum E.Mey.	4	7
Tridentea pachyrrhiza (Dinter)Leach	1	7

Asparagaceae

Myrsiphyllum asparagoides (L.) Willd.	7	6
Myrsiphyllum fasciculatum (Thunb.) Oberm.	7	2
Myrsiphyllum juniperoides (Engl.) Oberm.	7	2
Myrsiphyllum undulatum (L.f.) Oberm.	7	2
Protoasparagus acocksii (Jessop) Oberm.	4	2
Protoasparagus capensis (L.) Oberm.	4	3
Protoasparagus retrofractus (L.) Oberm.	4	2

Asphodelaceae

Aloe arenicola Reynolds	2	2
Aloe framesii L.Bol.	2	2
Bulbine aff. succulenta Compton	1	7
Bulbine frutescens (L.) Willd.	1	2
Bulbine sp.	1	6
Chlorophytum sp.	7	7
Trachyandra falcata (L.f.) Kunth	7	2

Asteraceae

Amellus epaleaceus O.Hoffm.	6	1
Amellus flosculosus DC.	6	2
Amellus microglossus DC.	6	2
Amellus tenuifolius Burm.	6	2
Arctotis diffusa Thunb.	2	2
Arctotis hirsuta (Harv.)Beauv.	6	2
Arctotis merxmeulleri Freidr.	6	2
Berkheya fruticosa (L.)Ehrh.	4	6
Chrysanthemoides incana (Burm.f.)T.Norl.	4	2/5
Didelta carnosa (L.f.)Ait. var. carnosa	6	2
Eriocephalus brevifolius (D.C.) M.A.N. Müller comb. nov.	4	7
Eriocephalus racemosus L.	4	2
Foveolina albida (DC.)Kallersjo	6	2
Gazania lichtensteinii Less.	6	6
Gazania schenckii O.Hoffm.	6	6/5
Gazania aff. heterochaeta	6	2
Gazania tenuifolia Less.	6	2
Helichrysum aff. oxybelium & asperum	6	3
Helichrysum marmarolepsis S.Moore.	6	2
Helichrysum micropoides DC.	6	2
Helichrysum pumilio (O.Hoffm.)Hillard&Burtt subsp. pumilio	6	2
Helichrysum sp.	6	6

Helichrysum tricostatum (Thunb.)Less.	4	2
Kleinia pinguifolius (DC.)Sch.Bip.	1	3
Onchosiphon grandiflorum (Thunb.)Kallersjo	6	2
Onchosiphon suffruticosum (L.)Kallersjo	6	2
Osteospermum microcarpum (Harv.)T.Norl.	6	2
Osteospermum oppositifolium (Ait.)T.Norl.	4	3
Osteospermum polycephalum (DC.)T.Norl.	4	7/1
Osteospermum sp.1	6	7
Othonna aff. furcata (Lindl.)Druce	2	6
Othonna aff. cuneata DC.	2	2
Othonna aff. opima Merxm.	2	2
Othonna clavifolia Marloth	2	6
Othonna cylindrica (Lam.)DC.	2	2
Othonna graveolens O.Hoffm.	2	2
Othonna lasiocarpa (D.C.) Sch. Bip.	2	2
Othonna lingua (Lees.) Sch. Bip.	7	2
Othonna sedifolia DC.	2	3
Pentzia sp.	6	1
Pteronia divaricata (Berg.)Less.	4	2
Pteronia glabrata L.f.	4	3
Pteronia onobromoides DC.	4	3
Pteronia paniculata Thunb.	4	6
Senecio aloides (DC.)Sch.Bip.	2	2
Senecio cakilefolius DC.	6	2
Senecio cardaminifolius DC.	6	2
Senecio citriformis	2	6
Senecio radicans (L.f.) Sch. Bip.	1	6
Ursinia aff. speciosa DC.	6	2
Ursinia calenduliflora (DC.)N.E.Br.	6	2
Boraginaceae		
Trichodesma africanum (L.)Lehm.	6	7
Brassicaceae		
Heliophila carnosa (Thunb.)Steud.	6	6
Heliophila lactea Schltr.	6	2
Lepidium africanum (Burm.f.)DC.	6	1
Campanulaceae		
Wahlenbergia psammophila Schltr.	6	2
Caryophyllaceae		
Dianthus namaensis Schinz.	6	6
Chenopodiaceae		
Atriplex cinerea Poir. subsp. bolusii (C.H. Wr.)Aell.	6	1
Atriplex eardleyae Aell.	4	1
Atriplex lindleyi Moq. subsp. inflata (F.Mull.)P.G.Wilson	4	1
Salsola nollothensis Aell.	4	2

Salsola tuberculata (Moq.)Fenzl	4	2
Salsola zeyheri (Moq.)Bunge	4	2
Suaeda fruticosa (L.)Forssk.	2	5

Colchicaceae

Ornithoglossum sp.	7	4
Ornithoglossum vulgare B. Nord.	7	2

Crassulaceae

Adromischus marianiae (Marloth)Berger var. hallii (P.C.Hutch.)Tolken	1	6
Adromischus marianiae (Marloth)Berger var. kubusensis (Uitew.)Tolken	1	6
Adromischus montium-klinghardtii (Dinter)Berger	1	6
Cotyledon orbiculata L. var. orbiculata	1	3
Crassula atropurpurea (Haw.)Dietr. var. cultriformis (Friedr.)Tolken	1	2
Crassula brevifolia Harv.	1	3
Crassula brevifolia Harv. var. brevifolia	1	4
Crassula columnaris Thunb.	1	3
Crassula cotyledonis Thunb.	1	6
Crassula deceptor Schonl. & Bak. f.	1	3
Crassula elegans Schonl. & Bak. f.	1	7
Crassula expansa Dryand. subsp. expansa	1	3
Crassula macowaniana Schonl. & Bak. f.	1	6
Crassula muscosa L.	1	3
Crassula pallens Schonl. & Bak. f.	1	3
Crassula plegmatoides Freidr.	1	3
Crassula pseudohemisphaerica Freidr.	1	6
Crassula sladenii Schonl.	1	6
Crassula sp.1	1	2
Crassula sp.2	1	2
Crassula subaphylla (Eckl. & Zeyh.)Harv. var. subaphylla	1	3
Tylecodon decipiens Tolken	1	6
Tylecodon fragilis (R.A.Dyer)Tolken	1	2
Tylecodon paniculatus (L.f) Tolken	3	3
Tylecodon reticulatus (L.f.)Tolken	1	2
Tylecodon schaeferianus (Dinter)Tolken	1	7
Tylecodon similis (Tolken)Tolken	1	6
Tylecodon wallichii (Harv.)Tolken subsp. wallichii	1	2

Curcurbitaceae

Kedrostis psammophila Bruyns	7	2

Euphorbiaceae

Euphorbia burmannii E.Mey. ex Boiss.	3	2
Euphorbia caput-medusae L.	3	2
Euphorbia celata R.A. Dyer	3	7
Euphorbia decussata E.Mey. ex Boiss.	3	2
Euphorbia ephedroides E.Mey. ex Boiss.	3	2
Euphorbia mauritanica L.	3	2

Euphorbia sp.1	3	7
Euphorbia stapelioides Boiss.	3	7
Euphorbia tuberculata Jacq.	3	2
Fabaceae		
Crotalaria meyeriana Steud.	6	1
Indigofera exigua Eckl.& Zeyh.	6	3
Lebeckia cinerea E.Mey.	4	2
Lebeckia multiflora E.Mey.	4	7
Lebeckia sericea Thunb.	4	2
Lessertia candida E.Meyer	4	7
Lessertia diffusa R. Br.	6	2
Lotonotis falcata (E.Mey.)Benth.	6	3
Medicago polymorpha L.	6	1
Geraniaceae		
Pelargonium carnosum (L.)L'Herit	4	2
Pelargonium ceratophyllum L'Herit.	1	7
Pelargonium crassicaule L'Herit.	4	4
Pelargonium crithmifolium J.E. Sm.	4	2
Pelargonium echinatum Curt.	4	2
Pelargonium fulgidum (L.)L'Herit	4	6
Pelargonium grandicalcaratum Knuth.	4	2
Pelargonium sibthorpiifolium Harv.	1	7
Sarcocaulon crassicaule Rehm	3	7
Sarcocaulon multifidum E.Mey. ex Knuth	3	7
Sarcocaulon patersonii (DC.) G.Don	3	4
Hyacinthaceae		
Albuca altissima Dryand.	7	2
Albuca aff. cooperi	7	3/7
Lachenalia klinghardtiana Dinter.	7	6/7
Massonia sp.	7	7
Ornithogalum xanthochlorum Bak.	7	2
Veltheimia capensis (L.) DC.	7	2
Illecebraceae		
Pollichia campestris Ait.	4	6
Iridaceae		
Babiana namaquensis Bak.	7	4
Babiana thunbergii Ker-Gawl., Koning & Sims	7	2
Ferraria divaricata Sweet	7	2
Ferraria shaeferi Dinter	7	2
Gladiolus orchidiflorus Andr.	7	2
Gladiolus viridiflorus G.J.Lewis	7	7
Lapeirousia barklyi Bak.	7	2
Morea fugax (Delaroche) Jacq.	7	2

Labiatae

Salvia lanceolata L.	4	2

Mesembryanthemaceae

Antimima aff. buchubergensis	1	6
Antimima maleolens L.Bol.	1	3
Antimima perforata L.Bol.	1	3/7
Aridaria noctiflora (L.)Schwant.	2	4
Brownanthus arenosus (Schinz.)Inlenf.&Bittrich	2	4/5
Brownanthus marlothii (Pax.)Schwantes	1	7
Cephalophyllum ebracteatum (Pax ex Schlecter & Diels)Dinter & Schwantes	1	4
Cephalophyllum spongiosum (L.Bol.)L.Bol.	1	2
Cheirodopsis robusta (Haw.)N.E.Br.	1	2
Cheirodopsis verrucosa L.Bol.	1	7
Conicosia elongata (Haw.)N.E.Br.	7	2
Conophytum saxeatum (N.E.Br.)N.E.Br.	1	6
Dracophilus dealbatus (N.E.Br.)Walg.	1	7
Drosanthemum curtophyllum L.Bol.	1	2
Drosanthemum ramosissimum (Schltr.)L.Bol.	1	4/5
Fenestraria rhopalophylla (Schltr. & Diels)N.E.Br. subsp. aurantiaca (N.E.Br.)H.E.K. Marth.	1	7
Jordaaniella cuprea (L.Bol.)H.E.K. Hartm.	1	2
Juttadintera deserticola (Marloth)Schwant.	1	7
Lampranthus hoerleinianus (Dinter)Friedr.	2	2
Lampranthus sp.1	2	2
Lampranthus sp.2	2	2
Leipoldtia uniflora L.Bol.	1	3
Lithops herrei L.Bol.	1	7
Mesembryanthemum barklyi N.E.Br.	2	1
Mesembryanthemum chrystallinum L.	1	2
Meyerophytum meyeri (Schwant.)Schwant. var. holgatense	1	6
Mesembryanthemum hypertrophicum Dinter	1	1
Phyllobolus ocultans (N.E.Br.) Gerbaulet	1	2
Phyllobolus quartziticus (N.E.Br.) Gerbaulet	1	2
Phyllobolus scintillans	2	1
Phyllobolus spinuliferus (Haw.) Gerbaulet	2	2
Psammophora modesta (Dinter & Berger)Dinter & Schwant.	1	7
Psilocaulon dinterii (Engl.)Schwant.	2	4
Psilocaulon subnodosum (Berger)N.E.Br.	2	2
Ruschia aff. subpaniculata	2	2
Ruschia cyathiformis L.Bol.	1	2
Ruschia fugitans L.Bol.	1	2
Ruschia hexamera L.Bol. subsp. longipetala L.Bol.	1	6
Ruschia namaquana L.Bol. var. quinqueflora L.Bol.	1	7
Ruschia paripetala L.Bol.(L.Bol.)	1	2
Ruschia rupis-arcuatae (Dinter)Friedr.	1	2
Ruschia sp.1	1	2
Ruschia sp.2	1	2
Ruschianthemum gigas (Dinter)Friedr	2	7
Stoeberia beetzii (Dinter) Dinter & Schwant	2	3
Stoeberia utilis (L.Bol.)L.Bol.	2	3

Neuradaceae

Grielium grandiflorum (L.) Druce	7	2
Grielium humifusum Thunb. var. humifusum	7	2
Grielium humifusum Thunb. var. parviflorum Hsrv.	7	2

Oxalidaceae

Oxalis sp.1	7	2
Oxalis sp.2	7	6

Plumbaginaceae

Limonium dregeanum (Presl) Kuntze	6	5

Poaceae

Centropodia glauca (Nees)T.A.Cope	5	7
Chaetobromus involucratus (Schrad.) Nees subsp. involucratus	5	2
Cladoraphis cyperoides (Thunb.) S.M. Phillips	5	2
Dregeochloa pumila (Nees) Conert	5	2
Erharta brevifolia Schrad. var. cuspidata Nees	5	2
Erharta calycina J.E.Sm. var. calycina	5	3
Erharta delicatula (Nees)Stapf.	5	6
Hordeum marinum Huds. subsp. gussoneanum (Parl.)Thell.	5	1
Karroochloa schismoides (Stapf ex Conert) Conert & Tuerpe	5	2
Phragmites australis (Cav.) Steud.	5	5
Schmidtia kalihariensis Stent	5	2
Stipagrostis ciliata (Desf.) De Winter var. capensis (Trin. & Rupr.) De Winter	5	2
Stipagrostis dregeana Nees	5	7
Stipagrostis geminifolia Nees	5	7
Stipagrostis lutescens (Nees)De Winter var. marlothii (Hack.)De Winter	5	7
Stipagrostis obtusa (Del.) Nees	5	2
Stipagrostis subacaulis (Nees) De Winter	5	7

Polygalaceae

Polygala mossii Exell	4	7

Portulacaceae

Anacampseros albissima Marloth	1	7

Rubiaceae

Kohautia cynanchica DC.	6	7

Santalaceae

Thesium elatius Sond.	4	2

Scrophulariaceae

Hyobanche sanguiea L.	7	2
Hyperia tristis (L.f.) Benth.	6	2
Jamesbrittenia fruticosa	4	6/5
Jamesbrittenia merxmeulleri	4	7
Manuela androsacea E. Mey. ex Benth.	6	2
Manulea aridicola Hilliard	6	2
Manulea minuscula Hilliard	6	7
Nemesia anisocarpa E. Mey. ex Benth.	6	2
Nemesia bicornis (L.) Pers.	6	2
Nemesia viscosa E. Mey. ex Benth.	6	2
Peliostomum virgatum E.Mey	6	7
Polycarena pumilum	6	2
Zaluzainskya affinis Hillard	6	2
Zaluzianskya benthamiana Walp.	6	7

Selaginaceae

Dischisma sp.	4	2
Dischisma spicatum (Thunb.)Choisy	4	7
Hebenstretia cordata L.	4	2
Hebenstretia parviflora E.Mey.	4	7
Hebenstretia repens Jarosz	4	2
Hebenstretia robusta E. Mey.	4	2
Hebenstretia sp.	4	2
Selago aff. robusta Rolfe	4	6/7
Selago robusta Rolfe	4	2

Solanaceae

Lycium cinereum Thunb. (Sens. Lat.)	4	3
Lycium decumbens Wel. ex Hiern	4	2
Lycium ferocissimum Miers	4	3
Lycium prunus-spinosa Dun.	4	2

Sterculiaceae

Hermannia heterophylla (Cav.) Thunb.	4	2
Hermannia pfeilii Schum.	4	3
Hermannia trifurca L.	4	2

Tecophilaeaceae

Cyanella ramosissima (Engl. & Frause) Engl. & Krause	7	2

Thymelaeaceae

Gnidia sp.	4	2

Zygophyllaceae

Augea capensis Thunb.	2	1
Zygophyllum clavatum Schltr. & Diels	2	2

Zygophyllum cordifolium L.f.	2	3/7
Zygophyllum morgsana L.	2	2
Zygophyllum prismatocarpum E. Mey. ex Sond.	2	4
Unknown Families		
monocot 'curly clumps'	7	2
monocot 3	7	2
monocot 4	7	2
monocot 8	7	2

Chapter 4 The Vegetation of the Coastal Belt Between Port Nolloth and Alexander Bay.

1 Introduction.

The vegetation of the Sandveld on the Namaqualand coastal plain has been poorly studied. Recent reviews of the succulent karoo and desert biomes of southern Africa by Low and Rebelo (1996), Jürgens (1991), Hilton-Taylor (in press), Milton *et al* (in press) and Jürgens *et al* (in press) provide a sound phytogeographic background in which to approach this area. These reviews, however, have concentrated on the delineation and description of the major phytochorological units at a regional scale within the biome based on classifications of the flora on broad structural groups of plants, patterns of endemism, climate and geology. At this level it is possible to obtain a good understanding of the regional floristics within the biome. These were discussed in the previous chapter.

At the level of plant communities or associations there has been surprisingly little work completed. Community level descriptions of the Namaqualand Sandveld is limited to Boucher and le Roux (1989 and 1993) and de Villiers *et al* (unpubl.). The previous chapter placed the flora of the study area in a regional and global context, and discussed patterns of species distribution in the landscape. In this chapter, the focus now turns to examine the flora of the study area at a community level.

2 Objectives, rationale and scope of this chapter.

The objective of this chapter is to undertake a comprehensive phytosociological analysis of the study area, looking firstly at the what the basic species assemblages or associations are and secondly at what environmental variables best explain the observed mosaic of species associations in the landscape.

The rationale for undertaking, this essentially descriptive study of the vegetation, is due in part to our current lack of knowledge of the flora of the Namaqualand coastal, belt and partly due to the original aim of the project, restoration. Firstly, restoration requires a goal (see Chapter 6). A phytosociological survey in this context sets the goals to which any restoration program should strive. Secondly, by understanding biotic or abiotic patterns or processes that influence the vegetation of the area, one can better understand the observed patterns of natural revegetation of disturbed areas and what the limitation to this process are. Such insights can provide restoration ecologist with clues as to how one can facilitate or actively promote the restoration of these disturbed areas through the manipulation of natural processes.

I have not focused on restoration directly in this chapter. This is discussed in Chapter 6. This chapter is descriptive, focusing on the following questions:

- What are the major species assemblages of the study area?
- What are the key environmental gradients that determine the distribution of plants in the landscape?
- Where do these assemblages grow in relation to one another and the major environmental variables?

Diamond mining activities concentrate on exposing tracer deposits of diamoniferous gravels buried beneath the dunes of the coastal margin. Consequently, the Sandveld is the primary focus of destruction. Distinct substrata such as the Buchu Twins, the canyon of the Holgat River and the Pebble Plains around Alexander Bay are essentially untouched. This phytosociological survey and analysis has focused explicitly on the plant communities of the Sandveld (viz. communities occurring on sandy as opposed to rocky substrata). The rocky substrata are home to unique plant communities (see previous chapter), distinct from those of the surrounding dune vegetation. As such, detailed descriptions of these communities, based on bio-inventories of these areas and available literature, are included in this chapter.

3 Study area.

See Chapter 2 for a description of the location, geology and climate of the study area.

4 Methods.

4.1 Plant community data.

Representative vegetation plots or relevés were sampled in a stratified manner throughout the dunes of the study area during the spring of 1994. Parallel line transects, perpendicular to the dominant wind direction were walked with sample plots being placed in homogeneous stands of vegetation along the length of the transect. The positioning of transects in the landscape was facilitated by the use of 1:10 000 orthophotographs (Surveyor General, Mowbray). Transects were laid so as to bisect the greatest observable variation in the landscape, yet keep with the predetermined angle to the coast. Circular relevés measuring 7.5 m diameter (176 m^2) were sampled using a modification of the method devised by McAuliffe (1990) for sparsely vegetated areas. The scale for logarithmic canopy cover classes used by McAuliffe (1990) was modified to take into account this small chamaephyte dominated vegetation (Table 4.1). All individuals within plots were counted.

Not all community/vegetation types were sampled. Only those areas directly impacted or having the potential to be impacted by mining were sampled and included in the relevé data-set. Those areas excluded from the relevé data-set were included in the bio-inventory of the study area (see previous chapter for methodological details). Plant community descriptions for these areas are based on the bio-inventory data-set. These areas include the Buchu Twins; the canyon of the Holgat River; the coastal cliffs on the Buchu Twins Peninsula, south of Peacock Bay; and, the pebble plains, inselbergs and lichen field in and to the east of Alexander Bay.

Table 4.1 Scale for logarithmic canopy cover classes as modified from McAuliffe (1990).

Cover Class	Diameter Range (cm)	Mid-point cover interval (m^2)
1	0-4	0.002
2	5-8	0.004
3	9-11	0.004
4	12-16	0.016
5	17-22	0.032
6	23-31	0.064
7	32-44	0.125
8	45-62	0.256
9	63-87	0.512
10	88-124	1.024
11	125-175	2.048
12	176-248	4.096
13	249-351	8.192

4.2 Description of environmental variables.

Environmental data collected for each relevé comprised both quantitative and qualitative data. These included quantitative abiotic environment variables, e.g. pH or soil resistance; qualitative abiotic variables deemed important in explaining the observed patterns, e.g. degree of fossorial rodent activity; and, biotic variables such as total species per plot or average cover per species per plot. Naturally, not all environmental variables were eventually used in the descriptions of plant communities. Indirect gradient analysis was used to establish which of the 20 environmental variables best described the observed patterns in the species-relevé data set.

Environmental variables were not selected haphazardly. *A priori* indications as to which variables would be useful were complicated by our general lack of knowledge of this system. Assumptions that guided the eventual choice of variables were:

1. The system is an arid coastal system, therefore soil pH and salinity (electrical conductivity) would probably be of importance. It is generally accepted that these are the two most important descriptive variables for soils (F. Ellis pers. comm.).
2. The coastal fringe is relatively young by southern African standards, comprising mainly mobile Tertiary and Quaternary sands (see Chapter 2). Variables 3,6,12 and 13 in Table 4.2 below, are related to sand age.

3. Wind is important and, related to this, sand movement and sand input would also be key variables. Therefore, variables were selected that gave an indication of these processes. The measurement of wind effect is complex as it is impossible to obtain an estimate of average wind velocity or sand movement in the landscape over a short period. One has to rely on wind and sand movement artefacts to act as surrogate measures of these processes. Variables 4,5,14,16,17,18 and 19 in Table 4.2 below, fulfil this role.

Variables 7 to 11 (Table 4.2) are not primary explanatory variables. These are biotic or secondary variables that are a consequence of the primary environmental variables. These variables were included in the ordination to ascertain if there was any observable pattern between the distribution of these variables and those of species, plant communities or the primary explanatory variables in the ordination space.

From the discussion on the properties of sand and sand movement (Chapter 2), it is plausible to consider that soil texture would prove to be a good indicator of wind activity. During the analysis of the soil samples, some soil textural analyses were conducted using the hygrometer method (Rowell 1994). At the time, no trend in the results was being detected and the analyses, due to their time consuming and costly nature, were discontinued. Subsequently, these results were re-analysed and a distinct pattern in the data relating to the different species associations was detected. These data were not included in the ordination analyses as they comprise an incomplete data set. The results of the soil texture analysis are, however, presented in Appendix III and have been incorporated into descriptions of the various plant association.

Table 4.2 Environmental variables used in the ordination of the species relevé data set. Bold text in parentheses refer to the abbreviations used in the text.

1.	pH (**pH**). Measured in water.
2.	Electrical conductivity (**Resistan**): measured in deciseimens per metre ($dS.m^{-1}$) in a 1:5 soil to water extract. For both soil analyses, the methods outlined in Rowell (1994) were used. Three soil samples were lumped per relevé and sub-sampled for each analysis.
3.	Altitude (**Altitud**).
4.	Distance to nearest deflating surface (**Deflll**): The straight line distance to the nearest deflating sand surface or aeolian sand source parallel to the dominant wind direction (SW).
5.	Distance south (**South**): Straight line distance to the sea shore or marine sand source parallel to the dominant wind direction.
6.	Distance from the coast (**West**): Straight line distance due west to the coast.
7.	Total plant cover per relevé (**totcover**).
8.	Average cover per species per relevé (**avgpersp**).
9.	Total number of species per relevé (**totcount**).
10.	Number of species per relevé with a cover in excess of 1% (**cnt>1.0**).
11.	Number of species per relevé with a cover exceeding 5% (**cnt>5.0**).
12.	Colour of dry soil (**COLOR1**). Colour of dry soil based on standard soil colour charts and classified on a scale ranging from 1 to 17 corresponding to white to dark orange brown.
13.	Colour in water (**COLOR2**). Colour of a water extract from sand rated on a scale of 1 to 10 where 1 represents a clear extract and 10 a black extract. This is a rough estimate of humic acid and organic matter build up in the soil.
14.	Phytogenic sand mounds (**MOUND**): A measure of mounds of sand accumulating around the aerial shoots of individual plants ranging from a flat, level surface (1) through to an uneven, undulating surface dominated by large mounds (4) approximately 1m high relative to the surrounding inter-mound area. In extreme cases, large mounds merge and begin to form small hummock or coppice dunes measuring up to several meters in height and diameter.
15.	Presence of burrowing rodents (**GOPHER**): Occupation of a relevé by Brant's Whistling Rat (*Parotomys brantsii*) on a scale of 1 (no rodent burrows) to 4 (high density of burrows).
16.	Biogenic soil crust (**CRUST**): Relative abundance and strength/thickness of soil surface biogenic crust measured on a scale of 1 (no crust, loose sand) through to 4 (well developed thick crust, present over greater than 75% of relevé area).
17.	Presence of pebbles or shells on the soil surface (**PEBBLES**): Boolean scale of presence or absence of small quartz pebbles or sea shells on the sand surface. These are indicative of a deflating surface.
18.	Catenal position (**SLOPE**): Dune crest, mid slope or dune slack.
19.	Sea shore type (**SHORTYPE**): Whether the shore type due south of the relevé was (1) a sandy beach or embayment, (2) a rocky shore or (3) was >10 km away.
20.	Transect number (**TRANSECT**): Number of the transect corresponding to the relevé as a surrogate indication of latitude. This was used as a co-variable in the gradient analysis to factor out the effect of latitude from axis-environmental variable regression analysis.

4.3 Analysis of relevé data set.

4.3.1 Phytosociological analysis.

Two-way indicator species analysis (Hill 1979) was used to produce a phytosociological table of dune communities represented within the study area. In this and the indirect gradient analyses, annual and incidental perennial plant species were excluded from the species-relevé data set (see Appendix I). Incidental species were those species that occurred in only one relevé. The Twinspan output was summarised in the form of an abbreviated summary table based on the relevé ordination with percentage constancy for each species per community type, constituting the body of the table (Meuller-Dombois and Ellenberg 1974). Delineation and description of plant communities was based on the Twinspan output, plant collection data, environmental variables and field notes.

The basic level of classification is that of association (Kent and Coker 1992). The association corresponds to the level of plant community or discernible groups or associations of species in the field. In the description of associations I have attempted to progress towards the concept of concrete communities (Kent and Coker 1992) where the description of characteristic species and associated environmental variables will enable the reader to locate and identify any given community in a field situation. Characteristic species listed under each description are those that occur in greater than 60% of community relevés. This corresponds to values of 4 or 5 in Table 4.3. Species that appear in all community types, so called companion species (Mueller-Dombois and Ellenberg 1974), were excluded from the list of characteristic species unless their absence from a community was considered characteristic. Where Twinspan listed differential species for the final association division, these are printed in bold under the list of characteristic species with each description. Associations have been grouped into formations, where a formation comprises a group of associations with a common, dominant species or group of species that distinguishes one formation from another. Structural descriptions of associations follows Shmida (1985).

4.3.2 Indirect gradient analysis.

The relationship between the relevé ordination and the environmental variables was explored using detrended correspondence analysis (DCA, Ter Braak 1987). This method was chosen as most appropriate as our knowledge of the system is limited. The objective was to gain an understanding of the systems environmental determinants or driving variables. Thus, the objective was not to constrain the ordination of the species-relevé data set within the selected environmental variables as would be the case with a direct gradient analysis technique (e.g. CCA). The objectives of the DCA analysis were (1) to determine how well the selected variables explained the pattern in the relevé and species data, through correlation analysis with the ordination axes, and (2) what environmental gradients or indices best determine the distribution of plant assemblages and species in the landscape.

5 Results.

5.1 Twinspan.

Twinspan is subjective in its approach to analysing phytosociological data. Basic assumptions need to be made and methodological parameters adjusted to suit the system and organisms involved and also the questions being asked. The assumptions were as follows. Firstly, there are distinct and predictable plant assemblages related to various environmental variables. These plant communities or associations are significantly different from one another in terms of both species composition and underlying determining variables. Secondly, throughout this project the importance of wind in the structure and functioning of this desert system is stressed. It is to be expected that the final Twinspan output will not comprise a discrete or clean delineation of plant communities. There will a degree of mixing of species creating a substantial amount of noise in the data set. No matter how strong the driving environmental variables are, individuals from other communities will always be encountered away from their "natural" community. Thirdly, the generally small size of plants needs to be taken into consideration when calibrating the analysis.

Many combinations of parameters for Twinspan were tested. Criterion for accepting a final phytosociological table were based very much on intuition and field observations. By comparing the Twinspan output with a selected number of known or intuitive associations, it was possible to gauge the effectiveness of the ordination in drawing out meaningful plant communities. A more objective criterion for accepting the Twinspan ordination would be to compare it to the DCA ordination. Both techniques, however, ordinate the relevé data based solely on the species composition using reciprocal averaging techniques (Kent and Coker 1992). Thus, a common resemblance between the two outputs would be expected. However, similarity of the two outputs combined with intuition was deemed better than intuition alone in reflecting "true" associations between relevés and consequently real, observable communities.

Annuals were omitted from the relevé data set as these species are not present in the landscape as plants for much of the year and, therefore, cannot be expected to act as indicator species. There is one exception, *Senecio cardaminifolius*. Despite the strong dispersive effect of the wind regime, this species was only ever encountered in one species association or habitat type and as such was awarded characteristic species status. This was the only annual species that demonstrated such conservative habitat tolerance.

There are some important parameters of the method that require clarification. The nine pseudo species cut-levels used reflects plant size and abundance (0 0.06 0.13 0.25 0.5 1 2 4 8). The weights corresponding to this scale pay less attention to species with low cover-abundance and emphasise those species with higher abundance (0 1 1 2 2 3 3 4 4). Pseudospecies indicator potentials reflect a similar down-playing of minor occurrences (0 1 1 1 1 1 1 1). This was deemed necessary for two reason. Firstly, the nature of the environment means that there is a high probability of encountering the odd individual from other associations. Except for species with strict habitat requirements, the strong dispersal effect of wind results in substantial mixing of communities. This is evidenced in the "noise" of species occurrences in the upper right and lower left hand sectors of the phytosociological table (Appendix II). Secondly, emphasis was placed on species abundance relationships based on the premise that associations are not defined solely as a function of species turn-over in space, but also on the basis of shifts in species abundances along the same spatial gradient.

Table 4.3 An abbreviated summary table of the phytosociological table (Appendix II) of 118 relevés representing the Namaqualand coastal plain dune vegetation between Port Nolloth and Alexander Bay on the west coast of South Africa. Association numbers correspond to their respective descriptions in the text below.

Classification of life forms follows Meuller-Dombois and Ellenberg (1974). Abbreviations used: P= phanerophyte; Ch= chamaephyte; t Ch= drought deciduous chamaephyte; G= geophyte; T= therophyte; herb= herbaceous; frut= woody or frutescent; suff= semi-woody or suffrutescent; rept= reptant; l succ= leaf succulent; st succ= stem succulent.

Percentage constancy of species in each association: + = Occurrence of species in 10% or less of relevés; 1 = Occurrence of species in 11 - 20% of relevés; 2 = Occurrence of species in 21 - 40% of relevés; 3 = 41 - 60% of relevés; 4 = 61 - 80% of relevés; 5 = 61 - 100% of relevés.

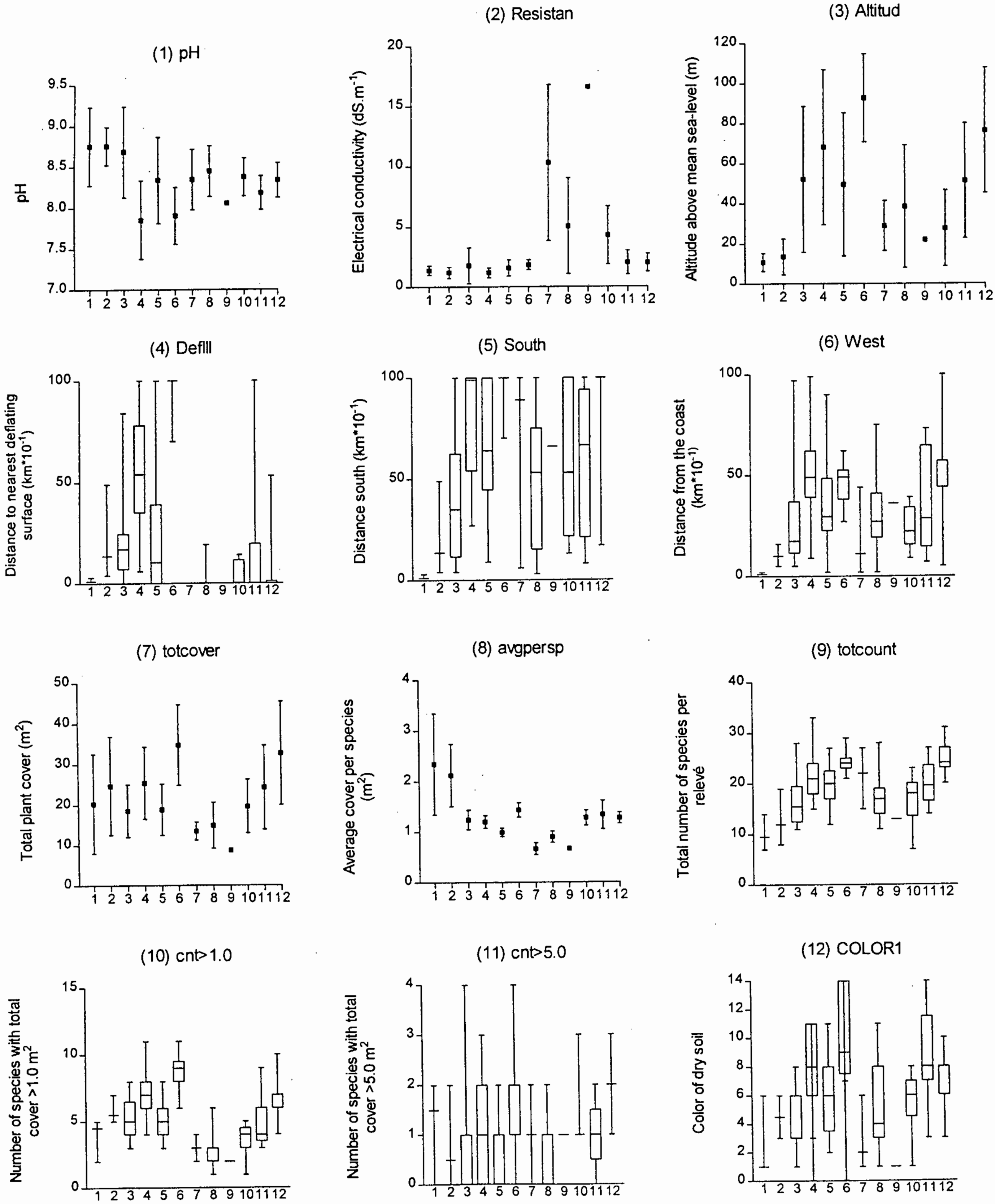
		Percentage constancy of species											
	Association number:	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
	Number of relevés:	**4**	**4**	**12**	**21**	**24**	**7**	**4**	**17**	**1**	**7**	**8**	**9**
Species	**Life form**												
Lebeckia sericea	P herb	3	5	3	3	+			+		+		
Othonna cylindrica	Ch herb l succ	2	5		1	+			+			+	
Amellus tenuifolius	t Ch herb		3			+							
Antholysa plicata	G		2	+	1	+							
Cladoraphis cyperoides	t Ch Herb (graminoid)	4	5	5	3	3			1				
Hebenstretia cordata	t Ch frut-suff rept	2											
Hebenstretia robusta	Ch herb		2	1	+								
Pteronia onobromoides	Ch herb			3	3	3			+			+	
Tetragonia fruiticosa	Ch herb l succ	5	4	5	5	5	5		2		2	2	
Arctotis diffusa	Hemichryptophyte		2	2	5	3	1						
Chaetobromus involucratus	t Ch Herb (graminoid)			2	5	3	5		+			2	
Crassula sp.1	Ch herb l succ				2	+	+						
Galenia collina	Ch herb rept l succ				1								+
Grielium grandiflorum	Hemichryptophyte		3	4	1		1						
Hebenstretia sp.1	Ch herb				+	+							
Helichrysum "perenials"	Ch herb			2	1	1							
Helichrysum tricostatum	Ch frut				4	+							
Jordaaniella cuprea	Ch herb rept l succ		2	2	4	3	3		2		1	1	+
Kedrostis psammophila	G l succ				1	1	1						
Lebeckia cinerea	P herb				2		1						
Lycium cinerea	P herb				3	1	3					1	
Lycium ferocissimum	P herb				+		1						
Microloma saggitatum	Ch herb				+		1						
Myrsiphyllum undulata	Hemicryptophyte			+	+	+	1						
Osteospermum oppositifolium	P- Ch herb		2	4	5	2	3		+	5			
Othonna lingua	Hemichry l succ				+		+						

Pelargonium fulgidum	t Ch frut-suff						2						
Phamaceum lanatum	Ch herb		3		1	1							
Protoasparagus acocksii	t Ch frut-suff				+								
Pteronia divaricata	P herb				2		1						
Lampranthus hoerleinianus	Ch frut l succ			+	2	2							
Stoeberia utilis	Ch frut l succ		3	2	5	4	5		2			1	
Tylecodon paniculata	Ch st succ				1	+	1						
Zygophyllum morgsana	Ch herb l succ		4	3	5	3	3				1		
Crassula brevifolia	Ch herb rept l succ				+	+	4					1	+
Erharta brevifolia	t Ch herb (graminoid)			1	2	2	2		1		1	1	+
Grielium humifusum	Hemichryptophyte			2	3	3	1		+		3	1	+
Hermannia pfeilii	Ch herb			2	1	2	2		2		1	1	
Lebeckia multiflora	Ch herb			1	+	2	3	2	2		1		2
Ruschia sp. 1	Ch frut l succ		2	2	3	5	1		1		1	2	
Crassula pallens	Ch herb l succ					+							+
Euphorbia burmannii	Ch st succ		2	3	2	4	3		4	5	3	3	+
Gladiolus/Morea	G				+	+	1		1			1	+
Jamesbrittenia merxmeulleri	t Ch frut-suff					+			+				
Othonna sedifolia	Ch herb l succ	2	2	5	5	5	5	2	4		5	5	5
Pelargonium grandicalcaratum	t Ch frut				1		2					1	+
Trachyandra falcata	G			2	2	3	5		3			5	
Cephalophyllum spongiosum	Ch herb rept l succ				2	+	4		+			2	
Didelta carnosa var tomentosa	Ch herb l succ	2		3	4	5	5	2	5	5	3	3	+
Protoasparagus capensis var. capensis	t Ch suff		2	2	4	4	5	4	4	5	3	5	4
Ruschia fugitans	Ch frut l succ				+	+	3					2	
Ferraria sp.	G	2		2	+	1			1				
Galenia crystallina	Ch frut l succ	4	3	5	+	4	+	4	3		5	1	+
Lycium decumbens	P herb	4	5	4	1	+		5	3	5	1	1	2
Ruschia rupis-arcuatae	Ch herb l succ	3	3	5	2	4		4	4		3	2	+
Chrysanthemoides incana	Ch herb rept	2	3							5			
Crassula atropurpurea	Ch herb rept l succ			+		+			+				
Lapeirousia barklyii	G					+						+	
Ruschia cyathiformis	Ch herb l succ				3	3	5		2		3	2	4
Senecio aloides	Ch suff rept l succ				1	1	2		+			2	3
Tylecodon fragilis	Ch l succ					+							+
Euphorbia mauritanica	P st succ			+	1	2	3				3	4	4
Lessertia diffusa	Ch herb rept			+							1		
Tylecodon wallichii	Ch l succ				+		1					1	
Salsola zeyheri	Ch herb		2	4	4	5		5	5		5	4	3
Mesembryanthemum chrystallinum	Ch herb rept l succ	3	4	3	2	3	2	4	3		5	4	4

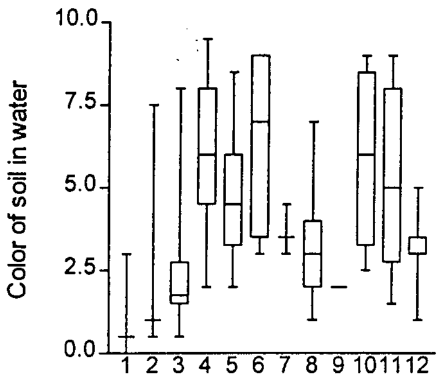
Atriplex cinerea	Ch herb l succ		2	1		+		2	+				
Hypertelis angrae-pequenae	Ch herb rept l succ	4	2	1				3	2	5	1		1
Salsola nollothensis	P herb	5		+					1				
Brownanthus marlothii	Ch frut l & st succ							3					
Chlorophytum sp.1	G			+				2	+		1		
Crassula columnaris	Ch herb rept l succ			+		+		4	1				2
Crotalaria meyeriana	Ch herb rept							2	+				
Dregeochloa pumila	t Ch Herb (graminoid)							2	1			1	
Drosanthemum ramosissimum	Ch frut l succ	4			+	+		5	3	5	3	1	+
Jamesbrittenia fruiticosa	t Ch frut-suff							2		5			
Lachenalia klinghardtiana	G							2	+				
Lessertia candida	t Ch frut-suff								+				
Limonium dregeanum	Ch herb	2		+				2	1	5			
Stipagrostis dregeanum	t Ch Herb (graminoid)							2	+		1		
Suaeda fruticosa fruiticosa	Ch frut st succ								+	5			
Zygophyllum clavatum	Ch frut l succ	2				+		4	5	5		2	
Zygophyllum prismatocarpum	Ch frut l succ							3					
Albuca cooperi	G					+	+		2		1	3	
Cotyledon orbiculata	Ch herb rept l succ							4					+
Euphorbia caput-medusae	Ch st succ G						1		1			3	2
Euphorbia ephedroides	Ch st succ				+	+			1			1	2
Euphorbia sp.1	Ch st succ							3			1		
Ornithogalum sp.1	G						2	2	1		1	1	+
Othonna graveolens	Ch frut l succ			+				2	3		3		3
Psilocaulon dinteri	Ch frut l & st succ	3						5	1				3
Sarcocaulon patersonii	t Ch herb							4	+		1	2	+
Stoeberia beetzii	Ch frut l succ			1	+	2	1	4	5		5	4	4
Trachyandra sp.1	G						1	3	+		1		4
Tridentea pachyrrhiza	Ch rept st succ							3	+				+
Zygophyllum cordifolium	Ch frut l succ						1	3	3	5	1	3	4
Antimima maleolens	Ch herb rept l succ				+	+	3	3	3		2	4	5
Aridaria noctiflora	Ch frut l succ												4
Brownanthus arenosus	Ch frut l & st succ					+		3	1		3	1	5
Cephalophyllum ebracteatum	Ch herb rept l succ				+	1	3	4	2		1	1	5
Cheirodopsis robusta	Ch l succ								+			3	5
Crassula elegans	Ch herb l succ				1		3		1		1	3	3
Crassula expansa	Ch herb l succ						1						+
Crassula muscosa	Ch herb l succ				1	+	1		+			2	2
Euphorbia decussata	P st succ				+	+	4					4	4
Hypertelis salsoloides	Ch frut l succ							2					3
Lampranthus sp.1	Ch frut rept l succ												4
Othonna cuneata	Ch frut l succ											2	
Pelargonium carnosum	t Ch frut			+	+		1		+		1		2
Protoasparagus capensis var. littoralis	t Ch suff						1	2			1	2	2
Psilocaulon subnodosum	Ch frut rept l & st succ			1		+		3	1		4	1	4
Pteronia glabrata	Ch frut				+	1	5	2	3		1	5	4

Salsola tuberculata	Ch frut												2
Senecio cardaminifolius	T												5
Phyllobolus quartziticus	Ch frut rept l succ	2		+		1		2	1		3	1	4
Tetragonia microptera	Ch herb rept l succ					+						1	2
Tylecodon reticulatus	Ch l succ											2	2
Total number of species	117	20	26	45	66	67	55	41	66	13	42	55	56

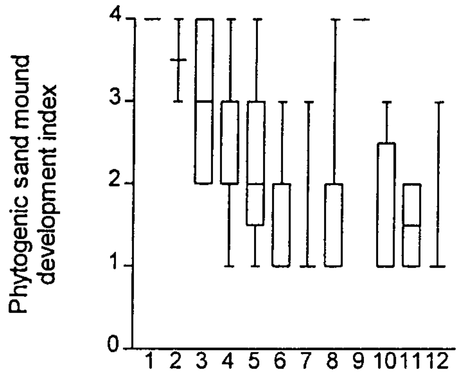
Figure 4.1 (following 2 pages) Summary diagrams of the environmental variables for the twelve plant associations shown in Table 4.3 and which are discussed below. Captions on each graph correspond to the abbreviations used in Table 4.2. Points on graphs represent means with standard error bars. Nominal data is graphed using box-whisker plots.


(1) pH
pH
(2) Resistan
Electrical conductivity (dS.m-1)
(3) Altitud
Altitude above mean sea-level (m)
(4) Deflll
Distance to nearest deflating surface (km*10-1)
(5) South
Distance south (km*10-1)
(6) West
Distance from the coast (km*10-1)
(7) totcover
Total plant cover (m2)
(8) avgpersp
Average cover per species (m2)
(9) totcount
Total number of species per relevé
(10) cnt>1.0
Number of species with total cover >1.0 m2
(11) cnt>5.0
Number of species with total cover >5.0 m2
(12) COLOR1
Color of dry soil

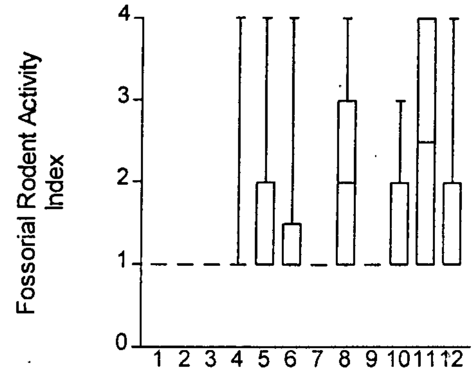
(13) COLOR2



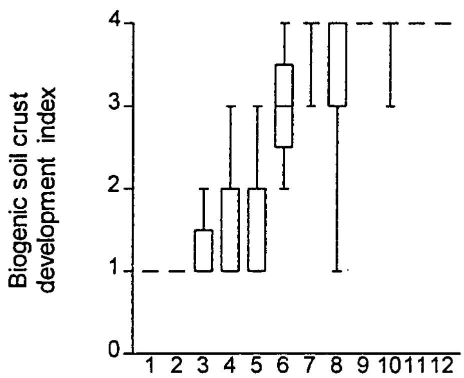
(14) MOUND



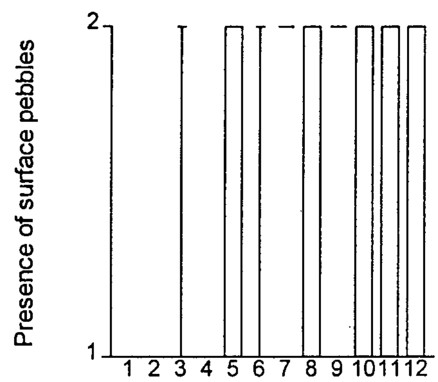
(15) GOPHER



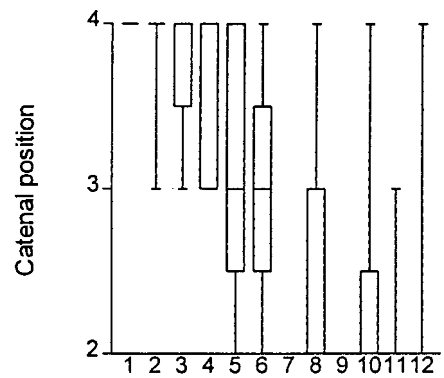
(16) CRUST



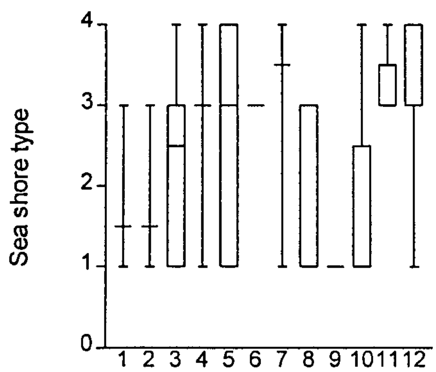
(17) PEBBLES



(18) SLOPE



(19) SHORTYPE



The final phytosociological table is presented in Appendix II. A summary is shown in Table 4.3. The 118 relevés sampled were eventually classified into 12 distinct communities. Elaboration and discussion of these and other communities not covered by the relevé data-set are discussed later in the text.

5.2 Description of plant communities.

Plant communities of the coastal belt between Port Nolloth and Alexander Bay can be divided into two broad groups based on substratum type (DCA axis 1). The first group of plant associations occupy deeper, loose sands on dune crests where sand accretion is the dominant process. Plants here are generally large, form phytogenic mounds and biogenic crusts are rudimentary to absent. Conversely, plant associations in zones of deflation, e.g. dune slacks where erosion is dominant and soils are generally shallow and compacted, the dominant plants are recumbent, mat-forming and phytogenic mounds are absent. These soils are more resistant to wind erosion and there is a strong development of biogenic crust, except in saline situations. The second axis along which plant associations or species can be arranged is latitude or a biogeographical gradient (DCA axis 2). This represents the turnover from Namaqualand Sandveld communities to those of the lower Orange River valley. The third axis of plant community division pertains to sand age (DCA axis 3). Within these broad environmental trends, soil electrical conductivity draws out a distinct subset of plant communities which do not fit into the general landscape model. Saline or halophytic habitats occur either as poorly drained littoral communities or as exposed pans or evaporites. Naturally, there is a distinct subset or indicator group of plant associated with these habitats.

Plant communities have been arranged according to these environmental gradients. Where possible references to the community types of Boucher and le Roux (1989) and Jürgens *et al* (in press) are made. The task of delineating and arranging "plant communities" is made simpler by the tools available to ecologists. The nature of this desert system makes hard and fast rules of assembly within the dune vegetation somewhat difficult. Clear delineation between certain communities occurring on different substrata (e.g., sand and schist) are comparatively easy to recognise both in terms of the species component and the environmental gradients (e.g. substratum). Throughout, the premise that plant associations be readily recognisable in the field, based on their descriptions, is maintained. A list of the plant associations recognised is presented in Table 4.4. Detailed descriptions of each association follows.

Table 4.4 Plant associations of the coastal belt between Port Nolloth and Alexander Bay.

***Stoeberia utilis* formations.**

Group 1: Strandveld Formation (White Dune associations).

Association 1: *Salsola nollothensis-Hebenstretia cordata.* Near Shore Strandveld.

Association 2: *Lebeckia sericea-Othonna cylindrica.* Back-Shore Strandveld.

Association 3: *Grielium grandiflorum.* White Sand Plume Strandveld.

Group 2: *Stoeberia utilis* Formation (Sandveld associations).

Association 4: *Stoeberia utilis-Helichrysum tricostatum.* "Rooi-Vye" Sandveld.

Association 5: *Ruschia rupis-arcuatae-Ruschia aff. subpaniculata.* Transitional Sandveld.

Association 6: *Euphorbia decussata -Euphorbia mauritanica.* Euphorbia Sandveld.

***Stoeberia beetzii* formations.**

Group 3: *Stoeberia beetzii* Formation (Non-halophytic deflating dune associations).

Association 10: *Stoeberia beetzii.* Swart Vye Veld.

Association 11: *Stoeberia beetzii-Pteronia glabrata.*

Association 12: *Cephalophyllum ebracteatum-Psilocaulon subnudosum.* Dune Slack Sandveld.

Group 4: Halophytic Formation.

Association 7: *Sarcocaulon patersonii - Drosanthemum ramosissimum.* Coastal Halophytic Pebble Pavement.

Association 8: *Stoeberia beetzii-Zygophyllum clavatum.* Sandveld Halophyte Association.

Association 9: *Drosanthemum ramosissimum-Limonium dregeanum.* Deflating Pan Association.

Association 13: *Phragmites australis.* Saline Seep Association.

Group 5: The lichen field (Association 14).

Group 6: Pebble plains of the Lower Orange River Valley (Associations 7c and 15).

Group 7: Inselbergs and rocky outcrops of the Buchu Twins, the Holgat River Canyon and the koppies to the east of Alexander Bay (Association 16).

***Stoeberia utilis* formations.**

The first division in the species-relevé data set by Twinspan is based on the occurrence of 2 species: *Stoeberia utilis* on deeper, loose sands (sand > 96%) with little or no soil biogenic crust; and, *Stoeberia beetzii* on shallow compacted sands (sand <96%) with well developed soil crusts. These two species are the key indicators of the plant associations encountered in the Sandveld north of Port Nolloth. Within the *Stoeberia utilis* Formations, the vegetation that occupies deeper sands is usually dominated by tall, relatively erect chamaephytes.

Group 1: Strandveld Formation (White Dune associations).

These are essentially the Strand Communities of Boucher and le Roux (1989) (Table 3.1 in previous chapter) that occur on dunes. Their definition of these communities, being located in a band approximately 200m wide along the coast, is extended somewhat to include those Strandveld communities that occur far inland away from the coast on active Quaternary sand plumes moving over older Tertiary sands. These substrata are young, coarse sands (sand > 98%, silt < 1%). They are generally white (COLOR1 <6), low in humic acids (COLOR2 < 2.5), and the pH is characteristically very high (pH 8.5 - 9.0) due to the high calcium content (Fig. 4.2). This character alone, separates this formation from other formations (see Section 5.3 on ordination). Despite the general near-shore location of this formation, soil electrical conductivity is not significantly different from other non-halophytic plant communities in the study area. This is probably due to the deep, well drained nature of this substratum. Due to the young age and activity of the substratum (near-shore dunes and plumes), processes of pedogenesis are not yet active (see Chapter 2). Consequently, the loose surficial sand are not underlain by the layers of replacement products common to the substrata of the other Sandveld formations. South of Kleinzee, rainfall is high enough to support deep rooted Dune Thicket species such as *Euclea racemosa* on these substrata where annual rainfall is less than 100 mm.

Association 1: ***Salsola nollothensis-Hebenstretia cordata.*** **Near Shore Strandveld.**

This association is characterised by the presence of large, active to semi-active hummock and coppice dunes; and very young, loose white marine sands, usually immediately upwind from a sandy beach. Where littoral sand activity is restricted (e.g. a cliff coast), older Quaternary or Tertiary surfaces reach to almost the high water mark, e.g. the Cliffs area between the Holgat River and Port Nolloth. This association is absent here and the near-shore zone may be occupied by a shingle beach association (see Boucher and le Roux 1993). For the most part, this association occurs along the entire coast of the study area.

This association is an open shrubland (0.5 to 1.5 m) dominated by very large individuals of *Salsola nollothensis* (>2x2 m), a woody phanerophyte. This species is primarily responsible for the large coppice dunes that characterise this association. The dominance of this species is diagnostic to this littoral association to which it is confined. It does, however, make minor appearances again in non-littoral halophyte communities (Community 8). *Hebenstretia cordata,* a creeping chamaephyte, is another species restricted to the littoral zone encountered only on the exposed sea facing dune slopes. It is, however, not necessarily characteristic of the community type as a whole. Stem and leaf (viz. Mesembryanthemaceae) succulent life forms are poorly represented in this association.

Characteristic species are:

Salsola nollothensis
Hypertelis angrae-pequenae
Tetragonia fruiticosa
Cladoraphis cyperoides
Drosanthemum ramosissimum

Association 2: ***Lebeckia sericea-Othonna cylindrica.*** **Back-Shore Strandveld.**

This association occupies the low hummock dunes immediately behind those of the near-shore zone (Fig. 4.2). This can be considered as a secondary succession strand community. Here the hummock dunes are smaller, however, sand movement is still a feature and phytogenic mounds or small coppice dunes are still prominent. Soil texture is still a coarse sand (sand > 98 %). There is, however, a significant increase in the clay content of these soils, and those of

Association 3, from < 1 % to between 1 and 2 %. Silt content remains unchanged for all three associations in this formation.

This is a deciduous shrubland to open shrubland (<1 m). *Salsola nollothensis* is conspicuously absent. *Cladoraphis cyperoides,* a perennial graminoid, is prominent in this association. The leaf succulent, leaf deciduous chamaephyte, *Othonna cylindrica,* separates this association from associations on older sands where it is replaced by *Othonna sedifolia.*

Characteristic species are:

Othonna cylindrica
Cladoraphis cyperoides
Zygophyllum morgsana
Lebeckia sericea
Tetragonia fruticosa

To the south of the study area, around Oubeep, a psammophylous, leaf deciduous asteraceous chamaephtye, *Arctotis merxmeulleri,* is a characteristic species in this community. This appears to be the most northern limit of this species distribution range as it is not found growing on similar substrata further to the north.

Association 3: *Grielium grandiflorum.* White Sand Plume Strandveld.

Up-wind of the back-shore hummock dunes, active linear sand plumes consisting of white Quaternary deposits moving over older Tertiary deposits (dunes, bedrock, hardpans or evaporites). As these constitute the oldest soils of the three associations in this formation, soils tend to be grey in colour, but never brown or orange.

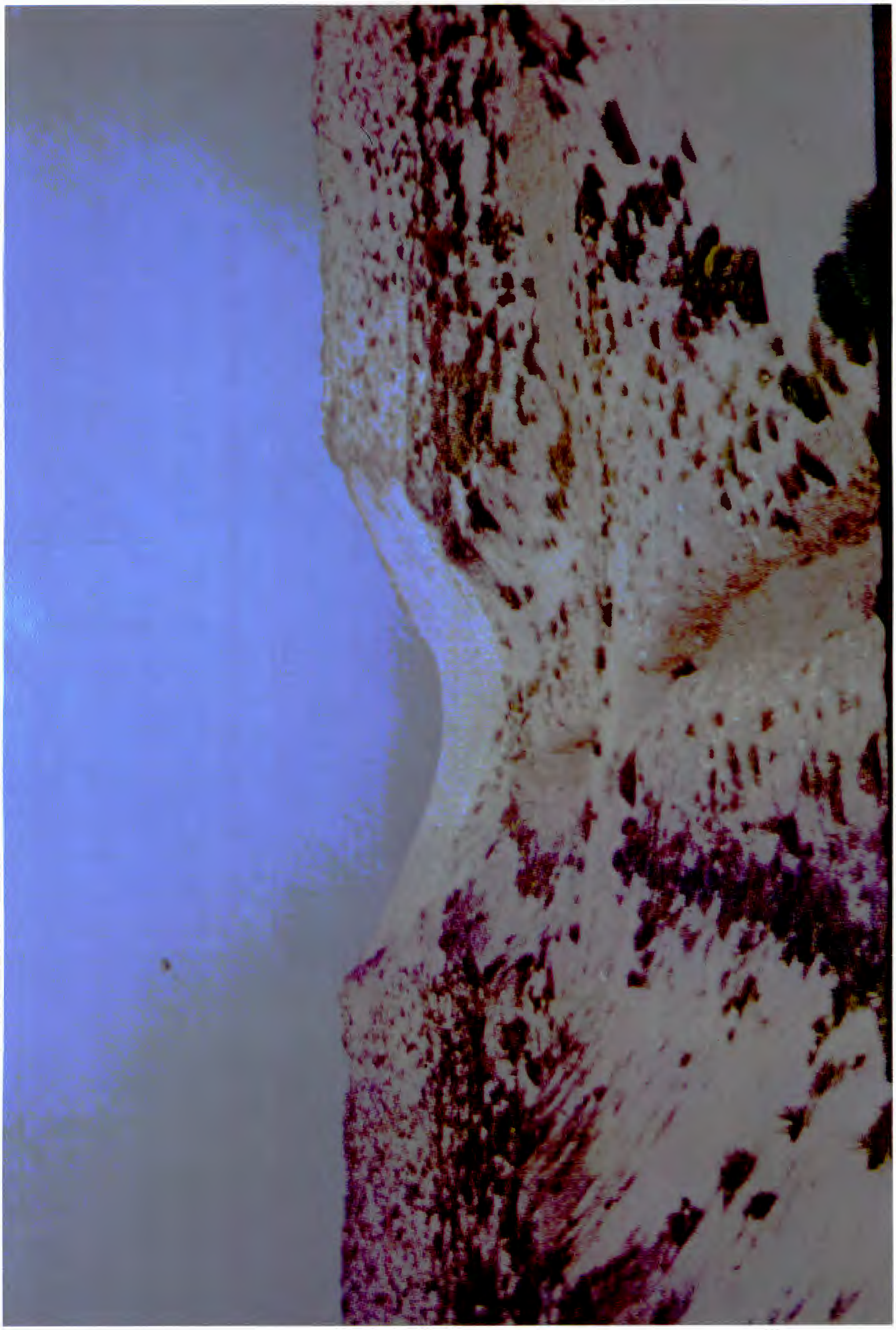
The association occurring on these plumes is an open shrubland (<1 m). It is similar to the White Dune Strandveld of Boucher and le Roux (1989) (Table 3.1). In places, e.g. south of Jam Pan, such plumes are reduced to discrete, low plumes (1-2 m high) carrying typically Strandveld species well into the proto-pebble plain communities (Association 7) of the Namib Domain.

Characteristic species:

Cladoraphis cyperoides | *Tetragonia fruiticosa*
Grielium grandiflorum | *Osteospermum oppositifolium*

In the above three communities, *Cladoraphis cyperoides* (spiny lovegrass) is always present. On DCA axis 1, this species is placed in line with the CRUST environmental vector (Fig. 4.16). This species is always associated with moving sand. As soon as sand activity declines through stabilisation by plants, then this species senesces and eventually disappears from communities. The graminoid component of the dune communities is then replaced by a tussock species, *Chaetobromus involucratus.* Wherever disturbance leads to re-activation of sand movement, then *C. cyperoides* makes its appearance in communities. This species, and its sister species *C. spinosa,* which occurs away from the coast on inland dune fields, act as good indicators of sand mobilisation.

Figure 4.2 (overleaf) Strandveld Formation on young, white hummock dunes adjacent to the coast, north of the Holgat River. A prospecting trench over the Lower Terrace bisects these near-shore dunes. This trench was about five years old when the photograph was taken. A calcrete layer consisting of consolidated marine gravels can be seen at the bottom of the trench.



Group 2: *Stoeberia utilis* Formation (Sandveld associations).

In this analysis, the term Sandveld is applied to all other, non-fynbos plant associations growing on loose dune soils as opposed to Strandveld used by Boucher and le Roux (1989) (Table 3.1 in the previous chapter). This has been done to avoid confusion with the term strandveld being associated with the strand or littoral zone. Many of these sandveld communities occur on the dunes of the coastal plain well beyond the boundaries of the study area and the zone of littoral influence into the interior. To the east of the Sandveld, where the dune substrata are replaced by more clay-loam soils of terrigenous origin, lowland succulent karoo vegetation of the Namaqualand coastal plain is encountered.

These Sandveld communities are characteristic of much of the study area south of the Buchu Twins and above the 40m contour. They are encountered close to the coast in places, even to just above the storm beach, where the shore-line runs parallel to the dominant wind direction; the coast line to the south lacks any sandy embayments; or, where the coastline consists of steep, wave-cut cliffs (e.g. the Cliffs area). Thus, where significant marine sand input into the terrestrial system is absent. These Sandveld communities occupy older predominately Late Tertiary to Early Quaternary sands. Soil colour ranges from yellow-orange through to brown, never white (COLOR1 3-14; COLOR2 3-9). Wind movement of sand is greatly reduced. In all these communities, *Cladoraphis cyperoides* is generally absent and replaced by the grass *Chaetobromus involucratus.*

Association 4: *Stoeberia utilis-Helichrysum tricostatum.* "Rooi-Vye" Sandveld.

This association occupies mid to top dune slopes (SLOPE 3-4) where sands are deep, loose and coarse (sand $\approx$ 98 %). Biogenic soil crusts are absent or rudimentary (CRUST $\approx$ 0). Dune crests are more exposed to wind action, therefore, phytogenic mounds are prevalent (MOUND 2-3). This association would fall into the Tall Strandveld group defined by Boucher and le Roux (1989) (Table 3.1).

This is a tall (1 to 1.5m), deciduous shrubland to open shrubland. It is called Rooi-Vye Sandveld as it is dominated by the large, leaf succulent chamaephyte *Stoeberia utilis*, rooi-vye being its vernacular name (Fig. 4.3). The presence of the branch-deciduous, asteraceous chamaephyte, *Helichrysum tricostatum,* and leaf deciduous, leaf succulent *Zygophyllum morgsana* set this community apart from other Sandveld communities.

Characteristic species:

Helichrysum tricostatum	***Zygophyllum morgsana***
Tetragonia fruiticosa	*Arctotis diffusa*
Chaetobromus involucratus	*Jordaaniella cuprea*
Osteospermum oppositifolium	*Stoeberia utilis*

Association 5: *Ruschia rupis-arcuatae-Ruschia* aff. *subpaniculata.* Transitional Sandveld.

This association occurs close to deflating areas on mid to bottom slopes. In places, pebbles are present on the surface. Phytogenic mounds are not a dominant feature in these areas (MOUND 2). The environmental variables (Deflll) suggest that this community type is at the leading edge of eroding areas. Thus, with time, areas occupied now by this community would approach the Short Sandveld Association (association 12).

This is an open shrubland (0.75 to 1.5 m). Structurally and floristically, it is similar to the previous community. However, *S. utilis* is not as dominant and there is an increasing presence of another woody Mesembryanthemaceae species, *Ruschia* aff. *subpaniculata* (Fig. 4.3). This association has been termed Transitional Sandveld as it appears to be an intermediate community between the Tall and Short Sandveld associations. This is supported by the DCA ordination. The species composition reflects the transitional nature of this association. There is no clear suite of dominating species and many species characteristic of Short Sandveld make their appearance, notably *Stoeberia beetzii*.

Characteristic species:

Tetragonia fruiticosa	*Stoeberia utilis*
Ruschia aff. *subpaniculata*	***Ruschia rupis-arcuatae***

Figure 4.3 (previous page) Tall Sandveld (back) and Transitional Sandveld (front) on orange-brown sands. The emergent species on the dune crest is *Stoeberia utilis*. The brilliant purple flower in the background belongs to *Lampranthus hoerlienanus* and the small yellow flower to *Othonna sedifolia*.

Figure 4.4 (overleaf) Euphorbia veld near Vyftienmylseberg, east of Port Nolloth. The developing dorbank layer overlying calcrete is clearly seen on the side wall of this excavation. The characteristic dark coloration of the sand in this community is also evident.

Association 6: *Euphorbia decussata -Euphorbia mauritanica.* Euphorbia Sandveld.

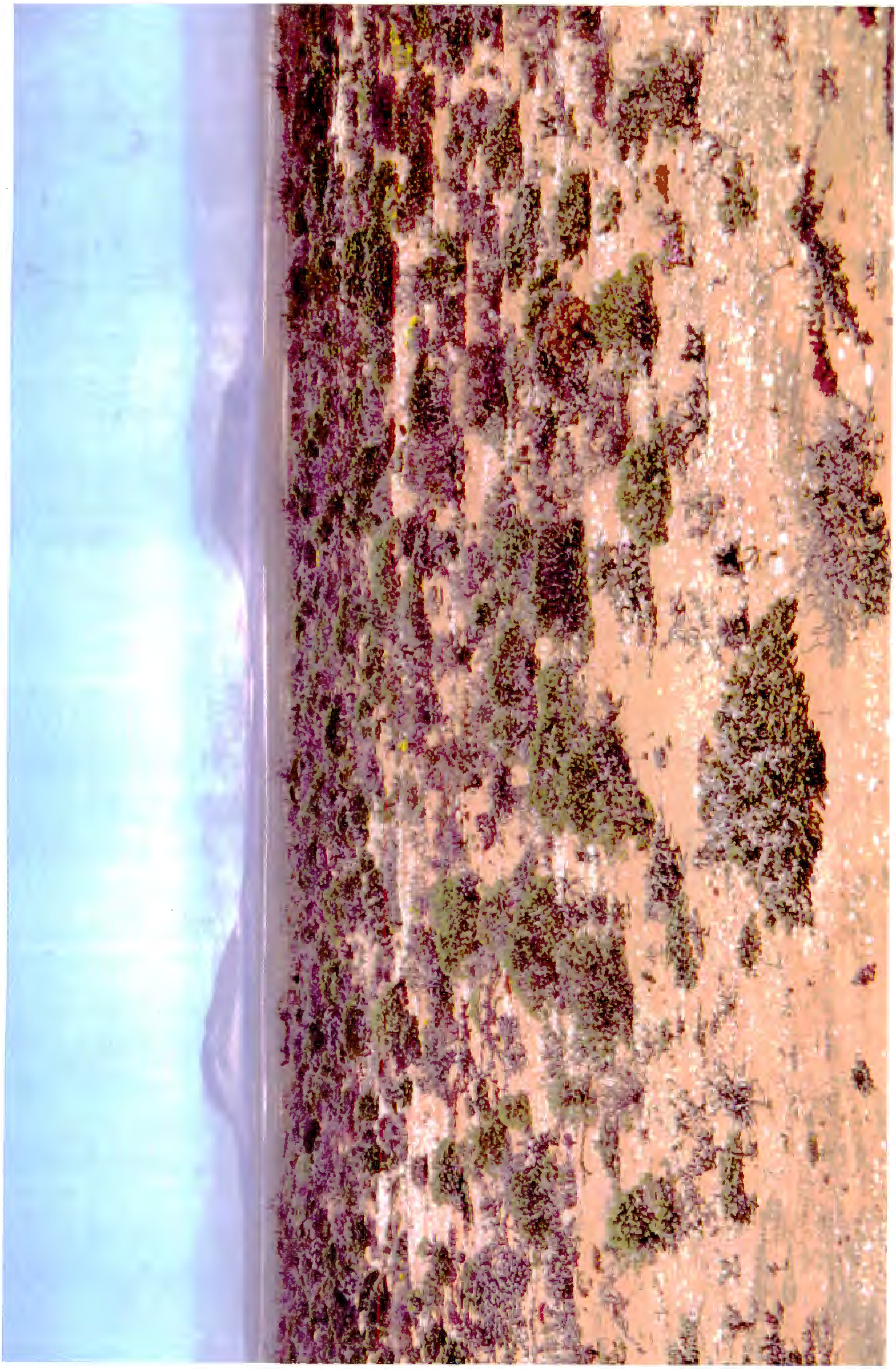
This association differs significantly from the previous two associations in that the surface is more stable (MOUNDS 1) and there is a well developed biogenic crust (CRUST 3). It occurs well away from actively deflating surfaces (Deflll >100) and plant cover is the highest of all dune communities (totcov 30-40%) indicating that sand movement is greatly restricted. It occurs on dark orange-brown sands (COLOR1>9), away from the coast (WEST ≈ 50; SOUTH 100) (Fig. 4.4) where the erosive force of the wind is much tempered in comparison to nearer the coast. The soils of this bottom slope position border on sandy-loam with sand ≈ 96 % and silt ≈ 3 %, but clay content not significantly different to the other associations in this group. Despite occupying bottom slopes, soil depth is still >1 m. Deeper soils sets the substratum of this association apart from that of the deflating-dune association where the hardpan lies in close proximity (<0.4 m) to the surface.

This is a shrubland (1 to 1.5 m) dominated by large (2x2 m), stem succulent (not cactoid) *Euphorbia* spp. Euphorbia veld at this latitude, as with Tall Sandveld (association 4), occurs across the breadth of the Sandveld. However, it appears to be more common on the eastern edges of the Sandveld. Due to the stable nature of the sand surface, many of the smaller deflating-dune association (association 12) species make their appearance in the relevés. Companion species common to the other dune communities are noticeably absent here such as *Ruschia rupis-arcuatae, Lycium decumbens* and *Salsola zeyheri*

Characteristic species:

Euphorbia decussata
Chaetobromus involucratus
Crassula brevifolia
Stoeberia utilis
Pteronia glabrata
Cephalophyllum spongiosum
Tetragonia fruiticosa

Figure 4.5 (overleaf) Swart Vye Veld east of the Buchu Twins (in the background).



***Stoeberia beetzii* formations.**

These are associations that occupy shallow sands (<1 m, usually <0.5 m) over hardpans of calcrete or silcrete, where the dorbank layer is in the process of being eroded away. Consequently, soil texture is slightly heavier than the *Stoeberia utilis* formations with a higher fines content (sand < 96 %, silt > 2 %, clay invariant). The surface of the soil is characterised by the presence of quartz pebbles left behind as the sand has eroded away. Nearer the coast, these pebbles can also be mixed with fossil sea shells or land snail shells. The higher fines content also promotes the development of biogenic crusts (see Chapter 2), a feature that characterises the non-halophytic associations here.

The vegetation differs visually from the *Stoeberia utilis* formations. Here, associations are dominated by short, recumbent to mat-forming, leaf succulent chamaephytes. The leaf succulent, *Stoeberia beetzii*, is characteristic of all these associations. South of Kleinzee, *S. beetzii* is replaced in these associations by *S. frutescence* as the key indicator species.

Group 3: *Stoeberia beetzii* Formation. Non-halophytic deflating dune associations.

In addition to the environmental correlates outlined above for these associations, the presence of dwarf leaf succulent species in the Mesembryanthemaceae and Crassulaceae is characteristic. The lower stature of this vegetation means that these associations are structurally classified as steppes as opposes to shrublands.

Association 10: *Stoeberia beetzii.* Swart Vye Veld.

This association is characteristic of the ecotone to the east of the Buchu Twins where the plant communities of the Namaqualand Sandveld merge with those of the Southern Namib Domain in the Lower Orange River Valley. The area to the east of the coastal communities between the Buchu Twins and Cape Voltas is dominated by this community (Fig. 4.5). Structurally, this association is classified as steppe (<0.5 m) dominated by near monospecific stands of *S.*

beetzii. The name not only refers to the vernacular name of this species, but also to the overall blackish colour of the vegetation (van Jaarsveld 1981).

Characteristic species:

Stoeberia beetzii	*Psilocaulon subnodosum*

Association 11: *Stoeberia beetzii-Pteronia glabrata.*

This association has similar environmental correlates to the previous association, but is a feature of the Sandveld to the south of the ecotone. This association overlaps with the previous on DCA axis 1 and 3, although it is cleanly separated along DCA axis 2, a latitudinal gradient.

Structurally and floristically, this association is similar to the previous. However, *S. beetzii* is a co-dominant with *Pteronia glabrata* and the overall species diversity is higher. This association can also be regarded as a transitional association between those of Group 2 and Association 12. This is suggested by the presence of Group 2 species such as *Cephalophyllum spongiosum* and *Ruschia fugitans* occurring together with those characteristic of Association 12, e.g. *Antimima maleolens*.

Characteristic species:

Pteronia glabrata	*Euphorbia decussata*
Antimima maleolens	*Stoeberia beetzii*

Association 12: *Cephalophyllum ebracteatum-Psilocaulon subnudosum.* Dune Slack Sandveld.

This association occupies bottom slopes or dune slacks of the dune catenal sequence. In contrast to the mid to top slope associations (Group 2), the surface is very low in micro-relief (MOUND 1), the biogenic crust is well developed (CRUST 4) and the community is dominated by low, spreading recumbent leaf succulents (Fig. 4.6). The soils represent the highest silt (silt ≈ 4 %) and lowest sand (sand ≈ 94 %) content of all 12 dune associations described here. This is a result of wind deflation of the illuviated dorbank hardpan layer.

Senecio cardaminifolius is restricted to this association and is a differential species. However, it was not considered appropriate for naming this association as it is an annual species. In this association plant cover is the highest in the group (totcov> 30%), and so is species diversity (56 species). This association closely resembles the lowland succulent karoo of the Namaqualand coastal plain found on the heavier terrigenous soils to the east of the Sandveld with low, leaf succulent species such as *Tylecodon reticulatus, T. wallichii, Cheirodopsis robusta, Lampranthus* sp. 1, *Cephalophyllum ebracteatum, Aridaria noctiflora* and *Hypertelis salsoloides* being prominent.

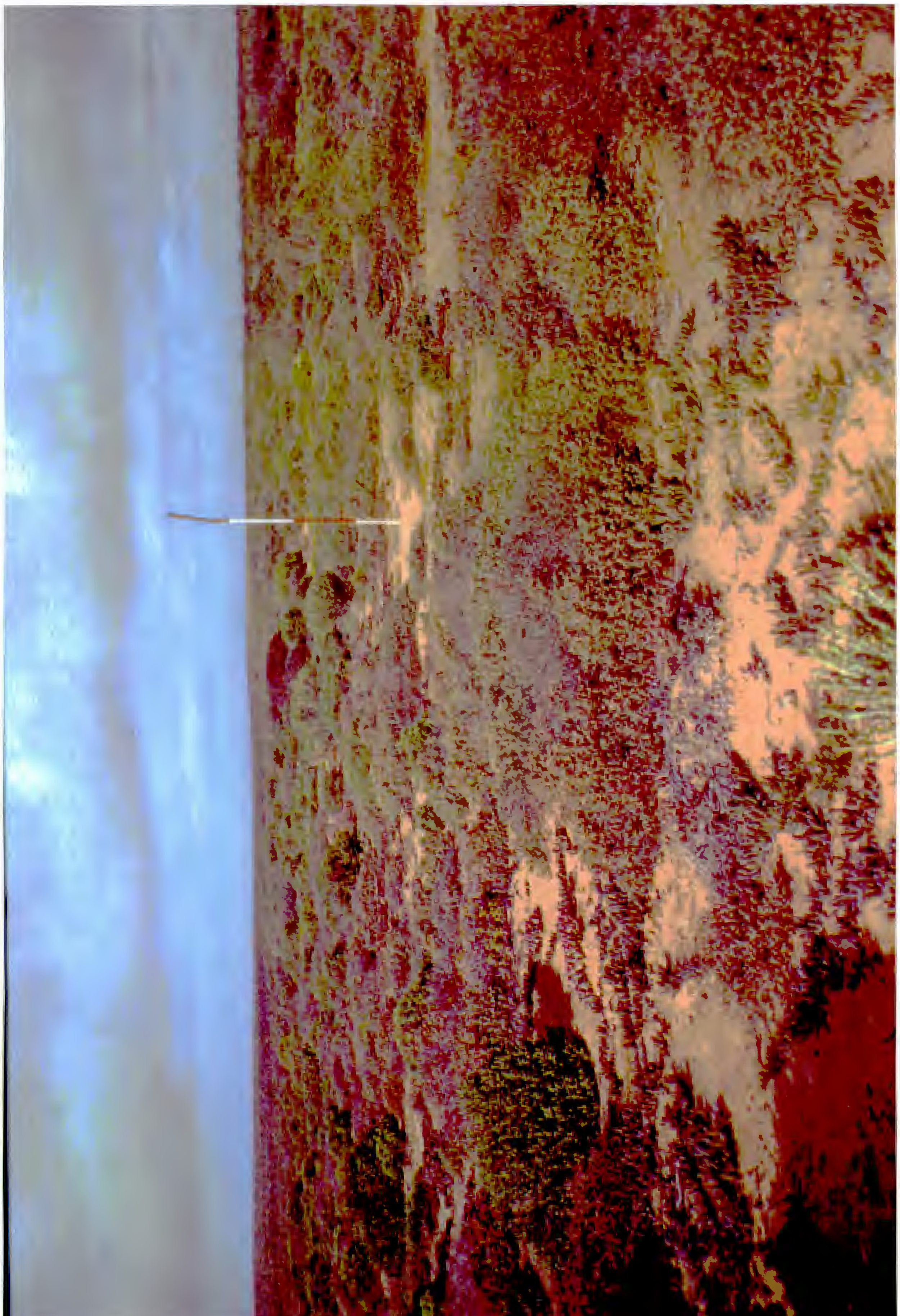
Characteristic species:

Psilocaulon subnodosum	***Cephalophyllum ebracteatum***
Phyllobolus quartziticus	*Pteronia glabrata*
Euphorbia decussata	*Cheirodopsis robusta*
Lampranthus sp.1	*Brownanthus arenosus*
Aridaria noctiflora	*Antimima maleolens*
Zygophyllum cordifolium	*Senecio cardaminifolius*
Trachyandra sp.1	*Stoeberia beetzii*

Group 4: Halophytic Formation.

A distinction needs to be drawn between the two groups of salt-affected soils encountered in the study area. Where there has been, or still is, direct sea inundation or ground-water seepage, the salt effect in soil is due to high concentrations of sodium chloride. These are typical saline soils with high osmotic pressure of the soil solution, and toxic effects are due to the presence of chlorides (Szabolcs 1993). Where surficial deposits of gypsum occur then the salt effect is a result of calcium ions, predominantly $CaSO_4$.. These are termed gypsiferous soils and have characteristically low pH (Szabolcs 1993). The differences between these two substrata are elaborated in relation to the different plant associations discussed below.

Figure 4.6 (overleaf) Dune Slack Sandveld east of the main road to Alexander Bay, in the Cliffs mining area.



Association 7: *Sarcocaulon patersonii - Drosanthemum ramosissimum.* Coastal Halophytic Pebble Pavement.

This association is characteristically a very low (<0.3 m), dwarf succulent, sparse (cover ≤10%) steppe (Fig. 4.7). It is considered halophytic (high EC) due to the occurrence of surficial gypsum deposits and not solely due to salt spray. Soil colour is similar to that of the near-shore dune communities (Group 1), an indication of the transitional nature of sand. Sand movement through these communities is very high, never being stabilised by the sparse vegetation cover. This is a feature of the pebble plains of the Lower Orange River Valley. Sand input is not necessarily restricted or absent - it is simply a permanently deflating or transient sand system. Species diversity in this association is high (66 species). This is probably a result of the ecotonal location of the association, and the proximity of a local flora rich in endemics specifically adapted to the extreme environmental conditions of the Lower Orange River Valley.

This association corresponds to the *Salsola zeyheri-Cephalophyllum ebracteatum* sub-community of Jürgens *et al* (in press). Three variants of this community can be recognised. The coastal halophytic pebble plain association (7a) is an ecotonal community between the Sandveld vegetation of the south and that of the pebble plain communities around Alexander Bay (sub-association 7c, Fig. 4.9, see Group 6 below). It is confined to the few remaining low lying proto-pebble pavements adjacent to the coast on the Buchu Peninsula, south of Peacock Bay, and the area immediately south of Alexander Bay harbour. This community was probably much more widespread, especially between Alexander Bay harbour and the southern bank of the Orange River. However, diamond mining activities have removed much of this distinctly halophytic coastal community type lying on gypsiferous soils.

Inland from the coast, a more widespread, less halophytic variant of this community is found to the east of Jam Pam (sub-association 7b). It is separated from the coastal variant by the presence of leaf-deciduous chamaephytes species such as *Crotalaria meyeriana* and *Jamesbrittenia merxmueleri* and the geophyte, *Lachenalia klinghardtiana*.

The area south of Peacock Bay is of interest floristically as *Gazania schenckii* and *Euphorbia c.f. decussata* occur here and nowhere else in the study area. As far as I can establish, this is the only occurrence of *G schenckii* in South Africa. The nearest other population is on the Buchu Mountains in the Sperrgebied of southern Namibia (G. Williamson, pers. comm.). *E. c.f. decussata* has been identified as a variant of the more widespread *Euphorbia decussata.* Its dwarf, prostrate nature would indicate that this is either a distinct, undescribed species or at least unique eco-type, since in cultivation it maintains its distinctive growth habit.

Characteristic species:

Crassula columnaris	***Drosanthemum ramosissimum***
Zygophyllum clavatum	*Cotyledon orbiculata*
Psilocaulon dinterii	***Sarcocaulon patersonii***
Stoeberia beetzii	

Association 8: *Stoeberia beetzii-Zygophyllum clavatum.* Sandveld Halophyte Association.

Although similar to the previous association, here communities occur on shallow sands over pans (old river channels or silcretes) or exposed calcrete south of the ecotone and below the 80 m contour. This association is a sparse (cover <15%) steppe or low, open shrubland. Many of the species characteristic of the previous community are also present, although in lower densities. Many Group 2 Sandveld species are also present. Their occurrence is probably due to this associations location in the landscape where the calcrete layer under the surficial dune soils and dorbank intersects the surface. Intersection of the surface by the calcrete layer is associated with sudden changes in bedrock altitude, creating exposed or pronounced surfaces prone to wind erosion. Such examples are the crests of ridges (e.g. Volstruisbult and Gifkop) or where one moves from the higher to middle, or middle to lower marine terraces. Naturally, surface topography is not an accurate reflection of bedrock contouring, however, by following the occurrence of this community in the landscape below the 80 m contour it is possible to approximate the location of buried marine terraces. Soils here are naturally light in colour, due to the calcrete, with high EC (average 5 mS). Deflation is dominant with surface deposits of quartz pebbles and sometimes calcrete nodules.

Characteristic species:

Zygophyllum clavatum *Stoeberia beetzii*

Association 9: *Drosanthemum ramosissimum-Limonium dregeanum.* Deflating Pan Association.

This association occurs on saline, deflating evaporites or pans at low altitudes near the coast. In places the soil surface has been eroded into a mesa-type landscape where the substrate has been eroded from around established plants. Soils have very high EC (>10 mS) and are white sands or, in places, green if a palaeo-estuary has been exposed, with low soil organic matter (COLOR2 2) and a high fines content (clay > 3%). This association forms a distinct, sparse (cover <10%) halophytic steppe vegetation.

Characteristic species:

Hypertelis angrae-pequenae *Drosanthemum ramosissimum*

Jamesbrittenia fruiticosa ***Limonium dregeanum***

Suaeda fruiticosa *Zygophyllum clavatum*

Zygophyllum cordifolium

Association 13: *Phragmites australis.* Saline Seep Association.

Pure stands of *P. australis* occur throughout the study area at low altitudes (<20 m) along the coast in low lying saline seeps such as dune slacks, overlying palaeo-river channels and evaporites. Places such as Rietfontein are thus named.

Characteristic species:

Phragmites australis

Figure 4.7 (overleaf) Coastal Halophytic Pebble Pavement north of Alexander Bay harbour. The "koppies" in the background are mine dumps at an ore processing plant.

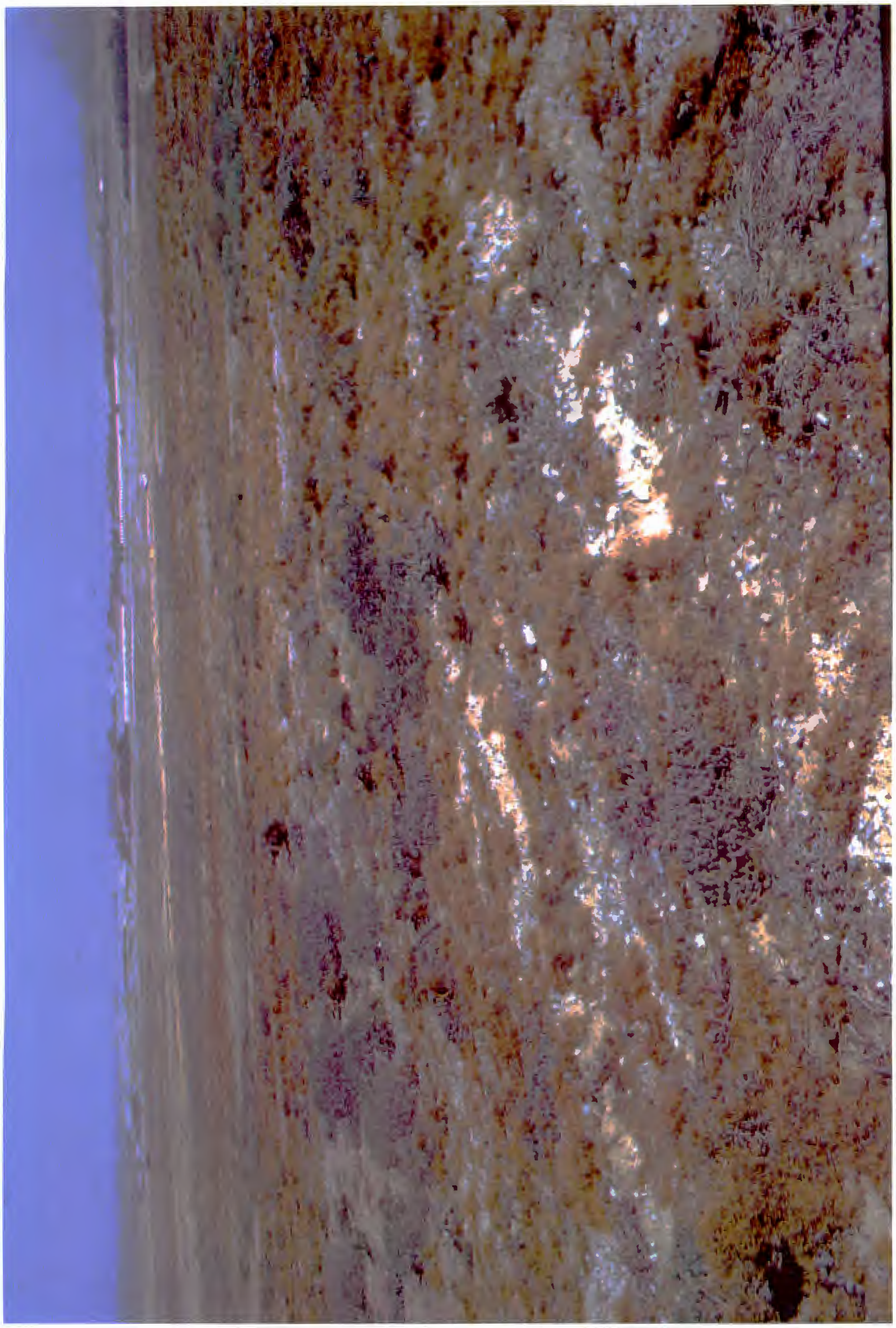


Figure 4.8 (preceding page) *Teloschistes capensis* growing in the lichen field south of Alexander Bay.

Group 5: The lichen field (Association 14).

This is a unique plant community. Globally, these desert lichen fields, dominated by foliose and crustose chlorophytes (lichens), are restricted to the four cool fog deserts discussed in the previous chapter. Regionally, the Alexander Bay lichen field is the most southern of the major Namib lichen fields (Schieferstein and Loris 1992, Jürgens and Niebel 1991) and it is also the only lichen field of its kind occurring within the borders of South Africa (Jürgens 1991). Smaller, less developed fields dominated by *Ramalina capensis* (sub-community *Ramalina capensis* of Jürgens *et al* in press) occur within the coastal fog zone as far south as Mitchell's Bay, south of Hondeklip Bay.

The lichen field at Alexander Bay covers an area of approximately 1.2 km^2 (calculated from 1:10 000 aerial photos). In the past, this lichen field has been abused to the extreme. A gypsum quarry was established in the middle of the lichen field, and the koppie on which it occurs has also been used as an informal motor-cross practice circuit. Despite its significance to the South African flora, at the regional scale, this lichen field is dwarfed by those north of the Great Sand Erg on the Skeleton Coast of Namibia. These occupy hundreds of square kilometres of the coastal fog zone (Schieferstein and Loris 1992).

Floristically, the lichen field has a unique community structure. Around the base of the low hill on which the field is located, commencing at about 60 m.a.s.l., lies a zone of dull lime green foliose lichen (*Ramalina* sp.). Above this and continuing to the summit of the hill, 94 m, the ground is dominated by the bright orange foliose species, *Teloschistes capensis* (Fig. 4.8). Thus, the slopes of the koppie have two well defined and striking lichen zonations. In addition to these two dominants there are a number of other species. Jürgens and Niebel (1991) noted a total of 29 species growing together on this single low hill. On the eastern slopes of the hill, the lichens only descend to about 80 m a.s.l., whereas the sea facing slopes are more densely covered with lichens, where they cover the ground to about 60 m. The west is also from whence fog arrives. This uneven east-west distribution has been ascribed to the sand blasting effects of hot, dry berg winds during winter (Jürgens and Niebel 1991), however, it is more likely due to the eastern slopes receiving less fog precipitation than the sea facing slopes. *T. capensis* appears to have a minimum altitudinal limit as it dominates only the higher strata of the main lichen field at Alexander Bay. *Ramalina* sp., on the other hand, is more widespread occurring at noticeable densities in other areas and lower altitudes such as around the radio tower to the north-west of the main field.

The chamaephyte community of the lichen field closely resembles the coastal halophytic pebble plain plant associations (Association 7 or sub-community *Teloschistes capensis,* Jürgens *et al* in press). It is dominated by *Sarcocaulon patersonii, Lycium decumbens, Drosanthemum ramosissimum, Zygophyllum clavatum* and *Stoeberia beetzii*. Most of the other species occurring in community 7 are also present. However, here the chamaephtyes form substrates on which numerous foliose and crustose lichens grow. Jürgens and Niebel (1991) encountered 41 higher plants in their census of the of the lichen field flora.

Soil analyses undertaken by Jürgens and Niebel (1991) illustrate an important limiting feature determining the distribution of lichen fields along the entire Namib coast and globally. There is no aeolian movement of sand through the system. This is listed by both Jürgens and Niebel (1991) and Schieferstein and Loris (1992) as the primary determinant, together with fog, of the lichen field location. Soils on the lichen field at Alexander Bay consists of "flour like" soil comprising the fine clay minerals: muscovite, chlorite and kaolinite. Muscovite and chlorite from weathered metamorphic bedrock. Kaolinite, derived from hydrothermal decomposition or weathering of feldspars in granite, is deposited by hot, dry winter berg winds sweeping down from the interior (see Chapter 2). There is no sand! Foliose lichens have little resistance to sand abrasion. The lichen field (especially *T. capensis*) at Alexander Bay occupies a well defined altitudinal range, as well as being located within a sand movement shadow, not a wind shadow. Life between the surface layer of pebbles is much tempered from the relentless summer southerly wind, thus allowing the build up of these powder-like minerals within the surface layer of the soil. A well developed gypsum layer occurs beneath the surface, hence the quarry. Alexander Bay experiences the highest evaporation values in South Africa (Schultze 1965). This strong evaporative demand applied by the local climate results in the capillary movement of the brackish groundwater to the sub-surface soil layers where it concentrates and eventually forms gypsum ($CaSO_4.2H_2O$).

Figure 4.9 (preceding page) *Fenestraria rhopalophylla* subsp. *aurantiaca* flowering on a pebble plain remnant in the middle of Alexander Bay, below the old water tower.

Group 6: Pebble plains of the Lower Orange River Valley (Associations 7c and 15).

In, around and to the east of Alexander Bay lie extensive wind-eroded, pebble pavements. These are not true pebble pavements such as those encountered further north in the Namib since the surficial lag gravel has not been eroded into a neat continuous pavement of wind-eroded pebbles. Thus, they should more aptly be referred to as gravel plains. These lag gravels over lie shallow sands (over calcrete), bed-rock outcrops or eroding river terraces. Species diversity and endemism in this unique flora is very high (see Chapter 3). Species such as *Ruschia namaquana* var. *quinqueflora, Ruschianthemum gigas, Dracophilus dealbatus, Juttadintera deserticola, Anacampseros albissima, Sarcocaulon multifidum, Lithops herrei, Cheirodopsis verrucosa, Euphorbia stapelioides* and *E. celata* are characteristic of these communities. These pebble plain communities correspond broadly to the sub-community *Salsola zeyheri-Chephalophyllum ebracteatum* of Jürgens *et al* (in press), but the high incidence of Western Gariep endemics sets this lower portion of the Orange River valley apart from similar communities further north in the southern Namib.

The salt effect is reduced as the surficial gypsum characteristic of the coastal pebble plains and lichen fields is not present. However, the abrasive effect of the transitional sand sheet is still very much prevalent and evident in the nature of the vegetation and life forms encountered. In addition to the vegetation being sparse and highly contracted, special adaptations to sand abrasion are a feature of this vegetation. Sand encrusted plants or psammophylly (Jürgens in press) are characteristic of the flora of the southern Namib, e.g. *Psammophora modesta* and *Strumaria bidentata.* Semi-geophyte habit is a common feature amongst leaf succulents, e.g. the endemic *Fenestraria rhopalophylla* subsp. *aurantiaca* (Fig. 4.9), *Lithops herrei* and *Cheirodopsis verrucosa,* and stem succulents, e.g. *Euphorbia stapelioides* and *E. celata.*

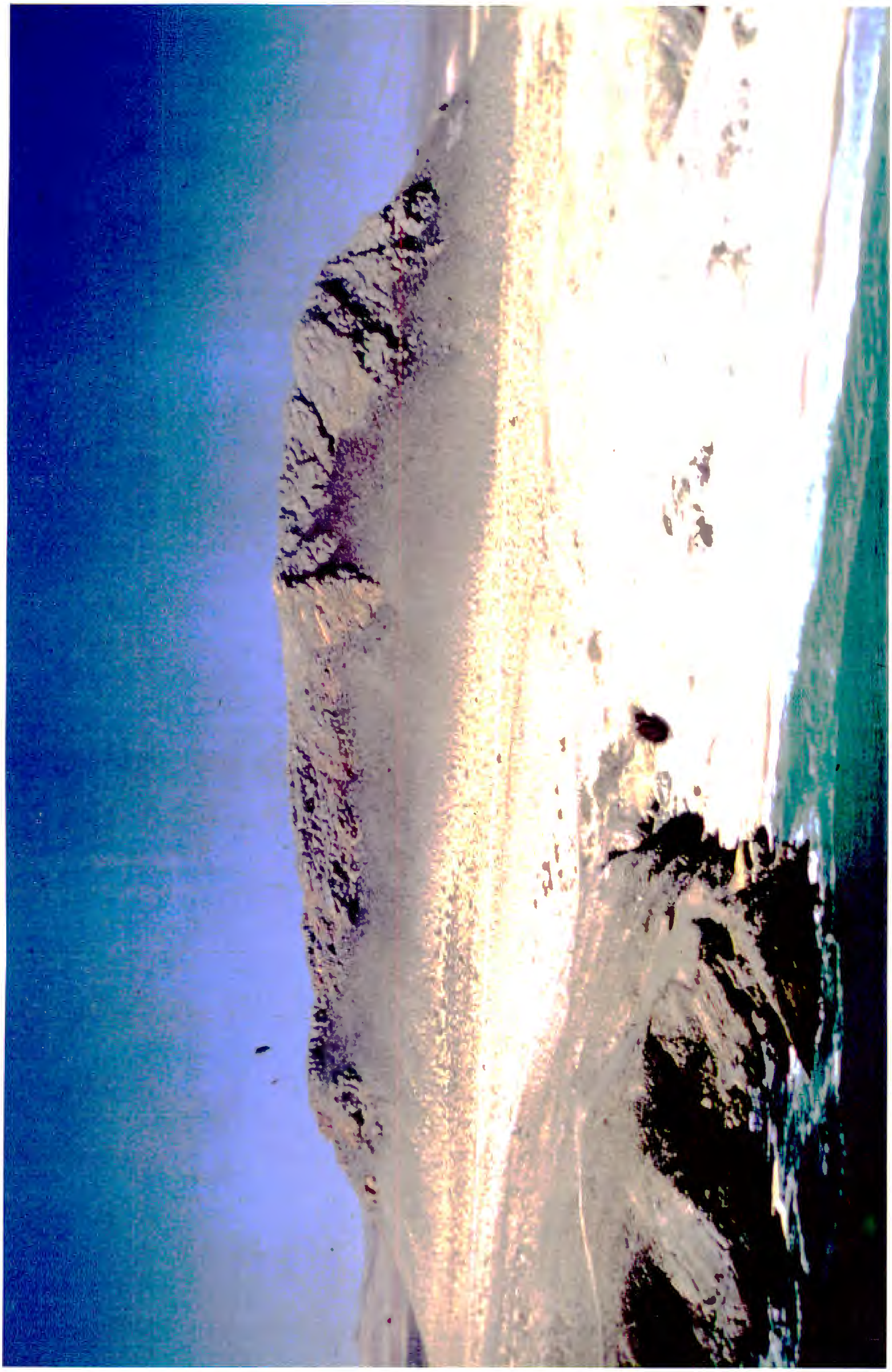


Figure 4.10 (previous page) The northern "brother" of the Buchu Twins (see Box 2.1 in Chapter 2) looking from the south-west.

Group 7: Inselbergs and rocky outcrops of the Buchu Twins, the Holgat River Canyon and the koppies to the east of Alexander Bay (Association 16).

These areas offer significantly different growing environments to plants. Consequently, these areas share little similarity with those of the surrounding sand covered coastal plain and pebble plains in both species composition and growth form. Patterns of diversity on these substrata have been discussed in the previous chapter

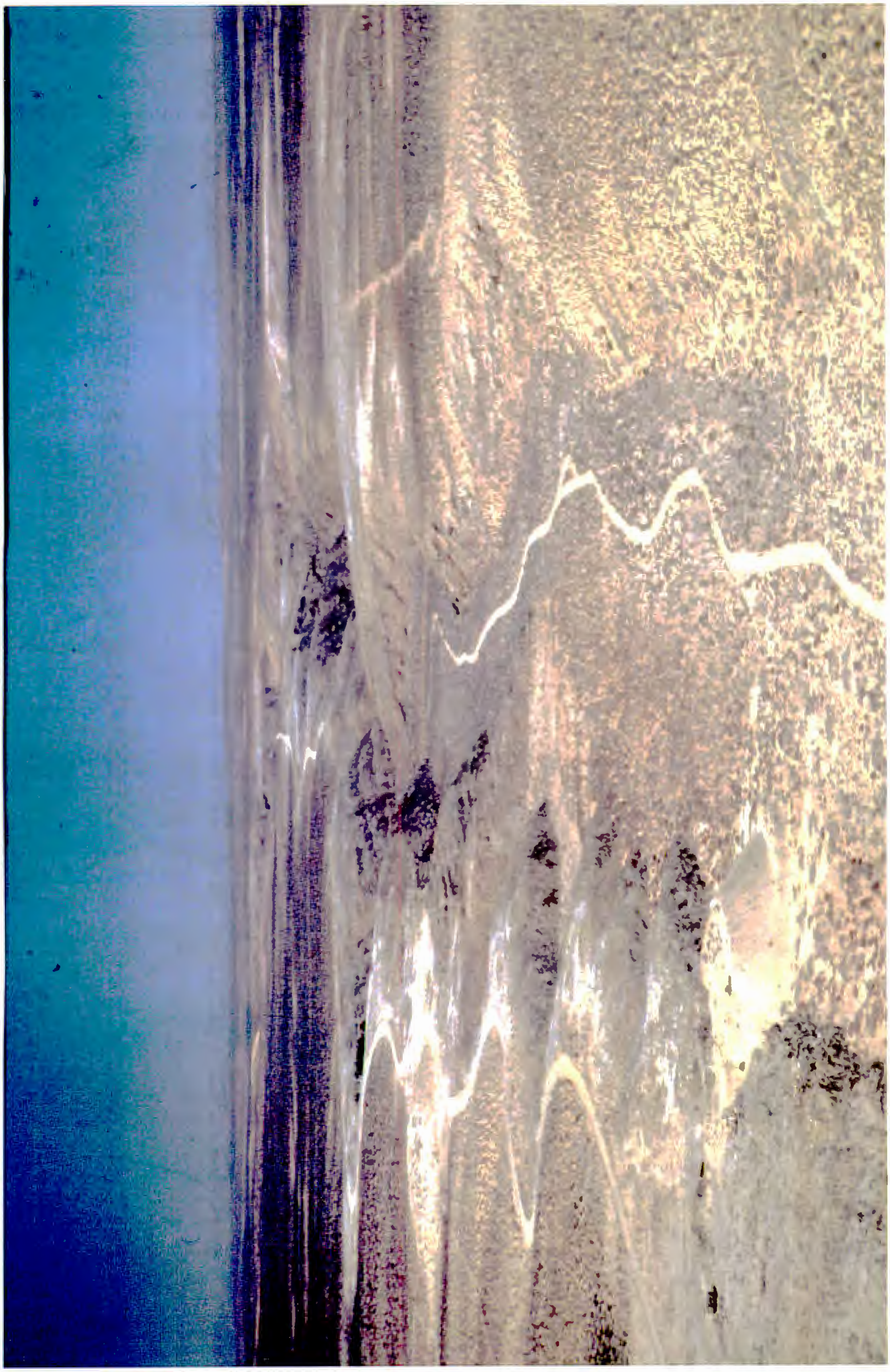
The koppies to the east of Alexander Bay support a slightly different flora to that encountered on the Buchu Twins (Fig. 4.10) or Holgat River (Fig. 4.11-13). The location of these koppies near to the Western Gariep circle results in a number of endemics of this centre and the Coastal Centre around Alexander Bay being encountered on these koppies. These are not encountered on similar substrata further to the south, notably *Crassula sladenii* and *Rhyssolobium dumosum* which are both endemic to this lower portion of the Orange River valley.

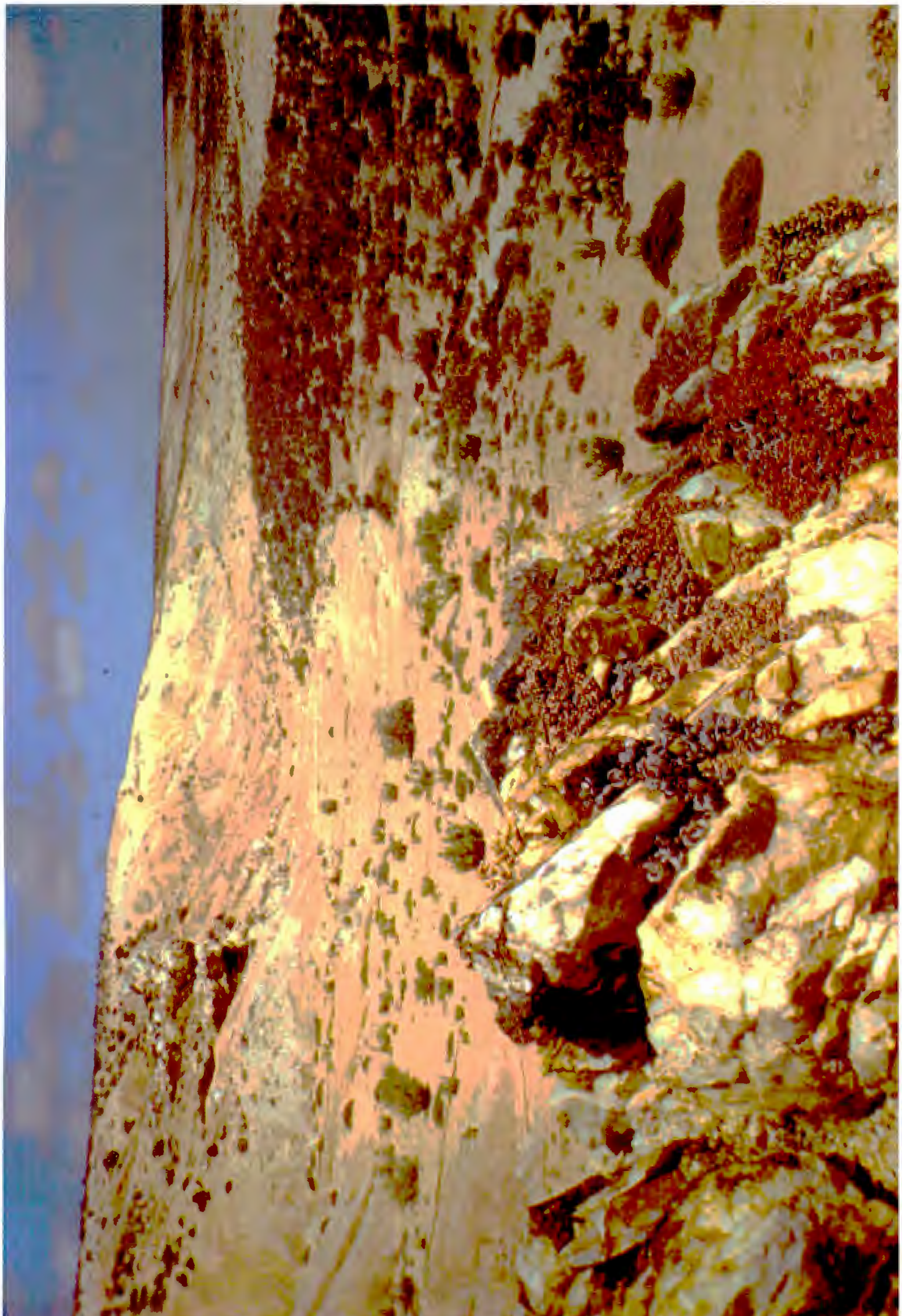
Figures on the following three pages:

Figure 4.11 The Holgat River Canyon, looking east from above the mouth of the river.

Figure 4.12 A rocky outcrop community of dwarf leaf succulents on quartz in the Holgat River Canyon, to the east of the main road to Alexander Bay.

Figure 4.13 A rocky outcrop community of dwarf leaf succulents on schist on the northern wall of the Holgat River Canyon, near the mouth.





5.3 Indirect gradient analysis.

Labelled species scatters, and relevé or species with environmental variables (envars) biplots are presented in Figures 4.14 - 4.17. For the relevé-environmental variables biplot, the symbols used to represent the relevés correspond to the 12 species associations presented in Table 4.3. In the final DCA ordination, relevés 94, 15, 37 and 52 (Association 1), and relevé 79 (Association 9) were excluded to obtain better spread amongst all remaining sites. These excluded sites represent extremes in pH and electrical conductivity, respectively.

The t-values for the regression coefficients of a weighted multiple regression of the sample (relevé) scores on the environmental variables, and the partial inter-set correlation of the environmental variables with the species axes, are presented in Table 4.5. This is a partial inter-set correlation because the environmental variable, TRANSECT, was used as a covariable in the analyses. This measure is deemed as a more stable measure of inter-set correlation as it is not affected by strong correlation's between environmental variables (Ter Braak 1987). This effect is observed for the first DCA axis where, in Table 4.5(b), CRUST is the single most important variable correlated with this axis. When the t-value of a variable is less than 2.1 in absolute value, then the variable does not contribute much to the fit of the species data in addition to the contributions of the other variables in the analysis (Ter Braak 1987). In Table 4.5(a), however, both CRUST, PEBBLES, SLOPE and MOUND show a strong correlation with the first axis. These variables are auto-correlated. This is to be expected since, all these variables were employed as surrogate measures of wind activity, sand movement and soil texture. Thus, this first axis could be described as a soil texture gradient that is a function of sand movement and sorting through wind action. Should soil texture have been included in this ordination analysis, then it would have emerged as the primary explanatory variable. Ordinations of other succulent karoo communities have shown a similar pattern. At Tierberg, Esler and Cowling (1993) showed that soil texture accounted for the greatest variation on the first CCA axis. Other soil properties, e.g. pH and EC, were also important in determining species distribution on the second CCA axis.

Axis 2 is problematic. The environmental variables explain less of the variability of this axis than they do for axis 3 (FR extracted, Table 4.5a and b). If the inter-set correlation for axis 2 is examined where TRANSECT was not used as a covariable (Table 4.6), the results change. There appears to be a latitudinal effect. As one moves north along the coastline so there is a significant turnover of species (Table 4.6a, FR extracted for axis 2>axis 1), but less so of communities (Table 4.6b, FR extracted for axis 2< axis 1). This turnover is more than can be explained merely by the measured environmental variables alone. Sampling of relevés straddles an important phytochorological boundary (see previous chapter). There is a turnover of species as one moves from the Namaqualand into the southern Namib Domain. However, the basic abiotic environmental variables defining the structure and composition of species associations, remain relatively unchanged across this boundary.

From the sample (relevé)-environmental variable biplot (Figure 4.14 and 4.15), electrical conductivity (Resistan) is also an important variable in explaining some of the variation in axis 1 and 2 for both species and samples (Table 4.5a and b). Electrical conductivity pulls out a subset of halophytic relevés with a characteristic group of halophytic plants. It does not, however, contribute much to explaining the overall variation in the data.

Both DCA axis 1 and 2 are correlated with totcover and avgpersp. This is an artefact of the turnover of species associations. As one moves from left to right on axis 1, or top to bottom on axis 2, there is a turnover of associations as a function of the change in environmental variables. From the statistics at the bottom of Table 4.3, this progression in associations is correlated with an increase in species or alpha diversity. As the driving environmental variables become less extreme, so the diversity of the associations increases.

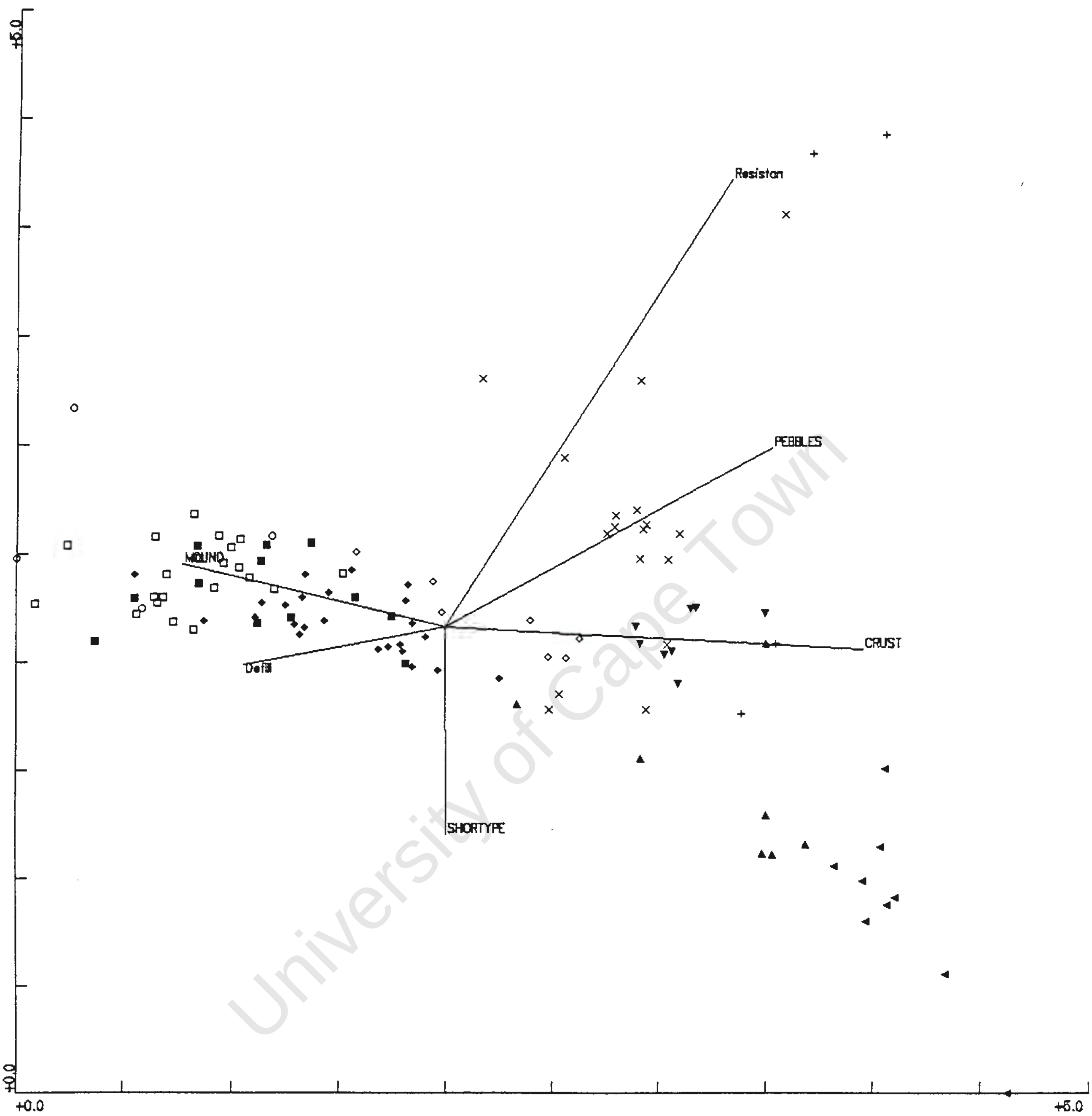


Figure 4.14 A biplot of sites and environmental variables with DCA axis I and II. Symbols refer to Twinspan classification of sites. O: Association 2; ■: Association 3; □: Association 4; ◆: Association 5; ◇: Association 6; +: Association 7; ×: Association 8; ▲: Association 10; ▼: Association 11; ◄: Association 12. See Table 4.2 for explanation of environmental variable abbreviations.

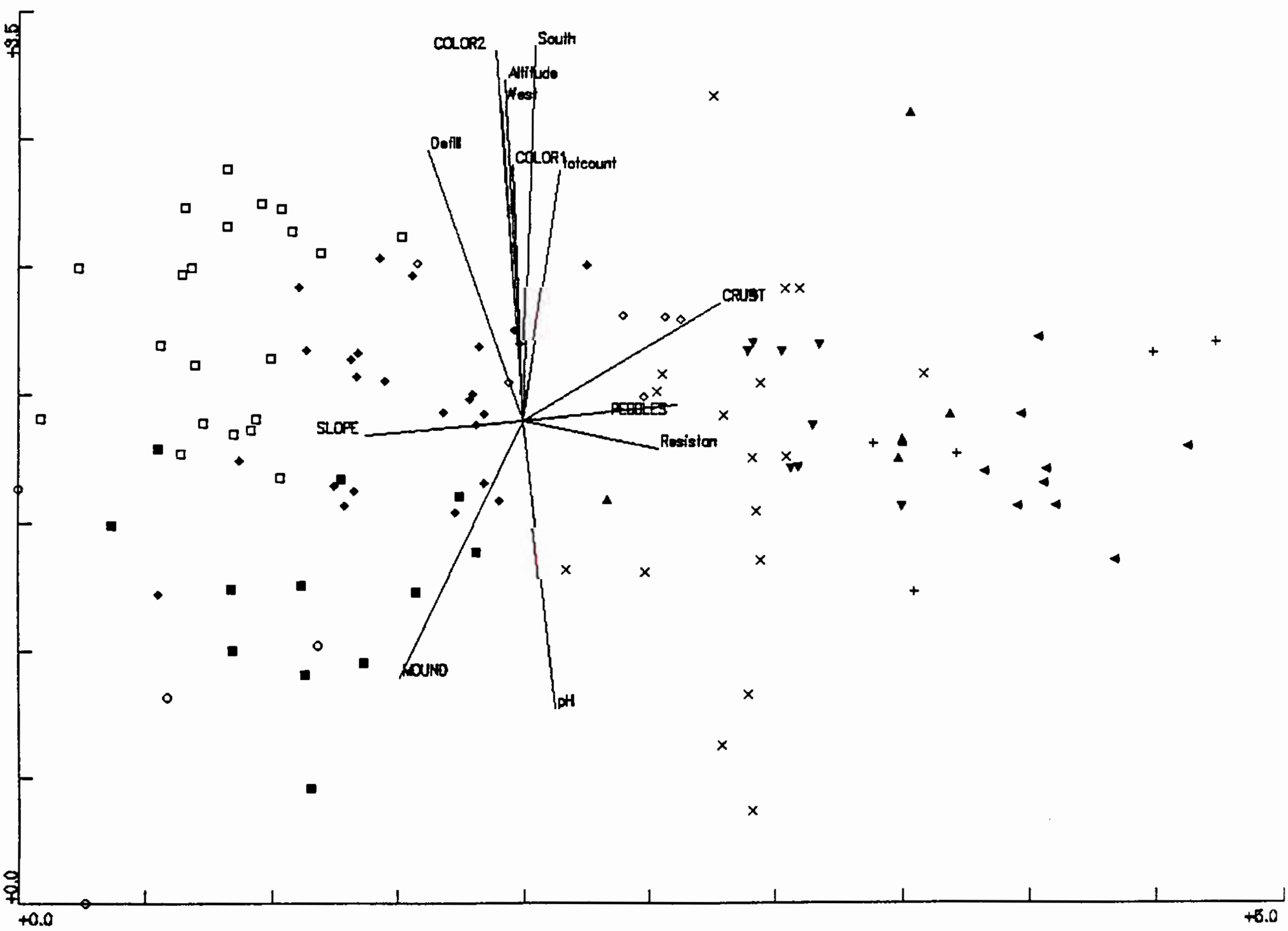


Figure 4.15 A biplot of sites and environmental variables with DCA axis I and III. Symbols and abbreviations the same as Figure 4.14.

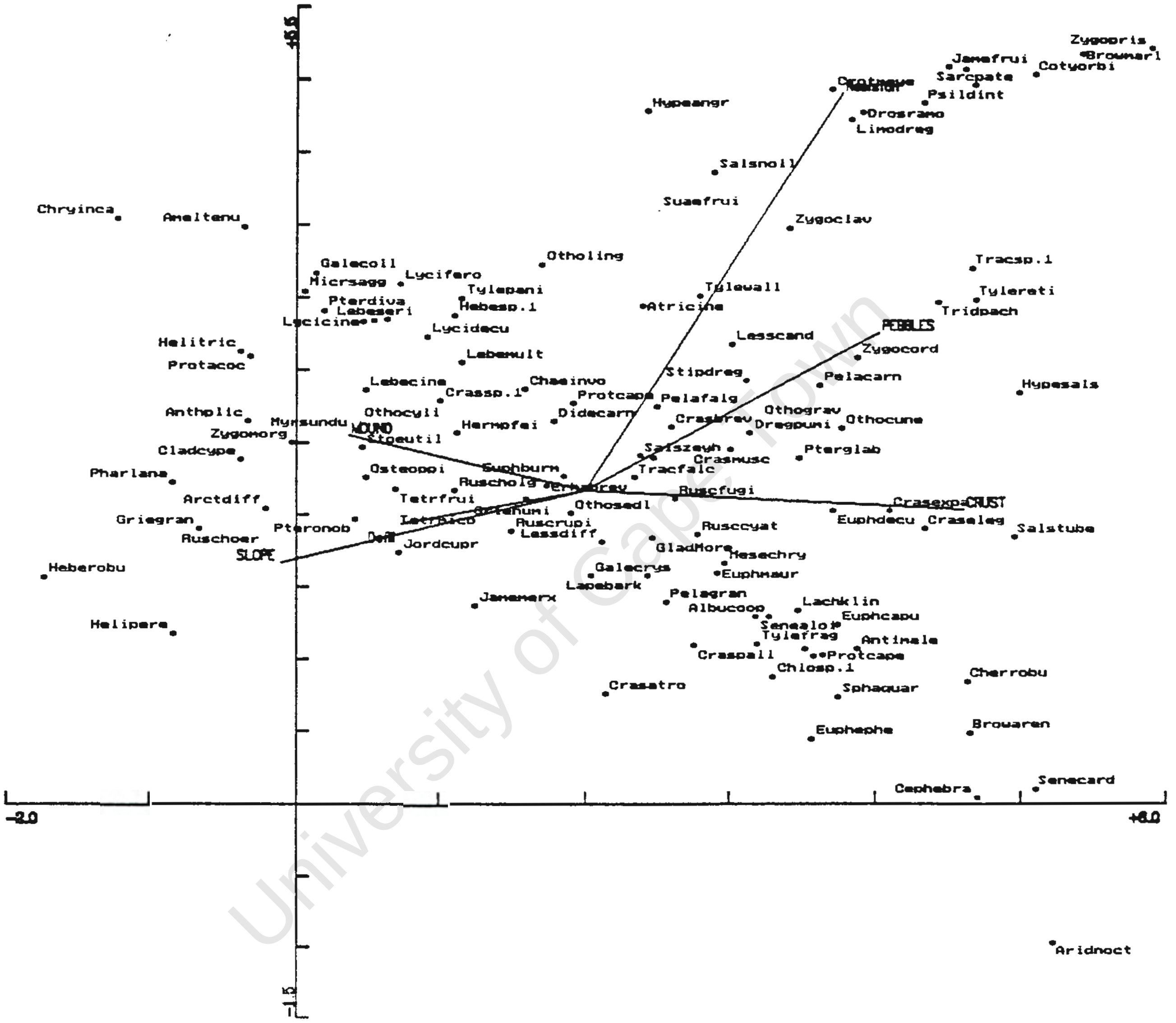


Figure 4.16 A labelled biplot of plant species and environmental variables with DCA axis I and II. Species codes represent the first four letters of the generic and the specific names. Full species names are given in Table 4.3. See Table 4.2 for explanation of environmental variable abbreviations.

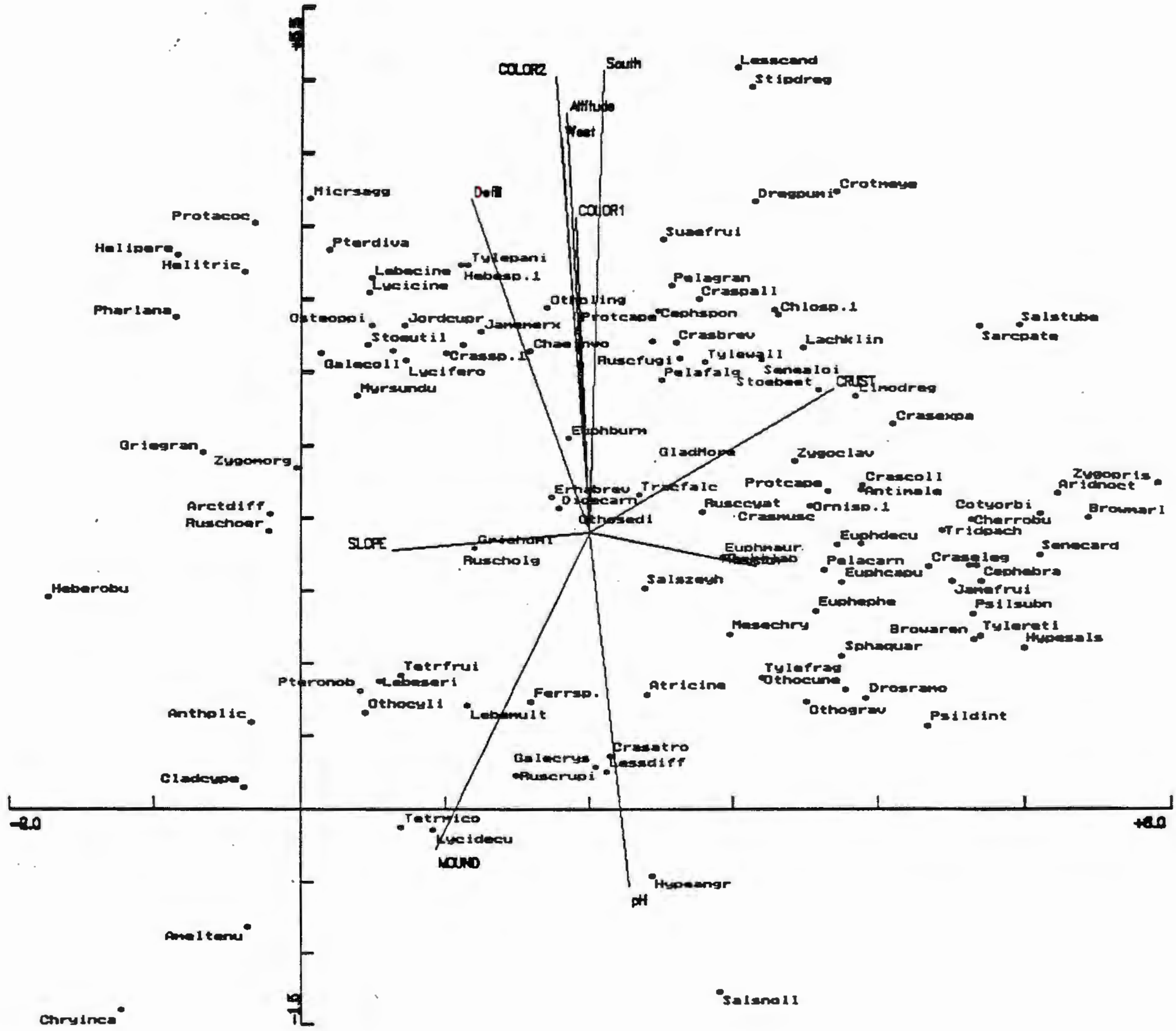


Figure 4.17 A labelled biplot of plant species and environmental variables with DCA axis I and III. Symbols and abbreviations used are the same as Fig. 4.16.

Table 4.5 (a) Partial inter-set correlation (TRANSECT was used as a covariable) of the environmental variables with the species axes consisting of the sample scores. (b) T-values of regression coefficients of a weighted multiple regression of the sample scores on the standardised environmental variables calculated for each axis. FR extracted: fraction of total variance in environmental data extracted by each species axis. Cumulative FR: cumulative sum of the fraction of variance extracted. It is the total variance explained by the first four axes. R(SPEC,ENV): species-environment correlation. EIG: the eigenvalue, multiplied by 100, is usually referred to as the percentage variance accounted for by the axis.

		(a) Partial inter-set correlation				(b) t-values of regression coefficients			
	DCA AXIS:	1	2	3	4	1	2	3	4
EIG						0.6396	0.4654	0.2287	0.1988
R(SPEC,ENV)		0.8866	0.6732	0.7708	0.6509				
FR extracted		0.1142	0.0389	0.1108	0.0551	0.253	0.0667	0.0782	0.0461
Cumulative FR		0.1142	0.1531	0.2639	0.319	0.253	0.3197	0.3979	0.444
1	pH	0.1445	-0.0938	**-0.4456**	-0.295	1.8762	-1.1056	-1.3442	-0.2344
2	Resistan	**0.4057**	0.2225	-0.0807	-0.0191	**3.0055**	**3.2136**	-0.8873	1.3713
3	Altitude	-0.026	-0.1484	**0.5196**	**0.4434**	0.3055	0.5404	-0.7852	**3.4646**
4	DefIII	**-0.3832**	0.1486	**0.4405**	**0.3528**	-1.733	**2.6633**	1.8184	1.1817
5	South	0.0854	-0.1882	**0.5573**	0.3057	0.0366	-0.7929	**2.2166**	1.0638
6	West	-0.0346	-0.1863	**0.4836**	0.2225	1.0964	-0.749	0.2796	**-2.2579**
7	totcover	0.1081	-0.2949	0.1035	**0.3666**	**2.7687**	**-3.1443**	0.3098	1.0385
8	avgpersp	-0.1009	-0.0264	-0.1661	0.2302	**-2.6934**	**2.7**	-1.1992	0.2599
9	totcount	0.1939	-0.2605	**0.3603**	0.1127	-1.7464	1.5067	-0.7144	-0.401
10	cnt>1.0	-0.2174	-0.1256	0.2796	**0.3797**	-0.8949	0.3233	0.6271	**2.2994**
11	cnt>5.0	0.1737	-0.2265	0.0446	0.1542	-0.0331	-0.2966	0.4193	**-2.5032**
12	COLOR1	-0.0029	-0.1435	**0.3861**	0.2351	0.4667	-0.5502	1.3114	0.0801
13	COLOR2	-0.1271	0.054	**0.5605**	0.1386	-1.4073	0.3861	**3.6482**	-1.1632
14	MOUND	**-0.5073**	0.2845	-0.3406	0.0149	-0.3242	0.9572	**-3.1769**	**2.0449**
15	GOPHER	0.2725	-0.0837	0	-0.0072	0.0787	-0.1682	-1.2591	1.8925
16	CRUST	**0.8005**	**-0.3727**	0.1104	0.0607	**7.0758**	**-2.5348**	0.5424	0.3572
17	PEBBLES	**0.5636**	-0.0943	-0.0291	-0.1211	0.7644	1.7907	0.9811	-0.0551
18	SLOPE	**-0.6182**	0.2005	0.0305	0.0248	**-2.6981**	-0.1946	1.7143	-1.3388
19	SHORTYP	0.0629	-0.2104	0.2237	0.1853	-0.4325	-0.2159	-0.3606	0.3991

Table 4.6 (a) Inter-set correlation (TRANSECT not used as a covariable) of the environmental variables with the species axes consisting of the sample scores. (b) T-values of regression coefficients of a weighted multiple regression of the sample scores on the standardised environmental variables calculated for each axis. Abbreviations same as for Table 4.5.

		(a) Inter-set correlation of environmental variables with axes				**(b) t-values of regression coefficient**			
	DCA AXIS:	**1**	**2**	**3**	**4**	**1**	**2**	**3**	**4**
EIG						.6421	.4491	.2751	.1769
R(SPEC,ENV)		0.8832	0.858	0.6716	0.5287				
FR extracted		0.1067	0.1501	0.0428	0.0119	0.2152	0.1436	0.0418	0.0215
Cumulative FR		0.1067	0.2568	0.2996	0.3115	0.2152	0.3588	0.4006	0.4221
1	pH	.1859	-.3370	.3357	-.0643	1.9515	.1645	.1169	1.7493
2	Resistan	**.4246**	**-.3555**	.0035	-.0252	**3.0979**	**-4.2924**	**-2.7039**	.8045
3	Altitude	-.0683	**.4973**	-.2166	.0897	.0528	.8391	.7708	.6433
4	DefIII	**-.4238**	.3053	-.2631	.0166	-1.3123	-1.3546	-1.0773	1.0356
5	South	.0382	**.5016**	-.2457	.1110	-.2472	**2.8540**	.7255	.9255
6	West	-.0650	**.3972**	-.3285	.1487	1.3458	-.4701	**-3.2363**	.7824
7	totcover	.0414	**.5197**	-.0665	.1342	**2.2104**	**2.5866**	-1.4879	-1.9453
8	avgpersp	-.1110	.0791	.2023	.1289	**-2.2429**	-1.8539	1.9766	**2.9975**
9	totcount	.1331	**.4977**	-.3250	.1071	-1.3646	-1.2260	1.0243	**2.4486**
10	cnt>1.0	-.2553	**.4998**	-.2341	-.0783	-.9908	**2.1012**	-1.1818	-1.7078
11	cnt>5.0	.1544	.2818	.0410	.0456	.1728	-.5626	.8036	-1.1350
12	COLOR1	-.0982	**.5169**	-.2274	.1722	.1113	1.2117	-1.2001	.6840
13	COLOR2	-.1626	.2849	-.1309	-.0162	-1.6529	.3660	1.2926	-1.2604
14	MOUND	**-.4662**	**-.4276**	-.0760	-.0380	-.2120	-1.4593	-1.3085	1.2889
15	GOPHER	.2626	.1276	-.1023	.1906	-.1494	.8186	-1.4387	1.6135
16	CRUST	**.7622**	**.4202**	.1309	.0458	**7.0245**	**3.2885**	1.7063	-.6188
17	PEBBLES	**.5678**	-.0590	.0714	.1122	.6727	-.9368	-1.7991	1.7863
18	SLOPE	**-.6136**	-.1904	-.1536	-.0913	**-2.7927**	-.3215	-1.1685	-.2230
19	SHORTYPE	.0237	**.4295**	-.0470	.1242	-.3995	.4254	1.2812	1.2272
20	TRANSECT	-.0727	.4580	**-.3439**	.1749	-.8407	1.3275	**-3.0613**	**2.4625**

The use of TRANSECT as a covariable separates the latitude effect from the third driving variable. Axis 3 is correlated with such environmental variables as pH, Altitude, Deflll, South, West, COLOR1 and COLOR2. These variables essentially represent a relevés position in the landscape relative to the ocean and various landscape features. Combined, these variables act as a surrogate measure for sand or substrate age or where a relevé is located in the landscape in relation to sand sources or palaeo-features. As marine sands age they turn from white to dark brown-red (COLOR1) and also the organic matter content increases (COLOR2)(see Chapter 2). Soil age is correlated with a number of other variables. As one moves further from the ocean, the incidence of fog decreases, altitude increases, sand movement decreases and pH decreases.

Axis 4 is correlated with altitude (Table 4.5). Altitude increases as one moves away from the coast. This is weakly correlated with vegetation properties such as the average cover of plants and total cover, both of which increase along the same gradient.

6 Patterns and processes in the Namaqualand Sandveld.

The Namaqualand Sandveld is not simply an amorphous mass of sand covered by plants. A complex, but predictable, landscape mosaic exists, a result of the interplay between the forces of time and wind on the distribution of sand. Nor are plants distributed in a random manner within this edaphic framework. Plant assemblages and functional groups are distributed in relation to subtle changes in the edaphic environment within the Sandveld. Across more obvious edaphic gradients, e.g. from sand to rock, the shift in plant associations and functional group types is more dramatic (see previous chapter).

Typical Strandveld and Sandveld species are distributed throughout the Sandveld of Namaqualand, occupying the deeper, loose more active sand substrates (e.g. dune crests, soil depth >0.75 m). The dominant species are typically erect leaf succulent chamaephytes up to 1.5 m tall in the Mesembryanthemaceae or Asteraceae. Creeping, mat or mound forming species are uncommon. Stem succulent species (viz. Euphorbiaceae) dominate communities locally, but these are finely branched, shrub-like species and not cactoid. Phanerophyte and Cactoid growth forms are entirely absent from Strandveld and Sandveld communities.

In between these communities, are communities particular to the Sandveld, but with a greater affinity, both in form and composition, to the lowland succulent karoo vegetation encountered further inland off the dunes of the Sandveld. These communities are encountered on shallow soils (<0.5 m) in dune slacks, characterised by well developed biogenic crusts. Here species are typically much shorter (<0.75 m), creeping or mound forming leaf succulent plants. The occurrence of leaf succulents, principally in the Crassulaceae and Mesembryanthemaceae, in these communities is much higher than that found on the deeper sands.

Together these assemblages of plants are arranged into a complex mosaic of plant associations. Wind is the driving variable in this system. The effect of latitude on species turnover is emphasised by the major biogeographical transition between two, floristically distinct phytochorion. The effect of time in shaping the landscape mosaic is expressed in the pedogenic processes that transform dune sands. Within the dune landscape, substrata that differ dramatically in their inherent properties, such as halophytic habitats or rocky outcrops, support suites of species not encountered in the dune landscape and these add to the overall diversity of the region.

Amongst the fog deserts of the world, the Sandveld is unique both geologically and climatically (Chapter 2), floristically (Chapter 3), and structurally (this chapter). Geologically, the Sandveld is the only one of the four fog deserts that has a near ubiquitous dune covering. Climatically, precipitation, although minimal, appears to be regular and predictable. Floristically, the diversity is exceedingly high, although this is a general trend amongst fog deserts in relation to other world deserts. Structurally, the dominant growth forms, or structural character of the vegetation stands alone. At a generic level Oceanic Sahara may appear similar to the Sandveld (see previous chapter), but as with the fog deserts in Chile and Baja California, the dominant succulent growth forms are cactoid or large, aloe-like leaf succulents (e.g. Agavaceae). The Sandveld of Namaqualand is, in every respect, a unique desert system.

References

Boucher, C. and le Roux, A. (1989) Heavy mineral sand mining project assessment vegetation report. Anglo American Corporation West Coast Heavy Mineral Sands Project Supplementary Report. EEU Report No. 4/90/49. Environmental Evaluation Unit, University of Cape Town, Cape Town.

Boucher, C. and le Roux, A. (1993) Dry coastal ecosystems of the South African coast. in van der Maarel, E. (ed.) Dry Coastal Ecosystems. Africa, America, Asia and Oceania. Ecosystems of the Worlds 2B. Elsevier, Amsterdam.

de Villiers, A.J., van Rooyen, M.W. and Theron, G.K. (unpubl.) Studies on the revegetation of saline mined soil at Namaqua Sands. Report for Anglo American Corporation.

Esler, K.J. and Cowling, R.M. (1993) Edaphic factors and competition as determinants of pattern in South African karoo vegetation. *South African Journal of Botany* 59: 287-295.

Hill, M.O. (1979) TWINSPAN. Section of Ecology and Systematics, Cornell University, Ithaca, New York.

Hilton-Taylor, C. (in press) Patterns and characteristics of the flora of the Succulent Karoo Biome, southern Africa. in Van der Maersen, L.J.G. (ed.) Proceedings of the XIVth AETFAT Congress, Wageningen, The Netherlands. Kluwer Academic Publishers, Dordrecht.

Jürgens, N. (1991) A new approach to the Namib Region. I: Phytogeographic subdivision. *Vegetatio* 97: 21-38.

Jürgens, N. (in press) Psammophorous plants and other adaptations to desert ecosystems with high incidence of sand storms.

Jürgens, N. and Niebel, A. (1991) The unknown lichen hill. *Veld & Flora* 77(1): 24-26.

Jürgens, N.; Günster, A.; Seely, M.K. and Jacobson, K.M. (in press) Desert. In The Vegetation of South Africa. Cowling, R.M. and Richardson, D.M. (eds.).

Kent, M. and Coker, P. (1992) Vegetation Description and Analysis. A Practical Approach. CRC Press, Boca Raton.

Low, B.A. and Rebelo, A.G. (eds.) (1996) Vegetation of South Africa, Lesotho and Swaziland. Department of Environmental Affairs and Tourism, Pretoria.

McAuliffe, J.R. (1990) A rapid survey method for the estimation of density and cover in desert plant communities. *Journal of Vegetation Science* 1: 653-656.

Meuller-Dombois, D. and Ellenberg, H. (1974) Aims and Methods of Vegetation Ecology. John Wiley & Sons, New York.

Milton, S.J; Yeaton, R.I; Dean, W.R.J. and Vlok, J.H.J. (in press) Succulent Karoo. In The Vegetation of South Africa. Cowling, R.M. and Richardson, D.M. (eds.).

Rowell, D.L. (1994) Soil Science: Methods and Applications. Longman scientific & Technical. Harlow, Essex.

Schieferstein, B. and Loris, K. (1992) Ecological investigations on lichen fields of the Central Namib. I. Distribution patterns and habitat conditions. *Vegetatio* 98: 113-128.

Shmida, A. (1985) Biogeography of the desert flora. In Evenari, M *et al* (eds.) Hot Deserts and Arid Shrublands. Elsevier Science Publishers B.V., Amsterdam.

Schultze, B.R. (ed.) (1965) Climate of South Africa. Part 8. General Survey (WB28). The Government Printer and Weather Bureau, Pretoria.

Szabolcs, I. (1993) Salt-affected soils as the ecosystem for halophytes. *Desertification Bulletin* 23:15-19.

Ter Braak, C.J.F. (1987) CANOCO - a FORTRAN program for canonical community ordination by correspondence analysis, principal components analysis and redundancy analysis (version 2.1). TNO Institute of Applied Computer Science, Statistics Department Wageningen, The Netherlands.

van Jaarsveld, E. (1981) A preliminary report on the vegetation of the Richtersveld with specific reference to the trees and shrubs of the area. *Trees in South Africa* Oct-Dec.: 58-84.

Appendix I: Plant species omitted from the species-relevé data set. * Signifies incidental perennial plants (viz. plants with only 1 occurrence) and not annuals.

Arctotis hirsuta

Foveolina albida

Gethylis grandiflora *

Hebenstretia parviflora

Hebenstretia repens

Helichrysum lactea

Hyperia tristis

Manulea aridicola

Nemesia anisocarpa

Nemesia bicornis

Onchosiphon grandiflorum

Pharnaceum croceum

Helichrysum pumilio

Ruschia hexamera *

Zaluzainskya affinis

Appendix II (overleaf): Phytosociological table of the sand dune associations as produced by Twinspan. No further sorting of relevés or species has been done.

	Strand Formations			*Stoeberia utilis* Formations			Halophytic Formations			*Stoeberia beetzii* Formations			
	1	2	3	4	5	6	7	8	9	10	11	12	
		1	1	111111	111	1 1		1111		1	1	11	
	9135	1330	335566777890	1123445566799001112	12222333444556778889011	8011790	6788	11444567890011	7	1445881	2569991	222361226	
	4572	6680	293405012062	791465561916579670580	670478013389573362678949	9823415	8835	45809127097151312	9	8046483	31820236	359447127	
Lebe seri	5--1	4566	3-4----63-85	54-7616-----84------3	---------4--------------	-------	----	----4-9----------	-	1------	--------	---------	0000
Otho cyli	-4--	7656	------------	7-8-887--------------	---88-------------------	-------	----	---3-------------	-	-------	7-------	---------	0000
Amel tenu	----	1-3-	------------	---------------------	-1----------------------	-------	----	-----------------	-	-------	--------	---------	0001
Anth plic	----	1---	-1----------	---1-----1-----1---	-------------1----------	-------	----	-----------------	-	-------	--------	---------	0001
Clad cype	-374	669-	-77598-96573	45---664836---5--6--5	--5------51-1-864--4-6-2	-------	----	11----3----------	-	-------	--------	---------	0001
Hebe cord	1---	----	------------	---------------------	------------------------	-------	----	-----------------	-	-------	--------	---------	0001
Hebe robu	----	-5--	-------33---	-----6--------------1	------------------------	-------	----	-----------------	-	-------	--------	---------	0001
Pter onob	----	----	-661-3--655-	1---4--75-42-4-4-3---	6--5-4-3-2--1--73-1--6--	-------	----	------------21---	-	-------	-------4	---------	0001
Tetr frui	5395	2-54	4563164862-6	444366254156816351431	752245253652--741-3-51-4	3456-63	----	1-1--2-1-5--21---	-	1-2----	1--2---1	---------	0001
Arct diff	----	2---	1-4--1------	-23121113455221-41-2	-1-1-3-3--21--611----3--	---1---	----	-----------------	-	-------	--------	---------	0010
Chae invo	----	----	----4-2-1--4	24461-1131-48-345445-	4--4-3-11-11---7--514214	7367756	----	--1-----------2--	-	-------	----32--	---------	0010
Cras sp.1	----	----	------------	--11---1----1--------	----------1-------------	----1--	----	-----------------	-	-------	--------	---------	0010
Gale coll	----	----	------------	------------4---2--1-	------------------------	-------	----	-----------------	-	-------	--------	-----1---	0010
Grie gran	----	77--	-----3--6---	9--4-8887972-7---5--6	------67-7-----------1--	--3----	----	-----------------	-	-------	--------	---------	0010
Hebe sp.1	----	----	------------	-------------------1-	-----------------------1	-------	----	-----------------	-	-------	--------	---------	0010
Heli pere	----	----	1--1-1------	-------------1-1----13	1------1-11------------1	-------	----	-----------------	-	-------	--------	---------	0010
Heli tric	----	----	------------	-627--623-2--476-63-3	----------1-------------	-------	----	-----------------	-	-------	--------	---------	0010
Jord cupr	----	1---	1----13--3--	--4--36263526-112-4-5	-----516626211--565-----	21---12	----	--------211--1-1--	-	-----1-	-----1--	--1------	0010
Kedr psam	----	----	------------	------------5---1-1--	------3-------------1--1	-----2-	----	-----------------	-	-------	--------	---------	0010
Lebe cine	----	----	------------	--------5--7---5-676-	------------------------	4------	----	-----------------	-	-------	--------	---------	0010
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Micr sagg	----	----	------------	---2-----------------	------------------------	1------	----	-----------------	-	-------	--------	---------	0010
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Otho ling	----	----	------------	-------------------1-	------------------------	-----1-	----	-----------------	-	-------	--------	---------	0010
Pela falg	----	----	------------	---------------------	------------------------	-3----2	----	-----------------	-	-------	--------	---------	0010
Phar lana	----	1--1	------------	---1--1-----1------1	---1-----------1--------	-------	----	-----------------	-	-------	--------	---------	0010
Prot acoc	----	----	------------	---7---5-------------	------------------------	-------	----	-----------------	-	-------	--------	---------	0010
Pter diva	----	----	------------	-3-4--4-4---1---7----	------------------------	5------	----	-----------------	-	-------	--------	---------	0010
Rusc hoer	----	----	-----8------	---------7---7-6---12--	--35--3---6---5----3-33-	-------	----	-----------------	-	-------	--------	---------	0010
Stoe util	----	-8-6	------3428--	788657879897778774787	--7776865589----6-6-86-7	83-2765	----	-3-----1----------	-	-------	-----1--	---------	0010
Tyle pani	----	----	------------	---4--------3---7----	--------------------3---	----5--	----	-----------------	-	-------	--------	---------	0010
Zygo morg	----	46-6	1562-4-56---	56556665662675577-543	---5-413-8---1526---54-4	55--21-	----	-----------------	-	1------	--------	---------	0010
Cras brev	----	----	------------	---5-----------------	---1--------------------	-1667-6	----	-----------------	-	-------	2-------	-----1---	0011
Erha brev	----	----	----11------	--1----1---11---1-11-	1-1----1--1---1---11---1	----11-	----	---1---1----------	-	1------	----1---	-----1---	0011

Grie humi	----	----	---6-4---4--	--8-6--4---574--41661	--747-----6-36---5273166	--3----	----	----4------------	-	6--4-2-	-1------	-----1---	0011
Herm pfei	----	----	-----3--2-2-	-----3---1-----61----	-5-----534--6--1-22-----	73-----	----	--2---111----13--	-	---1---	-------1	---------	0011
Lebe mult	----	----	----4-----2-	--8------------------	---4-7------1-7-3------2	-4-6-7-	1---	-----------141-2-	-	----1--	--------	1-----1--	0011
Rusc holg	----	4---	4----5---35-	62--6--8-445-44--17-5	75423545-73--15-35565326	-6-----	----	-4-----4-----6---	-	6------	--41----	---------	0011
Cras pall	----	----	------------	---------------------	-----------------------2	-------	----	-----------------	-	-------	--------	------1--	0100
Euph burm	----	2---	7---114-354-	----4--4-2-4-3-3---8-	-5---7-68--466-1173165-7	77--36-	----	------21145321111	1	13-5---	-213-5--	---3-----	0100
Glad More	----	----	------------	-------1-------------	-----11-----------------	----11-	----	----------1------	-	-------	----1---	------1--	0100
Jame merx	----	----	------------	---------------------	----------------2-------	-------	----	--------1--------	-	-------	--------	---------	0100
Otho sedi	---6	---6	578764287562	-8-6-4668688556687568	885--9888896884656478766	6688786	2---	-44-5--25-2155351	-	74-2161	-5464761	66-573747	0100
Pela gran	----	----	------------	------------------52-	------------------------	-----32	----	-----------------	-	-------	-------2	----4----	0100
Trac falc	----	----	----11-----1	---------1---1--1-11-	1-1-11---------1-1-1--111	111111-	----	--11------1--1111	-	-------	11-11111	---------	0100
Ceph spon	----	----	------------	---6---3-5-4---6-----	---1--------------------	-5756-6	----	---------3-------	-	-------	66------	---------	0101
Dide carn	1---	----	34-433---2--	-11-1--1-177513311--1	6-1117-1533-153-1111476-	7646785	1---	-15144115-1113111	1	1111---	---1-111	---1-----	0101
Prot cape	----	4---	6--------11-	--6552-4--3882-77-594	5656----2--633-7434-32-8	9642888	2-12	1-31---61-3131561	1	11--5--	2-257513	1121-21-2	0101
Rusc fugi	----	----	------------	------------4------6-	---4-3------------------	-776--7	----	-----------------	-	-------	-6-----8	---------	0101
Ferr sp.	-1--	----	1---1-----1-	-------1---1---------	------1---------11---1--	-------	----	-------------1-11	-	-------	--------	---------	0110
Gale crys	58-6	7--3	8586-3945766	-------1-2-----------	-777--2577-272-3155---1-	--1----	14-6	7331-5-1-7--61---	-	4435651	-3------	------2--	0110
Lyci decu	635-	3668	35-6--5853-8	7---3-----1--7-------	------------------4-4---	-------	3235	22---1-2-3-2---1-	1	--1----	-------1	---1--4--	0110
Rusc rupi	32--	8-5-	565661966658	1-----11-3---3---1---	25-4--5-366-64366535235-	-------	14-2	65-5-126-1--45431	-	3-241--	---2--2-	-1-------	0110
Chry inca	3---	5-8-	------------	---------------------	------------------------	-------	----	-----------------	3	-------	--------	---------	0111
Cras atro	----	----	------2-----	---------------------	----------------1-1-----	-------	----	----------1------	-	-------	--------	---------	0111
Lape bark	----	----	------------	---------------------	-------1----------------	-------	----	-----------------	-	-------	-1------	---------	1000
Rusc cyat	----	----	------------	31--3---1-11-12--1--	--244--5-2------3--33-41	412131-	----	1-4-----1-3--1---	-	2-1--11	-1---52-	5--3223-4	1000
Sene aloi	----	----	------------	------------22---4---	-----4---3-------8----4	---2--1	----	--------1--------	-	-------	6-----3-	2-1-5--35	1000
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Less diff	----	----	1-----------	---------------------	------------------------	-------	----	-----------------	-	1------	--------	---------	1001
Tyle wall	----	----	------------	-------------------4-	------------------------	----3--	----	-----------------	-	-------	----5---	---------	1001
Sals zeyh	----	---8	7-7-6467-6-7	4-6-8--57632-77--78--	78648777858951586676866-	-------	7644	86765857388-5-878	-	869646-	8787--56	-5-65-4--	1010
Mese chry	-11-	1-11	-11-11-1-1--	11-----1-1----------11	1--11--11111-11-11-11---	--11---	-111	111-1---1111---11	-	1111111	1111--1-	11-11111-	1011
Atri cine	----	--3-	-6---------3	---------------------	-1----------------------	-------	-5--	-------7---------	-	-------	--------	---------	1100
Hype angr	1-76	--7-	14----------	---------------------	------------------------	-------	61--	4-4------1--52---	1	-1-----	--------	----1----	1100
Sals noll	8799	----	----------6-	---------------------	------------------------	-------	----	9--7-------5----	-	-------	--------	---------	1100
Brow marl	----	----	------------	---------------------	------------------------	-------	7-8-	-----------------	-	-------	--------	---------	1101
Chlo sp.1	----	----	-----------1	---------------------	------------------------	-------	---1	--------------1--	-	----1--	--------	---------	1101
Cras coll	----	----	------1-----	---------------------	----------------1-11-----	-------	1-11	--11-----1-------	-	-------	--------	----1---1	1101
Crot meye	----	----	------------	---------------------	------------------------	-------	4---	--------------5--	-	-------	--------	---------	1101
Dreg pumi	----	----	------------	---------------------	------------------------	-------	---1	-------21-----2--	-	-------	---1----	---------	1101
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Jame frui	----	----	------------	---------------------	------------------------	-------	3---	-----------------	8	-------	--------	---------	1101
Lach klin	----	----	------------	---------------------	------------------------	-------	---1	--------1--------	-	-------	--------	---------	1101
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Zygo clav	6---	----	------------	--------------------	------------4----------	-------	3-24	628813798-57-8451	1	-------	---3--7-	---------	1101
Zygo pris	----	----	------------	--------------------	-----------------------	-------	3-7-	-----------------	-	-------	--------	---------	1101
Albu coop	----	----	------------	--------------------	------------1----------	----1--	----	--1-----------1--	-	---1---	11-1--1-	---------	1110
Coty orbi	----	----	------------	--------------------	-----------------------	-------	1-11	-----------------	-	-------	--------	----1----	1110
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Euph sp.1	----	----	------------	--------------------	-----------------------	-------	5-2-	-----------------	-	----2--	--------	---------	1110
Orni sp.1	----	----	------------	--------------------	-----------------------	--1--1-	---1	----------1--1-1-	-	---1---	-1-1----	---1-----	1110
Otho grav	----	----	---6--------	--------------------	-----------------------	-------	---3	5---657----55--79	-	-5--4-1	--------	-63---56-	1110
Psil dint	1--4	----	------------	--------------------	-----------------------	-------	5132	42----------5----	-	-------	--------	321----45	1110
Sarc pate	----	----	------------	--------------------	-----------------------	-------	3-52	--------------3--	-	----3--	--41----	------3--	1110
Stoe beet	----	----	------6--1--	---------6----------	-----------5--35685--4-	----6--	3-58	-556-9-179923471-	-	5988899	8687--6-	-7615-478	1110
Trac sp.1	----	----	------------	--------------------	-----------------------	---1---	--11	---1-------------	-	----1--	--------	1-111--11	1110
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Zygo cord	----	----	------------	--------------------	-----------------------	-3-----	--22	--44---1--5542---	3	--5----	4-6---51	33233-2-1	1110
Anti male	----	----	------------	---4-----------2----	--3-----------1--------	--45--5	1--1	--1--1-211--11---	-	-33----	63-3-423	532473-44	1111
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Brow aren	----	----	------------	--------------------	-----------1-----------	-------	-51-	----51---3-------	-	45-97--	------6-	866877977	1111
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Cras eleg	----	----	------------	------------1--1--1-	-----------------------	---1111	----	--11-1-----------	-	--1----	1----111	---11113-	1111
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Euph decu	----	----	------------	-----------------1--	--6--------------------	--98998	----	-----------------	-	-------	86--8765	69-866-87	1111
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Lamp sp.1	----	----	------------	--------------------	-----------------------	-------	----	-----------------	-	-------	--------	567-64--6	1111
Otho cune	----	----	------------	--------------------	-----------------------	-------	----	-----------------	-	-------	4-----3-	---------	1111
Pela carn	----	----	----1-------	-----------3--------	-----------------------	-----1-	----	-------------2---	-	-----1-	--------	3------3-	1111
Prot cape	----	----	------------	--------------------	-----------------------	-----4-	-3--	-----------------	-	-----5-	----3--1	-3---31--	1111
Psil subn	----	----	-----22-----	--------------------	-33--------------------	-------	-8-8	13--1------------	-	56978--	------3-	8898999--	1111
Pter glab	----	----	------------	------2-------------	--34---------------8---	864-147	2---	5-45---46-5-8--7-	-	--1----	98999987	61--68342	1111
Sals tube	----	----	------------	--------------------	-----------------------	-------	----	-----------------	-	-------	--------	-----1--7	1111
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Spha quar	1---	----	-----2------	--------------------	4-4-----5-------3------	-------	-3--	25----------1----	-	1-54---	------2-	4-353-1-5	1111
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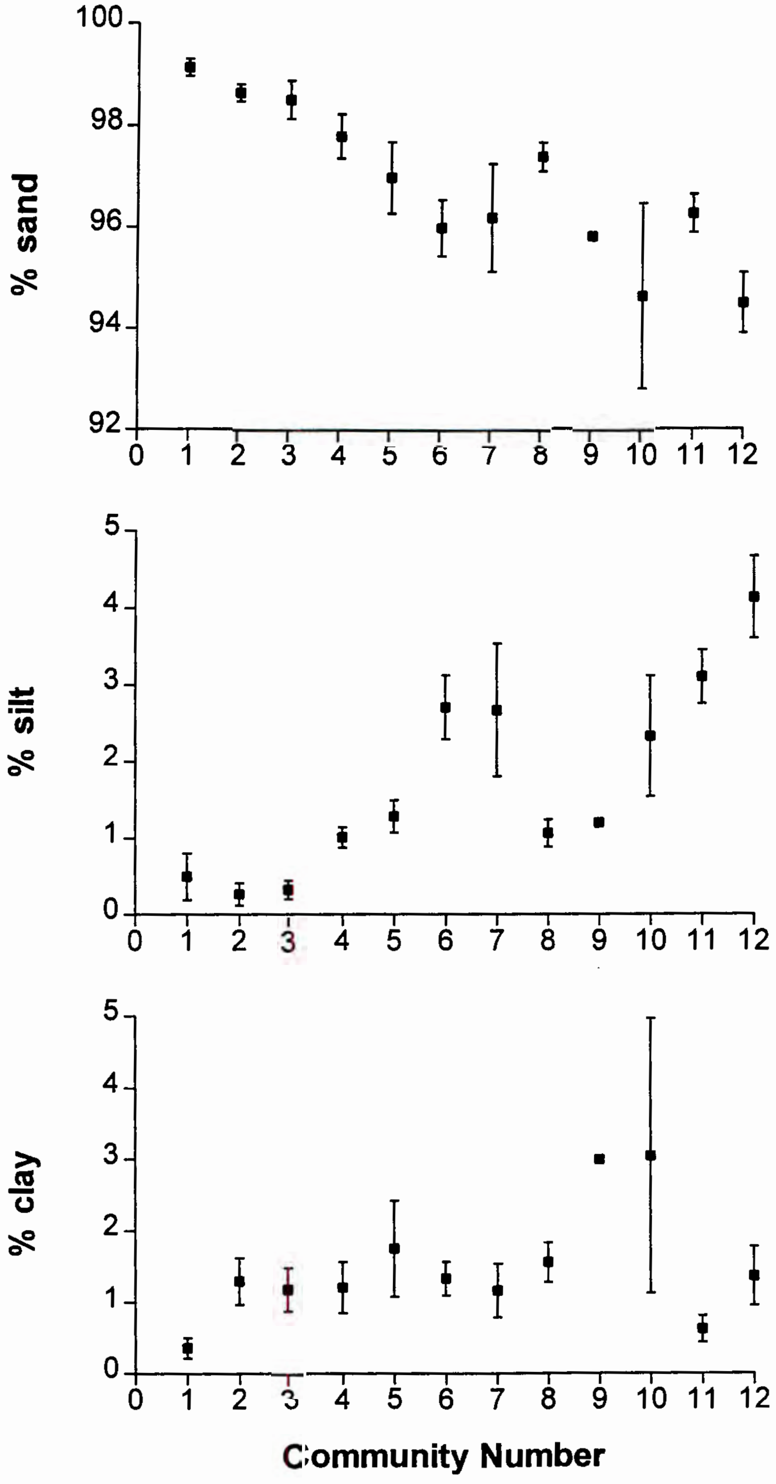
Appendix III: Soil texture for selected relevés.



Chapter 5 Patch Creation by Fossorial Rodents: A Keystone Process in the Revegetation of Severely Degraded Arid Soils.

Introduction.

Diamond mining activities along the west coast of South Africa have, over the past 50 years, resulted in the creation of large overburden dumps and other disturbed areas where the soil profile to bedrock (up to 30m) has been inverted and left in an unamended state. These overburden dumps created during the open cast mining for diamoniferous gravel horizons in the ancient colluvial dune soils are characteristically high pH, saline-sodic soils (Scott 1995). Although these exposed subsoils appear to contain adequate levels of most plant nutrients (Scott *et al* 1994), factors such as soil salinity; clay and sodium content causing defloculation; and dump architecture in terms of steep slopes, best explain the lack of natural plant re-colonisation (le Roux and Odendaal unpubl., Scott *et al* 1994, Scott and Johnson 1995, F. Ellis pers comm.). In addition to this, these sub-soils are biologically dead in terms of their microbial fauna and flora components. This is undoubtedly another contributing factor to the lack of plant colonisation. The presence of functional soil microbial communities is directly related to the establishment and maintenance of plant communities in arid systems (Allen 1988, Whitford 1988).

Some natural recovery of vegetation on overburden dumps does occur (le Roux and Odendaal unpubl.). A gradient of plant re-colonisation rate and degree exists perpendicular to the coast. As one moves away from the coast so the amount of sand movement decreases. Aeolian deposition of sand on overburden dumps is important in the revegetation process since this sand does not possess the chemical and physical properties of overburden dump soils, and as such, where sand is deposited on overburden dumps it provides sites for plant colonisation. Related to this west-east gradient is a gradient of soil depth. As one moves away from the coast so the depth to bedrock, as well as altitude and the degree of toxicity of subsoil increase. In an extreme case, a series of overburden dumps created on the farm Swartbank, 30km south of Alexander Bay, approximately 20 years ago are still totally bare today. The dumps occur at the eastern limit of marine-terrace diamond prospecting north of Port Nolloth, some 8km from the coast, and thus are the oldest colluvial soils disturbed by diamond mining. These overburden dumps represent the most extreme in terms of dump chemical and physical properties.

In addition to the these human topographic adjustments of the landscape, the northern Sandveld of the West coast is home to a burrowing rodent, Brant's Whistling Rat (*Parotomys brantsii*). A quiet walk through the dunes in this region will reveal the near ubiquitous presence of this shy rodent by its high pitched whistling. These fossorial rodents live in small colonies inhabiting intricate and extensive tunnel systems (De Graaff 1981). The number of entrances to a system may vary between 13 and 31 (De Graaff 1981, Dean and Milton 1991), but only some will be in constant use. At each burrow entrance, a small mound develops, a maximum area of 1x1 m, consisting of soil, faecal and organic matter deposited from the burrow network by the rodents. Their diet is entirely vegetarian consisting of shoots of low shrubs, grass and grass seeds (De Graaff 1981).

The keystone role of fossorial creatures in the structure of the edaphic environment and resultant effect on the structure and dynamics of plant communities in which they occur, has long been recognised by ecologists. The example of termite `heuweltjies' or mima-like mounds in the southern winter rainfall karoo is a well known South African example (Yeaton and Esler 1990, Dean and Yeaton 1993). Termites have also been associated with the creation of nutrient rich patches in nutrient poor tropical forests (Salick *et al,* 1983). Another insect, *Peltotrupes youngi* a burrowing scarabid beetle, has been shown to have significant patch-creating properties in Florida long leaf pine communities (Kalisz and Stone 1984). Amongst arachnids, Danin (1994) demonstrates the association between the establishment of *Salsola inermis* and scorpion burrows.

Probably the most studied fossorial creatures are American gophers (*Geomys* sp.). Kalisz and Stone (1984) also discuss the effects of Pocket Gophers (*Geomys pinetus*) burrowing in long leaved pine communities. Spencer *et al* (1985), Hobbs and Mooney (1985), Andersen (1987) and Hobbs and Mooney (1995) all discuss the spatial, temporal and intensity effects of various gopher species burrowing activities on the dynamics of North American plant communities. The effect on plant community structure and dynamics of another fossorial rodent that has received attention is the Indian crested porcupine, *Hystrix indica*, in Israel (Gutterman *et al*

1990, Shachak *et al* 1991). The general trend in all these studies is that soil mixing by burrowing animals results in the creation of patches in the landscape which differ both in their soil physical and chemical properties from those of the surrounding landscape. They also provide microsites for plants to colonise in an otherwise "homogeneous" vegetation matrix.

Not only are gopher activities instrumental in creating patches in existing vegetation matrices, but they can also play a keystone role in facilitating the return of vegetation by creating patches that favour plant establishment and growth. Anderson and Allen (1985) have shown that the burrowing activities of Northern Pocket Gophers facilitated plant re-colonisation on ash covered landscapes left after the eruption of Mount St. Helens in 1980. In their study it was shown that gopher mounds enhance seedling establishment and growth due to more favourable soil moisture, temperature, nutrients and organic matter. Gopher burrowing activities are also instrumental in the dispersal of mycorrhizal spores (MacMahon and Warner 1984). The soil associated with dung middens produced by rabbits (*Oryctolagus cuniculus*) on limestone quarry-spoil are areas of enhanced biological activity, increased soil moisture, higher nutrients, lower pH, and are more humic than surrounding spoil (Dixon and Hambler 1993). These sites were also the focus of enhanced pioneer plant colonisation of the mine spoil.

An active soil microbial community is necessary for the biogeochemical cycling of nutrients (Bolton *et al* 1993) and is a direct indicator of general soil fertility (Rowell 1994). The general soil microbial community is involved with the sequestering of soil nutrients and breakdown of organic matter and release of nutrients, and plays an integral part in determining general soil fertility (Nedler and Steinberger 1993). In a landscape characterised by poor soil growing conditions, the activities of fossorial animals can condition soil such that when a warren, burrow entrance or network is vacated by the animals, the mounds become foci for plant establishment.

At Swartbank, overburden dumps colonised by Brant's Whistling Rats are also colonised by plants. Where there is no apparent rodent activity there appears to be no plant colonisation. Thus, in the light the above discussion and this apparent association between fossorial rodent burrows (burrowing activity) and plant re-colonisation of overburden dumps, the aims of this study are to show that: (a) there is an association between rodent burrowing and plant re-colonisation of, and distribution on, overburden dumps; and (b) this association is due to the amelioration of soil conditions on burrow mounds which create sites suitable for plant establishment and growth.

Study site.

See Chapters 2 to 4 for a complete description of the study site geology, climate and vegetation. The farm Swartbank is located between the Holgat River and the Buchu Twins, approximately 35 km south of Alexander Bay, and to the east of the main road outside of the main diamond mining area. In the early 1970s the site at Swartbank was the subject of prospecting for marine diamond deposits, however, this did not come to anything and since then the site has remained relatively undisturbed.

Methods.

To determine whether there was an association between plant occurrence and rodent burrows, nine 5x5m quadrats, three each on three separate dumps, where placed over areas where Whistling Rats were or had been active. All plants present in each plot were counted. These data were compared to nine similar quadrats, three on each of the three dumps sampled, each placed over areas where there was no evidence of any rodent activity. Only perennial plants were recorded and any annual plants encountered were ignored. The mean number of plants per plot in the nine rodent plots was compared to the mean number of plants in rodent free-plots using the non-parametric Mann-Whitney test.

To examine the relationship between the occurrence of plants and burrow mounds at a finer scale, nearest neighbour distances between all burrow entrances (active and old) and their nearest plant neighbour were measured in each of the plots placed over areas of rodent activity. The cumulative distribution of these nearest neighbour distances was compared to that of point-to-plant distances in each plot. Points were stratified in each plot on a regular 1x1m grid (16 points in total per plot). The Kolmogorov-Smirnov test (Upton and Fingleton 1985) was used to test whether the cumulative frequency distribution of point-to-plant and burrow-to-plant distances were significantly different. If the two samples are distributed independently of one another then this test is applicable irrespective of the type of distribution of the data and also the size (n) of the two data sets (Upton and Fingleton 1985).

To be able to show that the edaphic properties of burrow mounds were different, six soil samples, two each from the three separate dumps, were collected from (a) control sites on overburden dumps away from any rodent influence (rodent-free plots); (b) uncolonised burrow mounds; (c) under established plants; and (d) topsoil from undisturbed areas in the surrounding the dunes (normal). Soil to a depth of 5cm was collected. For each sample, the pH, electrical conductivity (EC) and microbial activity was analysed. For all analyses, the methods outlined in Rowell (1994) were used. The pH of the soil was measured in both distilled water and a strong ionic solution (0.01M $CaCl_2$). EC was measured in deciseimens per metre ($dS.m^{-1}$) in a saturated soil paste extract. For microbial activity, a laboratory-based method to measure respiration of incubated soil, where activity is expressed in terms of grams carbon dioxide respired per gram air dried soil per second ($gCO_2.g^{-1}$ dw $soil.s^{-1}$), was used. A one-way Anova was used to compare the results of the four sites for each analysis. For pH, a matched t-test was used to test for significance of change in pH between water and calcium chloride for each site. The colour of the dry soil sample was determined using standard soil colour charts and a qualitative record of the colour of the saturated paste extract was made.

Results.

The association between rodent burrows and plant occurrence is very strong. No plants were encountered in any of the rodent-free plots. Rodents avoid constructing warrens on steep slopes. The maximum average slope angle measured in any of the rodent plots was 15^{o} (mean $8^{o} \pm 5.0$) compared with a maximum of 22^{o} (mean $12.4^{o} \pm 5.8$) for the comparison plots. A list of plant species encountered in the rodent plots is presented in Appendix I.

At the finer scale, within rodent plots there was no significant association between all burrow entrances (i.e. active and non-active) and the occurrence of plants (Fig. 5.1). There was however, a strong positive association ($p<0.01$) between active burrow entrances and plants, and a weaker negative association between non-active burrow entrances and plants.

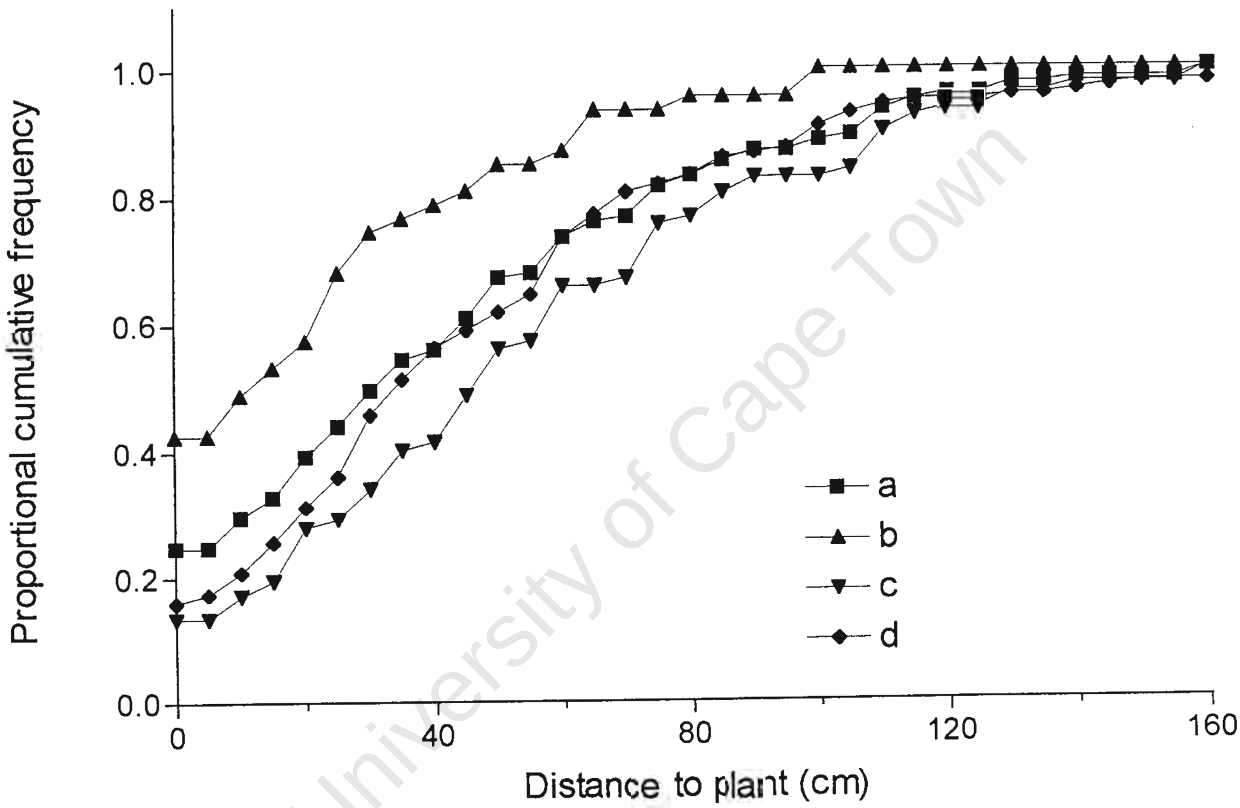


Figure 5.1 **Cumulative frequency distribution of nearest neighbour distances: (a) between all burrows and plants p=0.18; (b) between active burrows and plants, p<0.01; (c) between non-active burrows and plants, p=0.05643; and (d) between random points and plants.**

The effect of rodent activity on edaphic factors is marked. The pH of soils in water on uncolonised mounds and under plants increases by approximately 1.5 pH units compared to control and normal soils (Fig. 5.2a). For normal soils, and those from uncolonised mounds and under plants, the pH in calcium chloride showed a slight, although not significant, change in pH. The pH of the control soil, however, increased significantly ($p<0.01$) by approximately 1pH unit. Conversely, electrical conductivity was approximately half that of control soils in uncolonised mounds and under plant soils (Fig. 5.2b), but these were still approximately three times that of normal soils. Microbial activity on uncolonised mounds is comparable to rates in normal soils, approximately three times those of control soils, but only half those of soils from under plants (Fig. 5.2c).

The colour of the soils in each treatment changes from a dull orange in the control soils through to an orange or bright brown in the uncolonised mounds and under plants, to bright brown in the normal soils. Extracts from the soils also show a progression in colour from clear or white in the control soils, through to a yellow or black in the rodent affected soils and under plants. Raw data for soils is presented in Appendix II.

Discussion.

The burrowing activity of Brant's Whistling Rats has a significant effect on the re-colonisation of overburden dumps by plants. Where overburden dumps represent the edaphic extreme of factors limiting the plant re-colonisation, there is no re-colonisation of these surfaces by plants if the soil conditions have not been ameliorated in some way. The burrowing activities of rodents has a significant effect on the edaphic properties of those dump soils that are directly influenced by their burrowing, viz. burrow mounds. The activities of rodents introduce small patches of less toxic, biologically active soil into the homogeneous and inhospitable expanse of the overburden dumps in which they burrow.

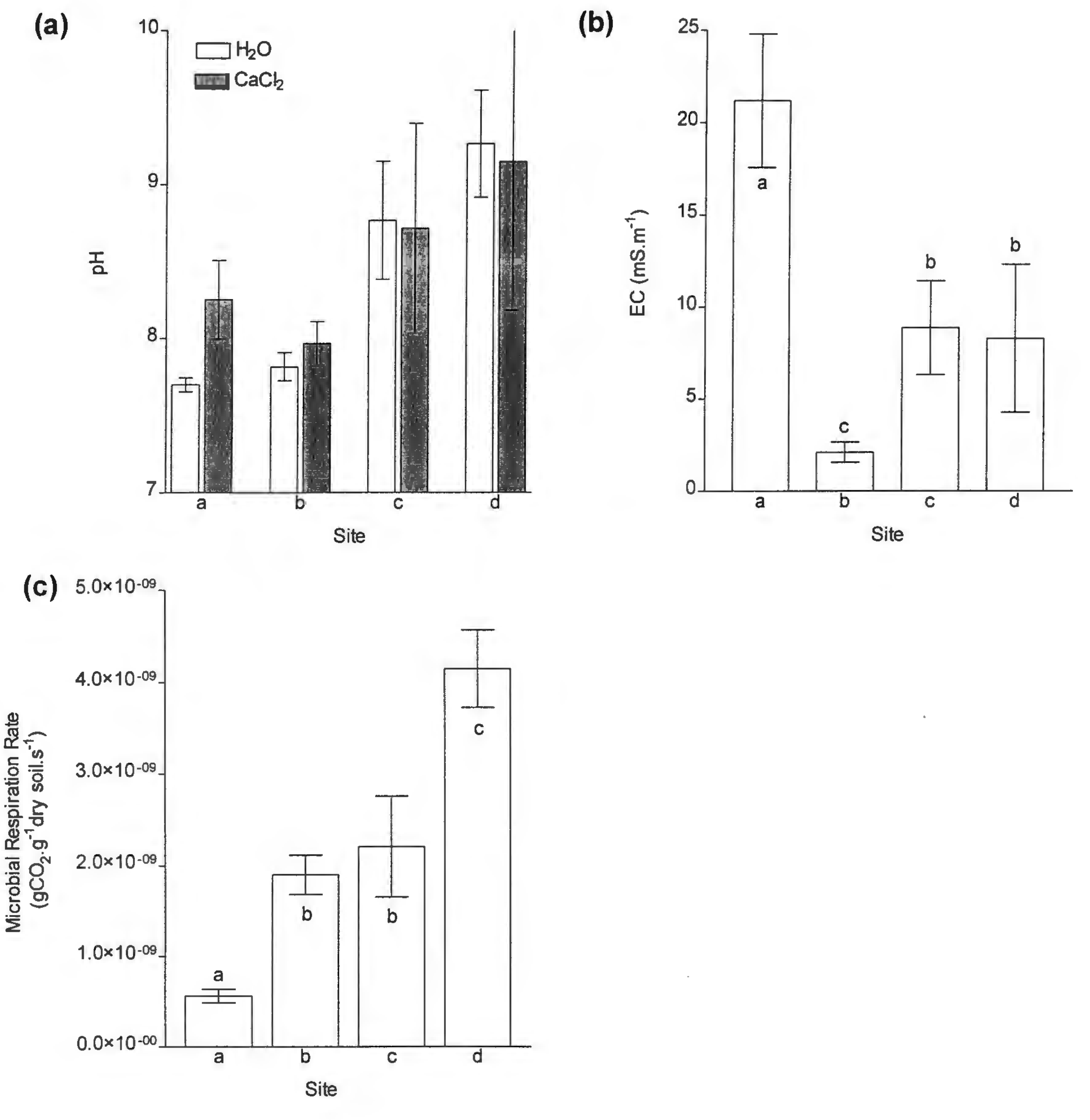


Figure 5.2 (a): Soil pH in water and a strong ionic solution (0.01 M $CaCl_2$). The sites are: (a) control soils from overburden dumps; (b) normal dune soils from the surrounding landscape; (c) uncolonised rodent burrow mounds; and (d) soil from under the canopy of plants growing on overburden dumps. (b) Soil conductivity. (c) Microbial respiration of soils. Different letters on each bar refer to treatments that are significantly different ($p<0.05$) from one another.

It is interesting that active burrows are associated with living plants and not the other way round. If plants were establishing on non-active burrow mounds, then one would expect old burrows to be associated with plants. Plant recruitment, however, is probably related to neighbourhood warren activity. Foraging rodents would invariably nosh[6] any emerging seedlings in the vicinity of their warren. Successful recruitment on a burrow mound could only realistically occur during a vacancy in the warrens occupation, viz. a recruitment window. There is some evidence for natural cycles in the populations of these rodents over a period of four to six years (T. Jackson and A. Spinks pers. comm.). Recruitment windows resulting from rodent population crashes could allow plants to establish on the edaphically favourable burrow mounds. At a later stage, when rodents re-colonise the over burden dumps, new burrows are constructed under or near established plants, explaining the positive association between burrows and plants. Established plants trap aeolinites in their canopies thus further ameliorating the immediate soil conditions. Repetition of this cycle could eventually result in the complete revegetation of the overburden dump surface over a period decades to centuries.

Examination of the soil colours from the different treatments suggests that rodents are capable of burrowing through overburden dumps into the buried topsoil layer and depositing this topsoil on the surface of the dumps in their burrow mounds. Additions of large quantities of organic matter to the lighter calcium rich subsoils soils of the dumps would turn them grey rather than the observed orange-brown. Lighter shades of brown can only be achieved when the typically bright brown dune topsoil is mixed with the dull orange dump soil. Another way in which soil, specifically under shrubs, can darken is throughout aeolian deposition (see Chapter 2). This mixing of the soil profile is supported by the lower EC values obtained for uncolonised mounds and under plants. Considering the aridity of the area, it is unlikely that salts could be leached out of the mounds. The variation in mound colour suggests that the degree of mixing is variable and a function of altitude of a burrow mound on the dumps, viz. depth to buried topsoil. Thus, flatter dumps (<2-3m high) would allow for more mixing of the overburden dump soils and buried topsoil, creating improved conditions for plant growth. Rodent colonisation of overburden dumps is also limited to shallow slopes (< 15°). Applying this to the mining process, by creating flatter, lower dumps one could facilitate rodent re-

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[6] nosh: to eat, to devour like a ravenous Killer-Ware-Pig on a full moon.

colonisation overburden dumps and employ nature to assist in the revegetation of these structures.

How does the burrowing activities of these fossorial rodents ameliorate the soils on overburden dumps? These are arid, saline-sodic soils. The rodents amend these soils with organic matter collected from the surrounding vegetation and their own excretions. The end result is an improvement in the soil fertility of the burrow mounds, expressed in terms of enhanced soil microbial respiration, but there are a number of important soil chemical processes which need to be considered. These are elaborated below.

Analysis of soil pH in both water and a strong ionic solution is not only indicative of the of the nature of these soils, but also the resultant changes due to rodent activity. That pH in an ionic solution, when compared to pH in water, increased significantly for the control soils but not significantly in the other treatments is very interesting. In the light of the high EC values measured for this treatment, the known sodic nature of the soil, and also the pH (~8.3 in $CaCl_2$), one can conclude that this observed increase in pH is a result of a high concentration of positive ions or strong salt effect (Rowell 1994). The presence of a high concentration of Ca^{2+} and Na^+ ions in the soil solution will contribute towards increasing the pH and with the addition of an ionic solution this effect is be exaggerated. For normal soils, pH in water is similar to that of the control soils, but there is no significant change in pH in an ionic solution, indicating that normal dune soils are not sodic. Thus, there is some chemical process in the soils of burrow mounds initiated by the activities of rodents that is resulting in the precipitation of ions out of the soil solution.

Below pH 8.0, soil exchangeable Ca^{2+} ion species and calcium carbonate or calcite ($CaCO_3$) are in equilibrium and CO_3^{2-} is inactive (Ross 1989). At pH above pH 8.0, CO_3^{2-} becomes very reactive resulting in the formation of metal carbonates imposing limits on the solubilities of metal ions and consequently their availability to plants (Lindsay 1979). Among these metal carbonates is calcite (see Appendix III for equations of the reactions). In alkaline soils the partial pressure of CO_2 gas is the controlling variable for calcite solubility (Lindsay 1979). The observed microbial respiration in rodent-affected soils results in an up to five fold increase of the soil CO_2 concentration. An increase in soil CO_2 concentration results in a decrease in calcite solubility as calcium ions are precipitated out of solution. In addition to the formation of calcite due to an increase in CO_2 concentration, calcite can also be formed by the addition of urea, e.g. in the form of rodent excretions (Ross 1989). Sodium ions reacting with CO_2 and water can form various sodium carbonate anion complexes and sodium hydroxide (Lindsay 1979). These sodium complexes will raise the pH of the solution which would explain the observed increase in pH in the uncolonised mounds and under plant soils. This process has been used to explain the existence of calcrete horizons under termite mima-like mounds (Moore and Picker 1991).

What one observes occurring on overburden dumps inhabited by these fossorial rodents is the creation of patches with distinctly different soil properties. As whistling rats are very common in the dunescape it is plausible to assume that their activity is creating mounds of soil which differ significantly from those of the surrounding landscape.

An active soil microbial community is necessary for the biogeochemical cycling of nutrients (Bolton *et al* 1993) and is a direct indicator of general soil fertility (Rowell 1994). The significantly higher microbial respiration rate in soils on uncolonised mounds is direct evidence for an improvement in general soil condition through amendment with organic material ejected from the warren by rodents. The even greater activity of the microbial community under shrubs is to be expected since microbial activity is enhanced under shrubs due to the moderated temperatures from shading effects; increased organic matter from both rodent, plant and aeolian inputs; increased water infiltration as a result of rodent digging and deposition of soil; and better moisture retention due to greater soil organic matter content that are associated with these desert microsites. These sites constitute islands of fertility in this desert ecosystem (Garcia-Moya and McKell 1970, Gutierrez *et al* 1993). It is interesting to note that the Aizoaceae and Mesembryanthemaceae, which are the dominant colonisers of the overburden dumps (see Appendix I), do not have mychorrhizal associations (Allsopp and Stock 1993). The microbial activity that is occurring on the burrow mounds is improving the "fertility" of the soil and there is probably no mycorrhizal link assisting in plant establishment.

The role that burrowing rodents play is essentially one of a large earth worm. Rodents forage off the overburden dumps and drag organic material back to their burrows both for use as food and also nesting material. At the same time these rodents are involved in expanding their underground burrow networks, hence subsoil is brought to the surface. Mixed in with this soil are the rodents faeces and old organic nesting material now in a state of decay. Two important processes are being fulfilled by the activities of the gophers, namely:

a) The faeces contain spores/propagules of soil micro-organisms, thus the soil ejected from burrows is seeded with soil micro flora (MacMahon and Warner 1984) and possibly plant seeds.

b) Organic matter is being introduced to the soil. This addition of organic biomass to the soil results in an increase in microbial activity (Aoyama and Tomohiro 1993). The addition of organic matter will also improve the soils physical properties (Nedler and Steinberger 1993).

In areas where the surface soil is drastically degraded in some way, e.g. the ash left after a volcanic eruption (Andersen and MacMahon 1985) or diamond mine overburden dumps, this conditioning and mixing of soil creates microsites where conditions for plant colonisation and growth are possible in an otherwise biologically sterile and uncolonisable environment.

Conclusions.

The role that Brant's Whistling Rat plays in the revegetation of diamond mine overburden dumps highlights two important processes in the functioning of arid systems. The first is that of patch creation. The creation of patches in the landscape that differ in some respect to the surrounding landscape are important in providing microsites for plants to establish. This emphasises the role of structure in arid system functioning. Secondly, the structure and functioning of the soil microbial community forms an integral part of the aboveground processes that we observe in these systems. Attempts to restore arid lands to self-sustaining functional ecosystems need to consider the integral role these two processes play in arid systems.

References.

Allen, M.F. (1988) Below ground structure: A key to reconstructing a productive arid ecosystem. In Allen, E.B. (ed.) The Reconstruction of disturbed Arid lands. AAAS Selected Symposium 109. Westview Press, Boulder.

Allsopp, N. and Stock, W.D. (1993) Mycorrhizal status of plants growing in the Cape Floristic Region, South Africa. *Bothalia* 23(1): 91-104.

Andersen, D.C. (1987) *Geomys bursarius* burrowing patterns: Influence of season and food patch structure. *Ecology* 68(5): 1306-1318.

Andersen, D.C. and MacMahon, J.A. (1985) Plant succession following the Mount St. Helens volcanic eruption: facilitation by a burrowing rodent, *Thomomys talpoides*. *The American Midland Naturalist* 114: 62-9.

Aoyama, M. and Tomohiro, N. (1993) Microbial biomass nitrogen and mineralisation immobilisation processes of nitrogen in soils incubated with various organic materials. *Soil Science and Plant Nutrition* 39(1): 23-32

Danin, A. (1994) Association of *Salsola inermis* and scorpion burrows in leached soils in the Judean Desert, Israel. *Israel Journal of Plant Science* 42: 37-40.

De Graaff, G. (1981) The Rodents of Southern Africa. Butterworths, Durban and Pretoria.

Dean, W.R.J. and Milton, S.J. (1991) Patch disturbances in arid grassy dunes: antelope, rodents and annual plants. *Journal of Arid Environments* 20: 231-237.

Dean, W.R.J. and Yeaton, R.I. (1993) The effects of harvester ant *Messor capensis* nest mounds on the physical and chemical properties of soils in the southern Karoo, South Africa. *Journal of Arid Environments* 25: 249-260.

Dixon, J.M. and Hambler, D.J. (1993) Wildlife and reclamation ecology: rabbit middens on seeded limestone quarry-spoil. *Environmental Conservation* 20: 65-73.

Eldridge, D.J. and Greene, R.S.B. (1994) Microbiotic soil crusts: A review of their roles in soil and ecological processes in the rangelands of Australia. *Australian Journal of Soil Research* 32: 389-415.

Gallardo, A. and Schlesinger, W.H. (1995) Factors determining soil microbial biomass and nutrient immobilisation in desert soils. *Biogeochemistry* 28(1): 55-68

Garcia-Moya, E. and McKell, C.M. (1970) Contribution of shrubs to the nitrogen economy of a desert-wash plant community. *Ecology* 51: 81-88.

Gutierrez, J.R.; Meserve, P.L.; Contreras, L.C.; Vasques, H. and Jaksic, F.M. (1993) Spacial distribution of soil nutrients and ephemeral plants underneath and outside the canopy of *Porlieria chilensis* shrubs (Zygophyllaceae) in arid coastal Chile. *Oecologia* 95: 347-352

Gutterman, Y., Golan, T. and Garsani, M. (1990) Porcupine diggings as a unique ecological system in a desert environment. *Oecologia* 85: 122-127.

Hobbs, R.J. and Mooney, H.A. (1985) Community and population dynamics of serpentine grassland annuals in relation to gopher disturbance. *Oecologia (Berlin)* 67: 342-351.

Hobbs, R.J. and Mooney, H.A. (1995) Spatial and temporal variability in California annual grassland: results from a long-term study. *Journal of Vegetation Science* 6: 43-56

Kalisz, P.J. and Stone, E.L. (1984) Soil mixing by scarabid beetles and pocket gophers in north-central Florida. *Soil Science Society of America Journal* 48: 169-172.

le Roux, A. and Odendaal, F.J. (unpublished) Report on the study of natural recovery of overburden dumps on DBCM properties in Namaqualand. Unpublished Report. Geology Department, De Beers Namaqualand Mines, Kleinzee.

Lindsay, W.L. (1979) Chemical Equilibria in Soils. John Wiley and Sons, New York.

MacMahon, J.A. and Warner, N. (1984) Dispersal of mycorrhizal fungi: processes and agents. In: Williams, S and Allen, M (eds.) VA Mycorrhizae Reclamation of Arid and Semiarid Lands. University of Wyoming, Agricultural Experimental Station, Laramie.

Moore, J.M. and Picker, M.D. (1991) Heuweltjies (earth mounds) in the Clansilliam district, Cape Province, South Africa: 4000-year-old termite nests. *Oecologia* 86: 424-432.

Nedler, A. and Steinberger, Y. (1993) Trends in structure, plant growth, micro-organism interrelations in the soil. *Soil Science* 155(2): 114-122.

Ross, S. (1989) Soil Processes: A Systematic Approach. Routeledge, London.

Rowell, D.L. (1994) Soil Science: Methods and Applications. Longman scientific and Technical. Harlow, Essex.

Salick, J.; Herrera, R. and Jordan, C.F. (1983) Termitaria: Nutrient patchiness in nutrient-deficient rain forests. *Biotropica* 15(1): 1-7.

Scott, D.F. and Johnson, M.A. (1995) Soil leaching trails on overburden soil from Kleinzee and Koingnaas. Report number FOR-C 283. The Division Forest Science and Technology, Pretoria

Scott, D.F.; Du Toit, B.; Johnston, M.A. and Burns, M.E.R. (1994) The effects of mining on soil properties and the ability of the soil to support vegetation after mining at Kleinzee and Koingnaas, on the west coast of South Africa. Project No. FL 719, Report No. FOR C-, Division of Forest Science and Technology, Pretoria.

Shachak, M.; Brand, S. and Gutterman, Y. (1991) Porcupine disturbances and vegetation pattern along a resource gradient in a desert. *Oecologia* 88: 141-147.

Spencer, S.R.; Cameron, G.N.; Eshelman, B.D.; Cooper, L.C. and Williams, L.R. (1985) Influence of pocket gopher mounds on a Texas coastal prairie. *Oecologia (Berlin)* 66: 111-115.

Upton, G.J.T. and Fingleton, B. (1985) Spacial Data Analysis by Example. Point Pattern and Quantitative Data. Vol.1 Wiley Series in Probability and Mathematical Statistics. John Wiley and Sons. Chichester.

Whitford, W.G. (1988) Decomposition and nutrient cycling in disturbed arid ecosystems. In Allen, E.B. (ed.) The Reconstruction of disturbed Arid lands. AAAS Selected Symposium 109. Westview Press, Boulder.

Yeaton, R.I. and Esler. K.J. (1990) The dynamics of a succulent karoo vegetation. *Vegetatio* 88: 103-113

Appendix I Plant species encountered in rodent plots.

	SITE 1			SITE 2			SITE 3				
Plot Number:	1	2	3	4	5	6	7	8	9		
Plant Species										**Occurrences**	
Mesembryanthemaceae											
Psilocaulon subnudosum	2		1		2				2	7	
Stoeberia beetzii				2					1	3	
Ruschia cyathiformis							2	4		6	
Phyllobolus scintilans						1				1	
Drosanthemum ramosissimum					1					1	
Aizoaceae											
Galenia crystallina									1	1	
Hypertelis salsoloides				1	1					2	
Tetragonia fruiticosa					1					1	
Other families											
Othonna sedifolia							1			1	
Zygophyllum clavatum	1									1	
Zygophyllum cordifolium		3					1			4	
Euphorbia mauritanica						2				2	
Lycium cinereum			1		1	2				4	
Cladoraphis cyperoides						2				2	
Ornithogaulum sp.					1					1	
Lebeckia multiflora				2						2	
Pteronia glabrata	1		1							2	
Salsola zeyheri		1								1	
Total number of plants										Average	STD
Alive	4	4	3	5	7	7	4	4	4	4.67	1.41
Dead	0	5	2	1	3	2	6	8	0	3	2.78
Total alive and dead	**4**	**9**	**5**	**6**	**10**	**9**	**10**	**12**	**4**	**7.67**	**2.96**

Appendix II Raw data for soil samples analysed.

Site	pH (H2O)	EC	Microbe	Soil Colour	Exudate Colour	Plant Species
C 1.1	7.9	20.00	0.743	dull orange	clear	
C 2.1	7.6	11.30	0.329	dull yellow orange	white	
C 3.1	7.7	22.90	0.555	dull orange	clear	
C 1.2	7.7	32.60	0.355	orange	white	
C 2.2	7.6	11.30	0.754	dull orange	white	
C 3.2	7.7	29.18	0.628	dull orange	yellow	
N 1	8.0	1.15	1.063	bright brown	brown	
N 2	7.8	1.64	2.565	bright brown	brown	
N 3	7.8	0.77	2.362	bright brown	yellow	
N 4	8.0	3.40	1.920	bright brown	yellow	
N 5	7.9	4.16	1.734	bright brown	yellow	
N 6	7.4	1.48	1.755	bright brown	yellow	
UM 1.1	8.6	1.20	0.894	bright brown	brown	
UM 2.1	10.0	14.40	3.574	orange	black	
UM 3.1	7.7	5.09	0.775	bright brown	brown	
UM 1.2	8.0	4.64	1.806	orange	yellow	
UM 2.2	9.8	10.54	4.022	orange	black	
UM 3.2	8.5	17.30	2.174	bright brown	brown	
UP 1.1	9.6	3.66	4.453	orange	yellow	*Psilocaulon subnudosum*
UP 2.1	8.1	0.88	3.870	orange	brown	*Lebeckia multiflora*
UP 3.1	9.3	2.3.00	2.263	bright brown	black	*Psilocaulon subnudosum*
UP 3.2	8.4	1.33.00	4.265	orange	brown	*Stoeberia beetzii*
UP 1.2	10.0	18.11	4.939	bright brown	black	*Psilocaulon subnudosum*
UP 2.2	10.2	23.40	5.087	dull yellow orange	brown	*Salsola zeyheri*

Abbreviations used:
C: control soils
N: normal soils
UM: uncolonised mound soils
UP: under plant soils
Microbe: Microbial activity expressed in g $CO_2.g^{-1}$ dry weight $soil.s^{-1} \times 10^{-9}$
EC: Electrical conductivity expressed in $mS.m^{-1}$

Appendix III Explanation of the soil bio-geochemical processes that occur as a result of increased soil carbon dioxide concentration due to increased soil microbial respiration.

Below pH 8.0 soil exchangeable Ca^{2+} ion species and calcite ($CaCO_3$) are in equilibrium and CO_3^{2-} is inactive. At pH above pH 8.0, CO_3^{2-} becomes highly reactive resulting in the formation of metal carbonates imposing limits on the solubilities of metal ions (Lindsay 1979). Among these metal carbonates is calcite (equations 1 and 2). In alkaline soils the partial pressure of CO_2 gas is the controlling variable for calcite solubility (Lindsay 1979). An increase in CO_2 results in a decrease in calcite solubility as equation 1 moves to the left.

$$CaCO_3 \text{ (calcite)} + 2H^+ \leftrightarrow Ca^{2+} + CO_2(g) + 2H_2O \quad \text{(equation 1)}$$

$$CO_2(g) + H_2O \leftrightarrow CO_3^{2-} \quad \text{(equation 2)}$$

In addition to the formation of calcite due to an increase in CO_2 concentration, calcite can also be formed by the addition of urea in the form of rodent excretions (Ross 1989):

$$CO(NH_2)_2 \text{ (urea)} + 3H_2O \leftrightarrow (NH_4)_2CO_3 \text{ (ammonium carbonate)} + H_2O \quad \text{(equation 3)}$$

Ammonium carbonate then dissociates in water:

$$(NH_4)_2CO_3 + H_2O \leftrightarrow 2NH_4^+ + HCO_3^- + OH^- \leftrightarrow 2NH_3 + CO_2 + 2H_2O \quad \text{(equation 4)}$$

In equation 4 ammonia is volatalised and lost to the atmosphere in a gaseous state. In equation 4, HCO_3^- and CO_2 will react with calcium ions to form calcite.

Chapter 6 An Ancient Arid Landscape: The Restoration Potential of Namaqualand Sandveld Disturbed by Open-Cast Diamond Mining on the West Coast of South Africa.

1 Introduction.

In recent years, the process of post-mining landscape revegetation in South Africa has been dominated by the "success" of coastal dune forest restoration by Richards Bay Minerals after heavy mineral mining, on the north coast of Kwazulu-Natal (van Aarde 1995, van Aarde *et al* 1996). It is commendable that both ecologists and industry could work together to achieve this success. However, dune revegetation in the humid and subtropical environment of the Kwazulu-Natal coast departs dramatically from the success, or lack there of, of dune restoration on the west coast of South Africa.

This chapter will focus on some aspects of the restoration potential of Namaqualand Sandveld vegetation. Embarking on a restoration program of the destruction wrought by the diamond mining industry in Namaqualand at this stage, is for all intents and purposes, an academic venture. Experience of the attempts made at the restoration of disturbed areas on the Namaqualand coast led to the stage where "sitting down" and deriving a framework for the restoration of the natural vegetation, within currently accepted philosophies of restoration practice and our knowledge of the natural vegetation, has become a necessity. It is hoped that this chapter, together with the knowledge of the natural environment gained from this thesis, will provide a philosophical framework for a concerted and directed programme of restoration and rehabilitation research and practice, on the part of the mines concerned, of the damage caused by diamond mining activities.

This chapter aims to provide a working framework or philosophy, and a set of goals which both researches and mine management can strive for in their attempts to mitigate the damage done in the mining process. A brief introduction to the process of ecological restoration is presented and discussed. The major types of destruction involved in the mining process and the problems involved with the mitigation of this destruction are outlined, to provide an idea of the scale and nature of the problems at hand. The focus will concentrate on the problems faced by any restoration attempt in terms of changes in the soil physical, chemical and biological environment, and also the constraints imposed by the natural abiotic environment of the west coast. The development of our understanding of the natural system, the restoration process and the problems faced, are all developed within the framework that the west coast of southern Africa or the Namib Desert is the oldest arid landscape in the world (Ward *et al* 1983). The full development of the current arid climate in the Miocene has dominated local geological and pedological processes since then. Mining activities on the west coast create problems in the abiotic environment that are in essence a consequence of this ancient arid landscape and which dune restoration in Kwazulu-Natal or other much younger Holocene arid dune environments do not have to contend with.

2 What is ecological restoration.

2.1 A definition.

Ecological restoration is the process of repairing damage caused by humans to the diversity and dynamics of indigenous ecosystems (Jackson *et al* 1995). Current approaches to ecosystem rehabilitation are extensions of traditional agronomic technologies developed under more hospitable environments (Whisenant 1995). Ecological restoration is an alternative that attempts to minimise management intervention (and expense) by stimulating natural successional processes to develop stable and functional ecosystems.

Related to the term ecological restoration are the activities of reclamation, rehabilitation, creation and mitigation (Jackson *et al* 1995). **Reclamation** is defined as resulting in a stable, self-sustaining ecosystem that may or may not include some exotic species and that includes a similar but not identical structure and functioning as the original land. Typically, this terms refers to the most severely degraded sites, such as open-cast mining. **Rehabilitation** is making land useful again after disturbance, such as creating a pasture where there was one a forest. It is a broad term that may refer to any attempt to restore elements of structure or function to an ecological system, without necessarily attempting complete restoration to any specified prior condition (MacMahon and Jordan 1994). Both of these terms are associated with mining activities and refer more to the goals and immediate outcome of the activity rather than the type of disturbance (Jackson *et al* 1995). **Creation** or **re-creation** involves activities that produce a persistent ecosystem, but undertaken in an area that did not previously support the created ecosystem (essentially rehabilitation). **Mitigation** refers to activities that lessen the degree of damage to an ecosystem and can include any of the above activities. Another important term or concept is that of **ecological recovery**. This involves leaving a system alone, generally in the expectation that it will regain desirable attributes through natural succession (MacMahon and Jordan 1994). This zero-order approach to restoration may or may not work. It is a key component of any restoration action - the contribution of the system itself. Where this approach is taken, restoration seeks to compliment and reinforce natural processes.

At a global or even regional scale, every restoration project is unique. All should include the following four elements: (1) judgement of need; (2) an ecological approach; (3) setting goals and evaluating success; and (4) limitations of ecological restoration. These are discussed in more detail below.

2.2 Judgement of need.

The process of ecological restoration begins with a judgement that an ecosystem is damaged by humans to the point that it will not regain its former characteristic properties in the near term (two generations, or 50 years set by the society for ecological restoration) (Jackson *et al* 1995), and that continued degradation may occur. Judgement depends very much on our perceptions of what a natural system is and what restoration attempts should be striving for. The generally accepted view is that nature is in constant flux and that what we see in the landscape today represents the transient product of a unique sequence of past climate changes and biotic invasions (Jackson *et al* 1995). Natural systems are characterised as open, strongly influenced by process outside of their boundaries, capable of reaching several temporary equilibria via a variety of successional pathways, and subject to continual disturbance (E. Allen 1988).

Humans are seen as a part of nature and our activities are yet another source of disturbance. This viewpoint provides a challenge to the restoration ecologists as there may exist many different ultimate ecological states reached via a number of different pathways. This might prompt people to suggest that restoration is never required if disturbance and invasions are considered natural, since human activity can disrupt the flux of nature itself (Jackson *et al* 1995). The potential for continued evolution of species, the persistence of species, and the complexity and flexibility of their interactions, is diminished. Most importantly, however, potential ecosystem services beneficial to humans are lost. Human destruction interferes with both natural processes as well as the ecosystem functionality, turning a renewable exploitable resource into a liability.

2.3 An ecological approach.

Ecological restoration implies that we wish to restore organisms and their interactions with one another and the physical environment. It concentrates on processes such as persistence of species through natural recruitment and survival; functioning food-webs; system-wide nutrient conservation via relationships among plants, animals, and the detritivore community; integrity of watersheds; and abiotic processes that shape the community such as periodic floods or fires. By working with the full diversity and dynamics of ecosystems, we can restore sustainable relationships between nature and culture (Jackson *et al* 1995). Restoration that initiates autogenic succession by using, rather than combating natural processes, is most appropriate for extensively managed areas (Whisenant 1995).

Agricultural or engineering based approaches to restoration, where species are replaced in the absence of an understanding of the processes and interactions that govern and maintain sustainable natural systems, will meet with little success. Ecologically restored areas, by contrast, should support healthy populations indefinitely, with minimum intervention. In practice, however, some processes must be maintained artificially, such as prescribed burning. Many seemingly natural systems have evolved and are maintained through the intervention of human activities. As humans are seen as part of nature, these “interventions” form an integral and necessary part of ecosystem dynamics, and if deemed the case, should form part of the ecological restoration process.

Practical ecological restoration can take one of two approaches, or both. There is the intensive approach where ecosystem elements are replaced immediately after disturbance to resemble the original system. This is a capital intensive approach suitable for small, high priority areas.

Implicit in this approach is that one's understanding of ecosystem structure and functioning is sufficiently advanced to allow the construction of functioning system from the start. The alternative or low intensity approach is to manipulate ecosystem processes which would ultimately result in a similar goal being reached, but over a longer period of time. This approach is more suited to large areas and relies very much on the concept of ecological succession, thus combining restoration with ecological recovery.

2.4 Setting goals and evaluating success.

Ecological restoration is a deliberate intervention that requires carefully set goals and objective evaluation of the success of restoration activities. Well-defined and attainable goals should provide the backdrop to the development of any restoration exercise (Holloway 1994). Goals and objectives provide benchmarks for later evaluation of a restoration project. Just as important, they should serve as the focal point for a broad-ranging discussion of the biological and ethical merits of the project.

A definition of what ecological restoration is trying to achieve is of value in setting goals. A natural landscape matrix comprises two broad components - structure and function. The distribution, not the movement, of energy, materials, kinds, and configuration of landscape elements makes up the structure of that landscape. Landscape function, or dynamics, is the interaction among the landscape elements that involves the flow of energy, materials, water, and species among the elements (Whisenant 1995). In order to evaluate a project objectively, specific criteria for success relating to the target landscapes' structure and function should be established, and should reflect the ecological approach described above. Such criteria might include the presence, cover and distribution of a plant species; the ability of the vegetation to respond to normal disturbance regimes and climatic fluctuations; use by particular animal species; soil condition and colonisation by particular invertebrates, fungi, and bacteria; characteristics of nutrient cycling; and the hydrological regime. These criteria should be used to assess both the progress and the process of restoration and, if necessary, to adjust strategy and carry out additional work to achieve the project's ultimate goals.

The society for restoration ecology have suggested that success should be demonstrable within 10-50 years (Jackson *et al* 1995). If restoration will result in a healthy ecosystem in 50 years or less, the evidence for this should be visible in 1-10 years (e.g. Mentis and Ellery 1994, van Aarde *et al* 1996). The use of this time framework is advantageous because it falls within one human lifetime, making it possible to hold those who inflicted the damage accountable for repairing it successfully. Tied to this is the nature in which restoration work is applied. It is imperative that the applied aspects be conducted within an experimental framework such that progress can be monitored in a scientific manner and that information can be extracted for application elsewhere (Holloway 1994).

2.5 Limitations of ecological restoration.

Ecological restoration is not always possible. It depends on four interrelated social and biological conditions (Jackson *et al* 1995): (1) how nature is valued by society; (2) the extent of social commitment to ecological restoration; (3) the ecological circumstances under which restoration is attempted; and (4) the quality of restoration ecologists' judgement about how to accomplish restoration. Without optimum conditions in all four areas, complete ecological restoration is not possible. On the ground, restoration is influenced by factors relating to the physical (climate, soil, physiography and disturbance) and biological (plants, animals and micro-organisms) conditions of a site (DePuit and Redente 1988). These impose practical limitations on the extent of restoration. Understanding how the components interact and affect one another, is central to the application of ecological restoration.

Complete ecological restoration is possible only where damage is reversible. Naturalisation of exotic species, climate change, soil loss, habitat fragmentation, depletion of fossil water supplies and other permanent hydrological modification, and species extinctions are examples. It is essential that restoration ecologists try to prevent irreversible damage as a primary goal and that the practice of ecological restoration is not a panacea or an antidote for short-term war on nature. The promise of restoration must not be viewed as fuel for destruction (Holloway 1994, van Aarde *et al* 1996). Often, "irreversible damage" is a matter of degree rather than kind, and with sufficient social commitment (and money) and farsightedness to a project, in terms of the effort it will take to put back what was undone, ecological restoration is possible. Society should be made aware, however, of the tremendous costs of such repair, and the inherent risk that such damage could turn out to be irreversible. Ecological restoration is also only possible once ecologists have a mechanistic understanding of the factors that influence the development and persistence of plant communities so that one is able to determine the potential and methodologies for establishing biologically diverse communities (Call and Roundy 1991). Natural, functional systems have an inherent value to humans. This value can be expressed in monetary terms by the cost involved in restoring the functionality of a damaged system. In most cases this cost would be very high.

3 Diamond mining on the west coast of South Africa - The case of Alexcor Ltd.

The impacts of diamond mining activities on the terrestrial, aquatic and marine environments of the west coast of South Africa are numerous. Discussion here will be limited to those mining activities that directly influence the terrestrial environment and which are the most extensive. Degradation caused as a result of human habitation associated with the mining industry, or the significant impacts that mining has on the marine, aquatic, estuarine or riparian habitats of the region, will not be discussed.

Alexcor Ltd. mine the coastal area below the 100 m contour between Oubeep, south-east of Port Nolloth, and Alexander Bay on the west coast of south Africa, an area of approximately 64 570 ha (Burns 1994). Terrestrial mining operations occur within 14 demarcated mining areas which supply diamoniferous gravel to seven processing plants and a final recovery plant (Burns 1994). Diamoniferous marine gravels associated with four palaeo-marine terraces are mined using open-cast mining techniques. In addition to mining blocks, numerous prospecting trenches, perpendicular to the coast, traverse the entire mining area (Fig. 6.1). The mining process involves the removal of overburden to expose the buried marine gravels by means of bowel-scrapers assisted by bull-dozers. In mining blocks, the overburden is removed in 50 to 100m wide sections spanning the marine terrace where the overburden from one section is used to infill the exposed bedrock in previously mined section. Prospecting trenches are typically a few hundred meters long and up to 20m wide and are used to expose a 1 m wide transect across the marine terrace which is then sampled for analysis (Figs 6.1 AND 6.2).

The thickness of the overburden varies between 0.5 and 20 m. It is typically composed of up to 1 m of loose surficial sand dunes; various layers of hard replacement products such as calcrete, dorbank and silcrete; and occasionally consolidated non-diamoniferous marine gravels (Fig. 6.2). Overburden is stockpiled in dumps *in situ*. In the case of mining blocks, this overburden is either replaced as the mining block progresses or is left. With the prospecting trenches, however, these dumps are left in the landscape unless the area is designated as a mining block in which case the overburden may be used as infill at a later stage (Fig. 6.1). In all cases, the top-soil is invariably buried under the lower strata of overburden. Thus, the layer of overburden lying closest to the diamoniferous layer is ultimately the last layer deposited on the surface of dumps. The primary and most widespread impact of diamond mining operations is this inversion of the soil profile to bedrock and the loss of top-soil.

The opening up or exposing of the soil surface results in significant secondary degradation to the natural environment. As all prospecting trenches are arranged perpendicular to the coast or the buried marine terraces, they lie perpendicular to the dominant wind direction. Thus, the exposed leeward side walls of the trenches and mining blocks are scoured out by the wind resulting in the formation of sand plumes, of often toxic subsoil, moving through the landscape. This has a serious multiplicatory effect on the impact of mining. Plume formation is not limited to mined areas. Sea water is employed in the processing of the diamoniferous gravels. The silt and clay held in suspension in the processing water is deposited in slimes dams near each of the seven processing plants. All of these slimes dams are the origin of wind generated, saline (EC >10 $ms.m^{-1}$), silt plumes. Similarity, sea water is sprayed onto the main roads that run through the mine to maintain their surfaces. This creates a wide saline phyto-toxic strip through the landscape which forms another origin for sand plume development.

Figure 6.1 (overleaf) An aerial view of prospecting trenches, overburden dumps and sand plumes developing down-wind of the exposed surfaces in the diamond mining area, to the north of Port Nolloth.

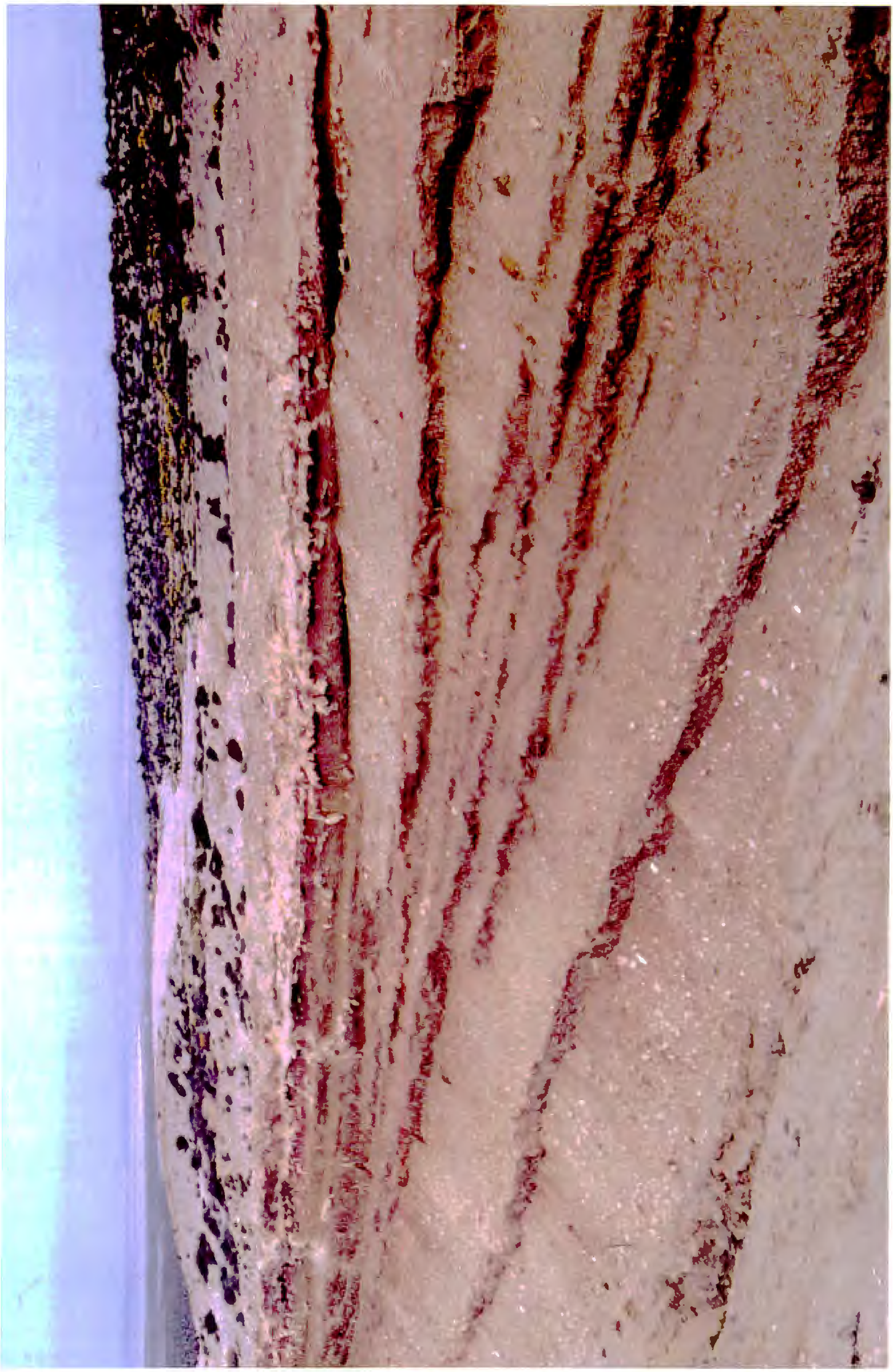

Figure 6.2 (previous page) A closer view of a newly excavated prospecting trench. The oil barrel in front of the small overburden dump and the pole in the of the trench (*ca.* 1 m, bottom left-hand corner of photograph), give an indication as to the depth of the trench. Note the cross-bedding of palaeo-dune series below the surficial calcrete layer and the consolidated marine gravels exposed at the bottom of the trench (see Chapter 2).

The extent of this degradation is significant. At present approximately 2400 ha (3.69% of the mines area) has been mined for diamonds since the proclamation of the mine in 1928 (Burns 1994). This figure does not include areas covered by overburden dumps, processing plants and slimes dams or any of the other artefacts of mine infrastructure in the landscape, nor does it cover secondary degradation effects such as plumes. A more realistic estimate of the extent of degradation would probably be in the order of 2 to 3 times this area (7.38-11.07%). It is difficult to relate the volume of earth moved in the mining process. Figures on annual or total carat production are not available in Burns (1994) nor are figures on the volume of overburden removed available. One could estimate the total volume of overburden removed by assuming an average excavation depth of 10 m (range 0.5 to 20 m, Table 6.1).

Table 6.1 An estimate of the volume of overburden moved by diamond mining activities in the Alexkor Ltd area prior to 1994 assuming an average excavation depth of 10 m (data from Burns 1994).

Area mined by end 1993	2 386 ha.
Average amount of overburden and ore removed per ha.	100 000 m^3
Estimated volume of overburden moved to date	**238 600 000 m^3**

This is a rough estimate of volume of earth moved. Most of this overburden is still lying in some form or another somewhere in the landscape. It is a tall order for the restoration ecologist to contemplate.

4 The problem.

The most important component in the restoration of degraded land is the biologically active surface layers - the soil (Bradshaw and Chadwick 1980). This provides the rooting medium for plants and the source of almost all the nutrients they require. As vegetation develops over periods, often of many hundreds of years, the soil structure and fertility build-up. Organic matter from the plant roots and surface debris is incorporated into the soil, along with animal remains. With time, a complex, stable and fertile soil system, with a well developed structure, is built up. It is this biologically active system that is so easily destroyed or degraded when mining activities produce degraded land. At the heart of the diamond mining restoration problem, is the inversion of the soil profile and the sterile land surfaces this creates.

To begin with, let us consider the geological history of the west coast (this topic is discussed more fully in Chapter 2). It is hypothesised that since the breakaway of South America from the African continent, the west coast of southern Africa has experienced an uninterrupted arid to semi-arid climate (Ward *et al* 1983), a feature shared with much of Australia (Taylor 1983). The dunes covering the coastal plain of Namaqualand have been accumulating for a somewhat shorter period in geological terms, at least since the beginning of the quaternary (Partridge and Maud 1987). As the mining activities only directly affects the coastal vegetation below approximately the 100 m contour our geological scenarios will be restricted to these more "recent" dune series.

The oldest of the marine terraces mined dates to the Early Pliocene (*circa* 7 Myr. BP). Although present day surficial dunes covering the oldest marine terrace are aeolian deposits of a much more recent origin (e.g. Pleistocene), a distinction can be made between these older dunes series, characterised by brown to orange-brown sands, and more recent Holocene dunes series, characterised by a white or beige-grey sands, nearer the coast. Diamond mining activities are concerned with locating and uncovering the wave-cut platforms or terraces of palaeo-strandlines buried beneath the dunes. There are four. There were more, but the very oldest were eroded by fluvial processes and others lie on the floor of the ocean, submerged relics of a lower Quaternary ocean level. Since the creation of these terraces and the later recession of the ocean, the exposed marine gravels were covered by marine sands, originally of terrestrial origin, washed down rivers into the sea, deposited on the receding strand-lines or estuaries and blown onshore by the dominating southerly winds. This process is still in action today. These accumulated sands form the overburden and range from 0.5 m near the coast, to 20 m in thickness over the older marine terraces (Burns 1994)

Once sand becomes stabilised, the processes of pedogenesis begin (Tinley 1985). Soluble components are leached or eluviated out of the surface sand profile, predominately calcium and silica. Added to these are aerosol inputs to the sand, namely salt spray from the ocean and clay in the form of dust blown from the interior during "berg winds". Thus the sub-soil profiles contain concentrated amounts of these materials, toxic to plants in their concentration, but locked away from their roots by the impervious dorbank and calcrete layers developing immediately beneath the most recent surface sand deposits. The present open-cast mining process inverts up to several million years of eluviation. Extreme subsoil physical and chemical conditions are characteristic of the overburden over older marine terraces. Recent Holocene dunes are more active, unconsolidated substrates and the toxicity of the overburden is much less.

A gradient of overburden toxicity or severity of the environmental problems facing restoration, exists from the coast inland. As one moves further inland so the depth of overburden that has experienced pedogenesis increases. Thus, near-shore dunes pose very few problems for rehabilitation as pedogenesis is still in a juvenile stage. Here overburden is soon (<10 years) covered by the still active sand of the near-shore environment or is sufficiently low in toxic elements to allow vegetation to recover naturally. With the increase in the depth of overburden as one moves away from the coast, so the natural recovery rate of vegetation on the mined areas becomes very slow, or is absent entirely absent. The lower aeolian movement of sand as one moves away from the coast combined with the low rainfall also means that scars created in the landscape remain fairly intact.

The extreme physical and chemical conditions created on overburden dumps have been investigated by Scott *et al* (1994). Overburden dump soils can be characterised as saline-sodic substrates. It is not so much that the salt is a problem nor the a micro-nutrient deficiency associated with the high pH values (>8, this is much the same as natural soils), viz. the chemical problems, as much as the physical problems that arise from the high exchangeable sodium content of the subsoil. On wetting, these soils are prone to dispersion and are easily eroded and on drying the surface is cemented into an impenetrable crust (Scott *et al* 1994).

The problems created as a direct result of human activities have been discussed, but what are the limitations imposed by the natural environment on the process of restoration?

Port Nolloth receives 67 mm rainfall annually and Alexander Bay 49 mm. Alternative sources of moisture are available in the form of frequent fog and heavy dew (see Chapter 2). The natural vegetation of the area is adapted to low rainfall and in theory this should not pose a problem to revegetation. The problem with dumps is that to improve the substrate for plant growth one requires rain (or another water source) to leach out the sodium from the surface soil in order to improve its physical properties. This will not be a rapid process under the current rainfall regime. The low electrolyte content of rain water causes massive defloculation of soil aggregates (Scott *et al* 1994). Consequently, these sodic soils are unstable, eroding habitats when wet, and hard, cemented surfaces when dry. These conditions are not conducive to plant establishment or growth. Low rainfall circumvents the problem of massive erosion associated with sodic soils. The indigenous flora of the coastal belt is adapted to the low rainfall, but not the erosion.

Wind has shaped the sandveld for millennia (see Chapter 2). Alexander Bay holds the reputation of being the windiest town in South Africa (Schultze 1965). Wind will remove anything that is not well cemented to the ground or sheltered from it. Natural vegetation cover is high enough to protect the sandy soil surface from wind erosion. Removal of the vegetation by mining exposes vast areas of soil to the erosive force of wind (see section on sand movement in Chapter 2). Damage due to mining tends to have a multiplicatory effect as exposed surfaces of especially toxic soils expand due to wind action.

The process of restoring functional plant communities on overburden dumps is faced with the creation of extremely inhospitable soil substrates in an arid environment dominated by high energy winds. What are the options for restoring this system?

5 Present approaches to and assessment of restoration.

le Roux and Odendaal (unpubl.) Have produced the only report on the natural recovery of vegetation on overburden dumps on the west coast south of the orange river. Success of natural recovery is related to, amongst others, depth of overburden. This emphasises the observed gradient of phyto-toxicity from the coast inland discussed earlier in the chapter. Related to this are the problems associated with these soils - pH, conductivity and sodicity. Also, dump architecture is significant as steeper slopes are more conducive to erosion and higher dumps more exposed to the wind.

Present recommendations for rehabilitation include:

1. **Conservation of topsoil**. The removal, storage or immediate use of topsoil to cover exposed overburden. Where this has been experimented with in the past there is near complete recovery of the natural vegetation. This simple step would make a major difference to the entire rehabilitation process.
2. **Dump architecture**. Limit the height and slope of overburden dumps. le Roux and Odendaal (unpubl.) Found that flatter slopes and lower dumps had improved natural recovery.
3. **Dump surface topography**. Furrows, plant canopies, rocks, old bulldozers, oil drums serve to break wind action leading to the deposition of sand, seed and organic matter. The significance of this is discussed below.

In addition to these changes in the physical structure of the overburden dumps, some measures for chemical amelioration have been proposed. Leaching trails conducted on overburden soils from Kleinzee and Koingnaas (Scott and Johnson 1995) demonstrate that marked improvements in the physical properties of soils can be achieved through the irrigation, with high electrolyte content water, of overburden dumps followed up with an application of gypsum to prevent later crusting. The high electrolyte water (brack ground water mixed with fresh water) as opposed to rain or fresh water is used to prevent the sodium from coming into solution, thus preventing dispersion of the soil aggregates during the leaching process. This would make the dump environment more favourable for plant growth and should be considered as part of a more comprehensive restoration program. In an environment where fresh water is a rare and expensive commodity, leaching would only be suitable for very high priority areas and would be costly.

Another widely applied and effective method of ameliorating the dispersive nature of sodic soils has been through organic matter amendments (Jayawardane and Chan 1994). The use of municipal wastes, straw and other rapidly decomposing organic amendments provide effective, but temporary relief from the problem (Lax *et al* 1994). The use of recalcitrant[7] organic amendments such as wood and bark chips provides a more long-term solution, as well as providing a substrate for soil biota development (Whitford 1988, Whitford *et al* 1989). In addition to improving soil aggregation, organic amendments contribute to the soil organic matter content, soil water holding capacity and leads to a general improvement in the soil fertility (Lax *et al* 1994, Itami and Kyuma 1995).

6 Ecological restoration.

The natural processes responsible for the origin and maintenance of natural systems needs to be understood as a prerequisite for ecological restoration (Burton *et al* 1988). We have established that the origin of the problem lies in the soil. Over and above the limiting soil physical and chemical properties, there is a severe biological limitation to restoration. The soil on overburden dumps is biologically dead. There are neither soil microbes nor organic matter in the soil for the microbes to live on, and nutrient cycling is non-existent. In arid systems where resources for plant growth are more limiting, a functioning soil microbial community is a critical factor in maintaining a systems "fertility" (Spain and Hutson 1983).

Beyond the edaphic environment, an understanding of successional processes is essential to ecological restoration (E. Allen 1988). Ecological restoration can be viewed as an attempt to hasten the rate of natural succession to produce a plant community that resembles the original plant community in structure and function. Where restoration, or a return to the pre-disturbance ecosystem is the goal, promoting succession may be especially important (E. Allen 1988, van Aarde 1996). The concepts of succession provide the theoretical basis for

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[7] recalcitrant mulch is one that is resistant to biological decomposition such as wood chips, thus it may persist in the soil for a number of years. Mulches, such as straw or leaf matter, are rapidly decomposed and are not considered recalcitrant.

revegetation. The processes of succession determine the rate and nature of initial revegetation and continue to influence plant communities long after treatments have been implemented (Call and Roundy 1991). Linked to our understanding of plant dynamics there must be a more mechanistic understanding of the soil biological processes that initiate and regulate the successional changes.

This returns us to the soil environment and its component biotic elements. Research on the restoration and succession in the arid lands of the united states has demonstrated that soil organisms (e.g. VA mycorrhizae) are pivotal to the rapid development of healthy plant communities (E. Allen 1988). Plant establishment and productivity in arid lands are primarily limited by water availability, nutrients and soil instability, which are in turn regulated by belowground interactions of roots, micro-organisms and soils (M. Allen 1988). Dune systems are prone to becoming dystrophic substrates for plant growth (Tinley 1985). Nutrients recycled from plant organic matter back into the soil solution are easily leached out of the rooting zone. Soil biota are involved in nutrient recycling and sequestration, thus their importance in the maintenance of system productivity assumes a greater role in arid dystrophic systems than in more mesic systems (Spain and Hutson 1983). At the other end of the spectrum, plant specific soil-borne diseases can drive the process of succession by forcing the degeneration of primary colonisers and their consequent replacement by a disease resistant and later-successional species (van der Putten *et al* 1993).

In arid ecosystems, plant succession appears to initiate in patches as "islands of fertility" such as under established shrubs, rather than in large homogeneous units (e.g. agricultural systems) (Call and Roundy 1991, Yeaton and Esler 1990, Milton 1995, see Chapter 5). Understanding the factors that regulate development of these islands may be critical to revegetating disturbed arid lands. Major changes occur in soil and microbial spatial patterning following disturbances. In the case of overburden dumps these are eradicated completely. Following plant establishment, micro-organisms and the processes they regulate, re-establish around the roots and where litter accumulates. The reconstruction of desirable ecosystems depends not only upon the establishment of plants, but on the concentration of initially diffuse nutrients to plant foci through the action of roots, mycorrhizae and abiotic processes such as wind (M. Allen 1988). In the absence of established plants, the problem that faces the restoration efforts of overburden dumps is the artificial recreation of these foci to "kick-start" the process of natural re-colonisation of mine spoils. Abiotic structures in the landscape that promote the concentration of resources (both water and nutrients) will enhance this process (Whisenant 1995).

In the sandveld environment, wind is a dominating abiotic force. In Chapter 4 it was shown that wind is a major determinant of plant community distribution in the sandveld through the many processes it regulates and drives (sand movement - erosion and deposition, particle size sorting). Wind is the major redistributor of plant resources in this dune landscape. The identification and manipulation of vectors controlling flows of limiting resources through the landscape is, in part, the essence of ecological restoration (Whisenant 1995, Whisenant *et al* 1995). Structures that promote the deposition of aeolian load, such as plant canopies or irregular surface macro-relief (e.g. leeward side of overburden dumps) or micro-relief (e.g. rocks, furrows and contours), will focus resources - non-toxic sand, seed, microbial spores, organic matter - and inevitably become the foci of plant re-establishment. In the context of the overburden dump, it is imperative that a technique be developed that contours the dump surface. Deep contours will catch water run-off; focus aeolian load and protect seedlings from the wind. Contours would also prevent the excessive erosion of the sodic soils on the dumps.

Wind is not the only major redistributor of resources in the sandveld. The activities of Brant's Whistling Rat is an interesting biotic vector that has been considered (see Chapter 5). Foraging behaviour off and burrowing activities on overburden dumps focus resources (nutrients, organic matter and micro-organism propagules) in their burrow mounds. These phyto-toxic soils, amended with a mulch of leaf matter, wood chips, rodent faeces and urine, later become the focus of plant establishment on overburden dumps. Their effect on dump soils is discussed in greater detail in the preceding chapter. In the light of this and the discussion on the biological properties of arid soils, placing a coarse wood chip mulch (or recalcitrant mulch) in the contours would further enhance the favourability of sites for plant establishment. This would be another crucial step to the development and sustainability of an active soil biota (Whitford 1988).

Turing our focus to the indigenous flora. Plants indigenous to the sandveld have some important traits that restoration ecologists need to consider: (1) shallow rooting depth; (2)

the ability to trap sand; (3) wind dispersal of seed; and (4) adaptations to many of the constraints imposed by the abiotic environment.

Scott *et al* (1994) noted that plants had very shallow rooting depths (<0.5 m) and my own observations agree with this. Most species appear to be confined to the top 30 cm of the soil profile. Very few species, however, root within the top 10 cm of the natural dune profile. Species such as *Stoeberia beetzii, Psilocaulon subnodosum, Cheirodopsis robusta* and *Zygophyllum cordifolium* have very shallow rooting profiles and have been found growing on overburden dumps (see Chapter 5). Species with shallow rooting profiles will be those species that colonise aeolian deposits or fertile microsites on dumps. Because these plants root so shallow, it should be possible to restore healthy plant communities on dumps even if there is thin layer of top soil (say >20 cm down) spread over the surface. The proximity of the phyto-toxic layer to the surface should not limit the growth of these plants. Other plants that would colonise small aeolian deposits on overburden dumps would be primary colonisers of recently deposited sand such as *Cladoraphis cyperoides*.

Dispersal by wind is another adaptation by plants to the local environment. Provided significant tracts of undamaged natural plant communities remain intact between the mining activities, the availability of seed for re-colonisation of suitable sites on dumps should not be limiting. If there are conditions conducive to plant growth on the dumps then plants will grow there. This has been well documented on overburden dumps (le Roux and Odendaal unpubl.). The natural re-colonisation process is edaphically and not propagule limited. Wind dispersal of seed allows plants to locate and colonise microsites with favourable soil conditions within the phyto-toxic dump landscape. A prerequisite for this is the maintenance of a matrix of undisturbed vegetation between mining activities. This action can be considered as maintaining a viable seed source. Not all species in the landscape disperse their seed via means of wind. Part of a comprehensive restoration program might include the reintroduction of poorly dispersed (e.g. water dispersed seeds) species at a later stage once a stable plant community has been reached.

Annual species are supposedly the first sign of a system in repair or the beginning of plant succession (le Roux and Odendaal unpubl.). On a dystrophic overburden dump surface, annual species may have a negative effect on the long term revegetation of the dump surface. In the light of the discussion on the role of recalcitrant organic matter in a system where resources are limiting, plant species that produce high quality non-woody litter should be discouraged, as resources once concentrated in the leaves are easily blown away by the wind or are rapidly broken down, leading to a shortage of persistent organic matter in the soil for the survival of the soil biota. Plant species that grow slowly, produce poor quality woody organic matter which takes time to decompose, promote the longevity of the soil biota, efficient nutrient cycling and integrity of the soil system (Whisenant 1995). Annual species occurrence on overburden dumps can serve as indicators as to the severity of soil toxicity or disturbance. However, absolute dominance in disturbed sites is indicative of a system in disequilibrium and not a system on the mend.

Past approaches to the restoration of diamond mine disturbance have focused on the physical, chemical or abiotic environment without explicit consideration for the advantages and disadvantages imposed by the natural biotic environment (viz. the engineering or agricultural versus the ecological approach). Amelioration of the soil physical or chemical environment will result in some restoration success, however, by considering ecosystem dynamics and incorporating these into a restoration plan will result in far greater success. Sustainable restoration strategies rely on landscape-level dynamics that contribute to ecosystem maintenance and development. Soil, vegetation and landscape-level strategies must be fully integrated and developed to maximise beneficial interactions (Fig. 6.3) (Whisenant 1995).

Figure 6.3 (overleaf) A flow-chart outlining an approach to ecological restoration adapted from Whisenant (1995), and placed in the context of diamond mining operations on the west coast. The text in the flow chart is linked to key questions in Table 6.2 that should be considered at the relevant stages during the restoration process. This protocol incorporates the ideas and philosophies discussed in this chapter, and maps out an integrated and sustainable way forward for the implementation of a successful restoration program.

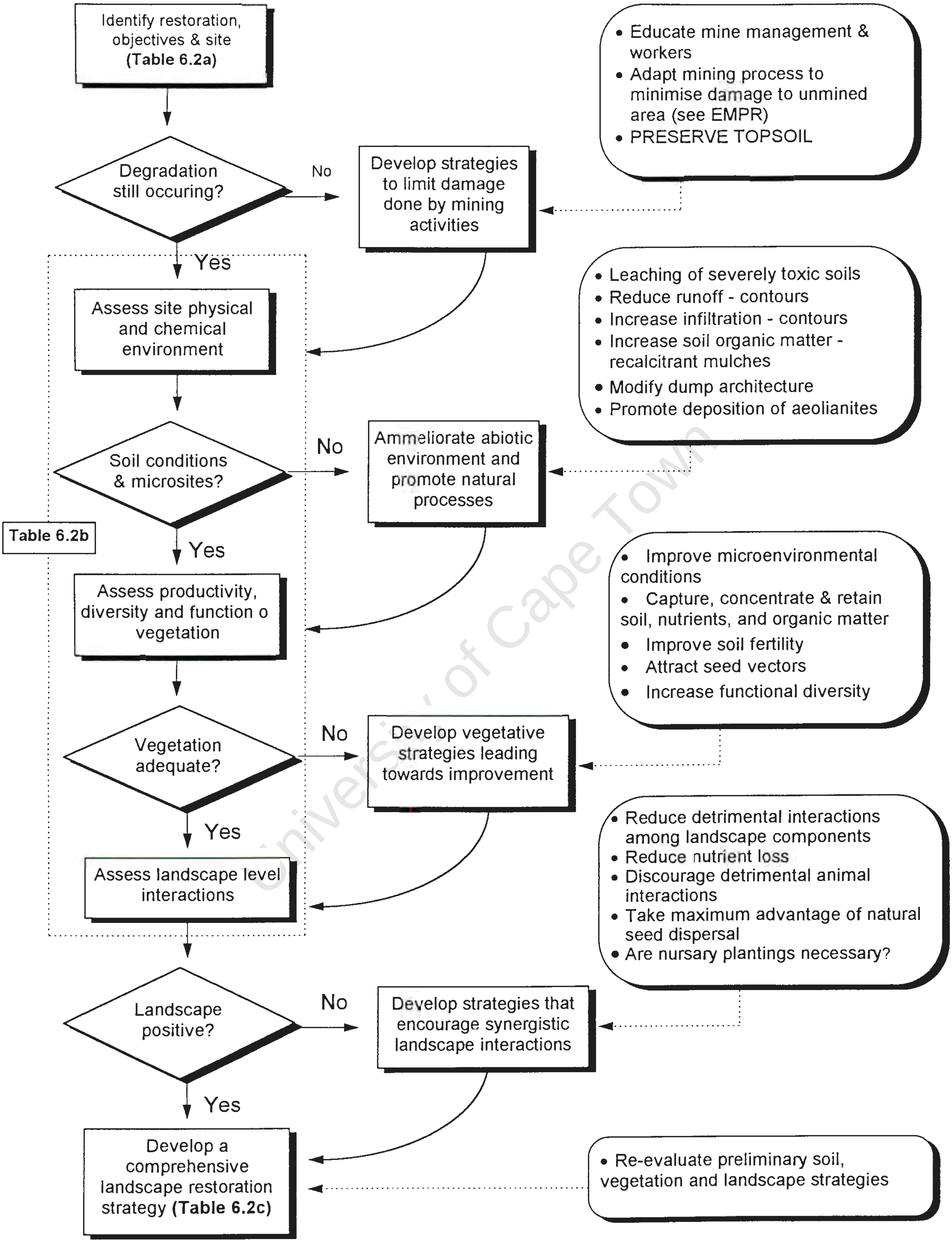
Identify restoration, objectives & site (Table 6.2a)
Degradation still occuring?
No
Develop strategies to limit damage done by mining activities
• Educate mine management & workers
• Adapt mining process to minimise damage to unmined area (see EMPR)
• PRESERVE TOPSOIL
Yes
Table 6.2b
Assess site physical and chemical environment
Soil conditions & microsites?
No
Ammeliorate abiotic environment and promote natural processes
• Leaching of severely toxic soils
• Reduce runoff - contours
• Increase infiltration - contours
• Increase soil organic matter - recalcitrant mulches
• Modify dump architecture
• Promote deposition of aeolianites
Yes
Assess productivity, diversity and function o vegetation
Vegetation adequate?
No
Develop vegetative strategies leading towards improvement
• Improve microenvironmental conditions
• Capture, concentrate & retain soil, nutrients, and organic matter
• Improve soil fertility
• Attract seed vectors
• Increase functional diversity
Yes
Assess landscape level interactions
Landscape positive?
No
Develop strategies that encourage synergistic landscape interactions
• Reduce detrimental interactions among landscape components
• Reduce nutrient loss
• Discourage detrimental animal interactions
• Take maximum advantage of natural seed dispersal
• Are nursary plantings necessary?
Yes
Develop a comprehensive landscape restoration strategy (Table 6.2c)
• Re-evaluate preliminary soil, vegetation and landscape strategies

Table 6.2 A checklist of appropriate questions for planning, conducting and evaluating restoration projects (from MacMahon and Jordan 1994).

A Project planning and design.

1. Has the problem requiring treatment been clearly understood and defined?
2. Is there a consensus on the restoration programs mission?
3. Have goals and objectives been identified?
4. Has the restoration been planned with adequate scope and expertise?
5. Does the restoration management design have an annual or midcoarse correction point in line with adaptive management procedures?
6. Are the performance indicators - the measurable biological, physical and chemical attributes - directly and appropriately linked to the objectives?
7. Have adequate monitoring, surveillance, management and maintenance programs been developed along with the project, so that monitoring costs and operational details are anticipated, and monitoring results will be available to serve as input in improving restoration techniques used as the project matures?
8. Has an appropriate reference system (or systems) been selected from which to extract target values of performance indicators for comparison in conducting the project evaluation?
9. Have sufficient baseline data been collected over a suitable period of time on the project ecosystem to facilitate before-and-after treatment comparisons?
10. Have critical project procedures been tested on a small experimental scale in part of the project area to minimise the risk of failure?
11. Has the project been designed to make the restored ecosystem as self-sustaining as possible to minimise maintenance requirements?
12. Has thought been given to how long monitoring will have to be continued before the project can be declared effective?
13. Have risk and uncertainty been adequately considered in project planning?

B During restoration.

1. Based on the monitoring results, are the anticipated intermediate objectives being achieved? If not, are appropriate steps being taken to correct the problem?
2. Do the objectives or performance indicators need to be modified? If so, what changes may be required in the monitoring program?
3. Is the monitoring program adequate?

C Post-restoration

1. To what extent were project goals and objectives achieved?
2. How similar in structure and function is the restored ecosystem to the target ecosystem?
3. To what extent is the restored ecosystem self-sustaining, and what are the maintenance requirements?
4. If all natural components of the ecosystem were not restored, have critical ecosystem functions been restored?
5. If all components of the ecosystem were not restored, have critical components been restored?
6. How long did the project take?
7. What lessons have been learnt from this effort?

8. Have lessons been shared with interested parties to maximise the potential for technology transfer?
9. What was the final cost, in net present value terms, of the restoration project?
10. What were the ecological, economic and social benefits realised by the project?
11. How cost-effective was the project?
12. Would another approach to restoration have produced desirable results at a lower cost?

Our view on the eventual outcome of any restoration attempts. In arid systems succession will not always result in the same ultimate, stable and persistent plant community being achieved (E. Allen 1988, Whisenant 1995, MacMahon and Jordan 1994). There are multiple pathways and multiple climax states that can be followed or attained. On the overburden dumps, the substrate has been irreparably changed, at least for the duration of our life times. The plant communities that eventually cover these structures will never fully resemble the dune vegetation that they displaced both in structure and function. The plant communities of the sandveld are strongly influenced by the nature of their substrate (see Chapter 3). There are, however, elements of natural plant communities within the sandveld adapted to living on shallow (<20 cm) sands overlying impenetrable or toxic subsoil. It is highly unlikely that the phyto-toxic nature of overburden dumps will be ameliorated in the short term (<50 years) without intensive capital inputs. In the absence of top-soiling, those plants that do colonise the dump surface with the assistance discussed above will promote the deposition of aeolian load, thus building up a layer of non-toxic soil. There are many shallow rooted plant species capable of exploiting this habitat and one will eventually see a dominance by these species. Naturally these will be fragile systems due to the thickness of the soil and also highly unpalatable. Future land-use options will be severely limited. Options that have the potential to reduce plant cover such as grazing or 4x4 vehicles, run the risk of rejuvenating the process of aeolian erosion resulting in renewed ecosystem degradation. This factor needs to be considered during the goal definition process.

7 Conclusion: Lessons to be learnt from our understanding of the problem, knowledge of the system and an ecological restoration philosophy.

Natural systems are not agricultural systems. Agricultural systems require frequent and expensive inputs and intervention to maintain their integrity, and are not sustainable. Natural systems are self-sustaining, self-regulating systems that, if not abused, will endure and continue to be productive. Using traditional agricultural or engineering methods or mind-set to recreate natural systems will inevitably result in the long-term failure of any restoration project (many examples already exist along the west coast). From our knowledge of how the natural plant communities are structured and function, we can manipulate certain keystone processes to facilitate or accelerate the return of healthy natural systems. From the evidence available, dealing with the restoration of arid systems, a healthy soil biota plays a keystone role in maintaining the integrity of arid systems. Efforts to rehabilitate the damage done by diamond mines should focus on restoring the soil and its biological properties, and manipulating natural processed to obtain self sustaining natural systems.

References

Allen, E.B. (1988) Some trajectories of succession in Wyoming sagebrush grassland: Implications for restoration. In Allen E.B. (ed.) The Reconstruction of Disturbed Arid Lands. An Ecological Approach. AAAS selected symposium #109. Westview Press, Boulder.

Allen, M.F. (1988) Below ground structure: A key to reconstructing a productive arid ecosystem. In Allen E.B. (ed.) The Reconstruction of Disturbed Arid Lands. An Ecological Approach. AAAS selected symposium #109. Westview Press, Boulder.

Bradshaw, A.D. and Chadwick, M.J. (1980) The Restoration of Land. University of California Press, Berkeley, Los Angeles.

Burns, M. (1994) ALEXKOR. Environmental Management Programme Report. Volume 3. EMATEK - CSIR, Stellenbosch.

Burton, P.J.; Robertson, K.R.; Iverson, L.R.. and Risser, P.G. (1988) Use of resource partitioning and disturbance regimes in the design and management of restored prairies.

In Allen E.B. (ed.) The Reconstruction of Disturbed Arid Lands. An Ecological Approach. AAAS selected symposium #109. Westview Press, Boulder.

Call, C.A. and Roundy, B.A. (1991) Perspectives and processes in revegetation of arid and semiarid rangelands. *Journal of Range Management* 44: 543-549.

DePuit, E.J. and Redente, E.F. (1988) Manipulation of ecosystem dynamics on reconstructed semi-arid lands. In Allen E.B. (ed.) The Reconstruction of Disturbed Arid Lands. An Ecological Approach. AAAS selected symposium #109. Westview Press, Boulder.

Holloway, M. (1994) Nurturing Nature. *Scientific American*. April: 76-84.

Itami, K. and Kyuma, K. (1995) Dispersion behaviour of soils from reclaimed lands with poor soil physical properties and their characteristics with special reference to clay mineralogy. *Soil Science and Plant Nutrition* 41: 45-54.

Jackson, L.L.; Lopoukhine, N. and Hillyard, D. (1995) Ecological restoration: A definition and comments. *Restoration Ecology* 3:71-75

Jayawardane, N.S. and Chan, K.Y. (1994) The management of soil physical properties limiting crop production in Australian sodic soils-A review. *Australian Journal of Soil Research* 32: 13-44.

Lax, A.; Diaz, E.; Castillo, V. and Albaladejo, J. (1994) Reclamation of physical and chemical properties of salinized soil by organic amendment. *Arid Soil Research and Rehabilitation* 8: 9-17.

le Roux, A. and Odendaal, F.J. (unpubl.) Report on the study of natural recovery of overburden dumps on DBCM properties in Namaqualand. Unpublished Report. Geology Department, De Beers Namaqualand Mines, Kleinzee, South Africa.

MacMahon, J.A.and Jordan III, W.R. (1994) Ecological restoration. In Meffe, G.K. (ed.) Principles of Conservation Biology. Sinauer Associates, Inc. Sunderland, Ma.

Mentis, M.T. and Ellery, W.N. (1994) Post-mining rehabilitation of dunes on the north-east coast of South Africa. *South African Journal of Science* 90: 69-74.

Milton, S.J. (1995) spatial and temporal patterns in the emergence and survival of seedlings in arid Karoo shrubs. *Journal of Applied Ecology* 32: 145-156.

Partridge, T.C. and Maud, R.R. (1987) Geomorphic evolution of southern Africa since the Mesozoic. *South African Journal of Geology* 90: 179-208.

Schultze, B.R. (ed.) (1965) Climate of South Africa. Part 8. General Survey (WB28). The Government Printer and Weather Bureau, Pretoria.

Scott, D.F. and Johnson, M.A. (1995) Soil leaching trails on overburden soil from Kleinzee and Koingnaas. Report Number FOR-C 283. The Division Forest Science and Technology, CSIR, Pretoria

Scott, D.F.; Du Toit, B.; Johnson, M.A. and Burns, M.E.R. (1994) The effects of mining on soil properties and the ability of the soil to support vegetation after mining at Kleinzee and Koingnaas, on the west coast of South Africa. Report Number FOR-C, Project Number Fl 719. The Division Forest Science and Technology, CSIR, Pretoria.

Spain, A.V. and Hutson, B.R. (1983) Dynamics and fauna of the letter layers. In Soils: an Australian viewpoint. Division of Soils, CSIRO, Melbourne/Academic Press, London

Taylor, J.K. (1983) Dynamics and fauna of the letter layers. In Soils: an Australian viewpoint. Division of Soils, CSIRO, Melbourne/Academic Press, London

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

van Aarde, R.J. (1995) Workshop on the rehabilitation of the coastal dunes of Kwazulu-Natal, 30.and 31 August 1995, Richards Bay. Mammal Research Institute, University of Pretoria, Pretoria.

van Aarde, R.J.; Coe, M. and Niering, W.A. (1996) On the rehabilitation of the coastal dunes of KwaZulu-Natal. *South African Journal of Science* 92:122-124.

Van der Putten, W.H.; Van Dijk, C. and Peters, B.A.M. (1993) Plant soil-borne diseases contribute to succession in foredune vegetation. *Nature* 362(4 March): 53-56.

Ward, J.D.; Seely, M.K. and Lancaster, N. (1983) On the antiquity of the Namib. *South African Journal of Science* 79: 175-183.

Whisenant, S.G. (1995) Landscape dynamics and arid land restoration. In Roundy B.A.; McArthur, E.D.; Haley, J.S. and Mann, D.K. (comps.) Proceedings: Wildland Shrub and Arid Land Restoration Symposium; 1993 October 19-21; Las Vegas, NV. Gen. Tech. Rep. INT-GTR-315. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.

Whisenant, S.G.; Thurow, T.L. and Maranz, S.J. (1995) Initiating autogenic restoration on shallow semiarid sites. *Restoration Ecology* 3: 61-67.

Whitford, W.G. (1988) Decomposition and nutrient cycling in disturbed arid ecosystems. In Allen E.B. (ed.) The Reconstruction of Disturbed Arid Lands. An Ecological Approach. AAAS selected symposium #109. Westview Press, Boulder.

Whitford, W.G.; Aldon, E.F.; Freckman, W.; Steinberger, Y. and Parker, L.W. (1989) Effects of organic amendments on soil biota on a degraded rangeland. *Journal of Range Management* 42: 56-60.

Yeaton, R.I. and Esler, K.J. (1990) The dynamics of a succulent karoo vegetation. *Vegetatio* 88: 103-113.

Chapter 7 General Discussion.

This thesis is lengthy. However, I believe that the questions asked at the outset and the background against which this research was conducted, necessitated the effort that has gone into the production of this document. Detailed scientific research dealing with the vegetation of this corner of the karoo is meagre. That which is available deals with neither ecological patterns nor processes in this system. This project has attempted to change this. To say that this thesis provides a comprehensive analysis of ecological structure or processes would be misleading. On the contrary, I believe that this thesis barely scratches the surface of our understanding of the ecology of this unique flora. The information contained here does, however, provide a solid groundwork for further ecological studies in this system, especially with regard the restoration of diamond mining activities.

There are several key points that have emerged from this thesis, and which I consider significant. These points could provide important foci for future research in this area.

- This coastal fog desert is unique, not only in a southern African context because of its unique geology and climate, but globally because of the unique (structurally) and diverse (floristically) flora.
- Broad scale patterns of plant diversity can be predicted on the basis of habitat diversity. "Hot spots" of plant diversity are encountered on rocky substrata where one encounters unique assemblages of dwarf leaf succulent plants. These assemblages are rich in local endemic species. Non-rocky substrata (e.g. the dunes of the coastal plain) are characterised by having a more widespread, generalist type vegetation. These patterns in plant diversity can, I believe, be extrapolated to the whole of Namaqualand. Further research that builds upon these themes, elsewhere in Namaqualand, will prove to be invaluable in developing a model that can isolate key areas of high conservation value in the region.
- At a finer scale, the distribution of plant communities in Sandveld is intimately linked to wind, and the manner in which wind distributes and sorts sand within the landscape. Probably the biggest failing of this project was the premature termination of soil texture analysis. In hindsight, it should have been obvious to me that soil texture should be the overriding signature of sand-sorting by wind. I should have read Chapter 2 more closely. A

key biological indicator of patterns in soil texture, however slight, are biogenic crusts. This was born out in both Chapter 2 and 4.

- The Brant's Whistling Rat story intrigued me, and continues to intrigue me. This proved to be a turning point in this thesis. It provided the seed for developing the link between the biology of the system and the ecological restoration thereof. The actual experimental aspect of the rats involvement was minor in relation to ideas and insight gained from the restoration literature, especially the American arid rangelands. Soil biology is a keystone variable in the structure and dynamics of arid rangelands. I believe that potentially significant gains towards understanding karoo ecology are to be made in the study of soil biological structure and function. It is important that this avenue of research be pursued.
- Restoration severely degraded arid lands is not an exercise in agronomy, nor engineering. There is a need to create an understanding amongst practitioners of restoration (e.g. managers and ecologists) that "healing" a damaged ecosystem is a far cry from producing a successful wheat crop. It is imperative a functional understanding of ecosystem biological and environmental attributes be integrated into the planning and implementation of an restoration project. This thesis does not provide adequate insight into the functioning of vegetation described. Future ecological research in this system should concentrate on integrating plant biological processes with soil biological and environmental processes to provide a better functional understanding of observed patterns in the landscape.