

## Preface

The fynbos has attracted both scientists and naturalists for many years, decades and even centuries. Numerous research papers have been published, dealing with an extensive array of topics related to floristics, vegetation, ecology and conservation of fynbos. Answers to many questions were suggested, but many problems remain unsolved. The private Grootbos Nature Reserve, situated at the W edge of the Agulhas Plain, is right in the middle of the Fynbos Biome and bears a considerable diversity of plant species and ecosystems. The reserve is run as a five star lodge, providing its guests with 17 kms<sup>2</sup> of natural fynbos and forest scenery for relaxation. Since the establishment of the reserve and the lodge in 1995, much emphasis has been placed on ecological issues. A lot of effort has been put into the catalogization of the flora, into the gaining of understanding of the distribution of ecosystems and the generation and implication of a management plan directed towards the conservation of the near-natural ecosystems. However, a comprehensive account of the reserve's ecosystems on both a descriptive and an analytic basis was still missing, as well as a detailed map of the vegetation, these both being important tools for further management action. This thesis has been written in order to generate such an account, based on existing knowledge on the one hand and on new studies on the other hand.

A project of this scale can hardly be the product of a single person. This thesis would not have come about without the support of a considerable number of people. Dr. Andreas Erhard from the Department for Geography, University of Innsbruck, has installed the networks necessary for all the studies connected to the thesis. Dr. Erschbamer, from the Botanical Department, University of Innsbruck declared her will to provide support, contributing important help especially during the initial and the final stages of the work.

Nothing would have been possible without the support of Michael Lutzeyer and of the management of Grootbos Private Nature Reserve, arranging the possibility for a stay during the field work on the reserve. I am very grateful for the patient support with

species identification that I received from Heiner Lutzeyer and John Manning, from the nature guides of the reserve, especially Carla, Shelly and Silence, and above all from the Conservation Director Sean Privett, who, though always busy, patiently provided valuable additional information and suggestions constituting a major contribution to this thesis. Much would have been more difficult had it not been for the organizational help from and valuable discussions with the German student researcher Sandra Gernandt.

Dr. Pieter De Necker and Jaco Kemp from the Geography Department of the Stellenbosch University invested time to enable me access to the library and computer facilities of the University. The same is true of Sandy Smuts, to whom I want to thank for the access to the library of the Botanical Department of the University of Cape Town. From a financial point of view, I am grateful for the generous grants I received from the Office for International Relations, University of Innsbruck and the Dean's office of the Faculty for Natural Sciences, University of Innsbruck.

Claire Cochrane as well as my colleagues Reinhard Starnberger and Matthias Kaufmann provided valuable tips for improving the quality of the thesis.

Last but not least I would like to thank my mother Edith for the invaluable help that I received from her in many respects, as well as my father Walter and my grandfather Franz Mergili for their financial support.

I hope that everyone reading this thesis has the opportunity to walk through the shady Milkwood Forest, to descend into the forest valley through bright orange pincushions in order to admire the distinctive fernlands and to penetrate the tall, calm Afromontane Forest, to ascend the heights of Protea Peak through a sea of magnificently flowering proteas, and to explore a post-fire environment in spring in order to admire the carpet of flowering geophytes. May this thesis contribute to a better understanding of the complex and wonderful world of fynbos, leading to an even more focused conservation of these ecosystems in order to keep them alive for future generations.

Martin Mergili  
Innsbruck, January 2005

## Summary

### Abstract

Grootbos Private Nature Reserve (located between Stanford and Gansbaai, Overberg Province, Western Cape, South Africa) is maintained as a Five Star Lodge with a hinterland of 1700 ha of near-natural ecosystems.

The reserve is situated in the heart of the Fynbos Biome. The Southern tip of Africa experiences a mediterranean-type climate with hot, dry summers and moist, temperate winters. These conditions, in connection with fire as frequent disturbance factor and nutrient-poor soils, support a species-rich heath-like shrubland which is called fynbos ("fine bush") due to the abundance of species with small leaves. Typical families are the Proteaceae, Ericaceae and Restionaceae. The fynbos is not only characterized by a high species diversity, but also by a high degree of endemism, so that even the 90,000 km<sup>2</sup> area is sometimes recognized as a separate floral kingdom.

According to a survey in 1997, different plant communities are present, being related to an array of environmental variables. The major objective of this study was to refine the knowledge obtained in 1997 and to survey some properties recently included into the reserve in order to obtain a comprehensive picture of the vegetation of Grootbos Nature Reserve in order to support further management activities directed towards nature conservation.

23 relevés (sampling sites) were set up, in addition to the existing 48. The cover of each identifiable species was recorded, as well as several environmental variables describing topography, soil physics and soil chemistry. For 127 more sites, the dominant and easily identifiable species and the topographic data were recorded to increase the dataset available for subsequent numerical vegetation analysis and mapping.

A numerical classification was applied to the dataset (two-way indicator species analysis), as well as an indirect (Detrended Correspondence Analysis) and a direct ordination (Canonical Correspondence Analysis). The three methods provided results which were largely in line. Three levels of vegetation units were established: a biome level, a complex level and a formation level. At the biome level, Forest, Wetland and Fynbos, which are floristically very distinct, were discriminated. The patchily distributed forests are

characterized by a low species diversity and the absence of wildfires. Afromontane Forest covers S-facing ravines and patches of Milkwood Scrub Forests are present on lower slopes. For the species-rich fynbos, occupying the majority of the reserve, one complex associated with alkaline sands (corresponding to Coastal Fynbos) and another with acid sands (corresponding to Mountain Fynbos) were clearly separated in both the classification and the ordinations. In contrast, continuous transitions prevailed on the formation level, so that the units had to be based on structurally dominant species, partly reseeding Proteaceae. This is connected with some problems as the group is well known to show an unstable pattern of distribution caused by fire-induced shifting of populations. Tab. S.1 summarizes the major features of all vegetation units.

In order to generate a vegetation map, an array of reflection classes was attempted to be extracted from true color orthophotos by numerical methods. Spatial datasets illustrating a vegetation index and surface texture were generated, but their value for distinguishing different fynbos units was limited. Vegetation units were available from the 1997 survey, but the new properties had to be mapped manually by using GPS, as did some poorly surveyed patches of the remaining reserve. The map was adapted to the classification results, but includes an additional level of detail not supported by the numerical vegetation analysis.

The relationships between topography and vegetation were investigated on a spatial basis by a geostatistical analysis: The distribution of the vegetation if it fully mirrored the topographical conditions was predicted. The three levels of vegetation units as dependent variables were related to certain combinations of the following topographical features as independent variables: elevation (DEM obtained from contour lines), slope, aspect, solar irradiation, flow accumulation and exposition to the fire-bearing SE winds (all calculated from the DEM). The prediction scores ranged from 17.7 to 77.5 per cent, depending on the combination of variables. The most obvious mispredictions were that a certain share of the Alkaline Sand Fynbos was predicted as Milkwood Scrub Forest, many S-facing slopes supporting fynbos were predicted as Afromontane Forest and the prediction of

Neutral Sand Proteoid Fynbos was very poor in general.

One of the major threats for the natural ecosystems of the reserve are introduced plant species, particularly the Australian *Acacia cyclops* (Rooikrans). Control and eradication measures are therefore essential for conservation issues, as well as a reasonable fire management and the protection of red-data species.

## Zusammenfassung

Das private Naturreservat Grootbos liegt zwischen Stanford und Gansbaai in der Provinz Overberg (Region Westkap, Südafrika). Das 1700 ha grosse Naturschutzgebiet wird als Fünfsternhotel betrieben. Es befindet sich inmitten des so genannten Fynbos Bioms. Das mediterrane Klima der Suedspitze Afrikas (heisse, trockene Sommer und milde, niederschlagsreiche Winter), zusammen mit häufig auftretenden Buschfeuern und den oft sehr nährstoffarmen Boeden erlaubt kaum Waldvegetation, dafür jedoch ein sehr artenreiches Buschland, das aufgrund der kleinen Blaetter vieler Arten fynbos ("feiner Busch") genannt wird. Neben dem Artenreichtum ist auch der hohe Anteil an Endemiten charakteristisch, weshalb die nur etwa 90.000 km<sup>2</sup> grosse Kapregion oft als eigenes Florenreich (Capensis) aufgefasst wird. Die charakteristischen Pflanzenfamilien sind Proteaceae, Ericaceae und Restionaceae.

Die Vegetation des Reservates wurde im Jahr 1997 untersucht, resultierend in einer überblicksmässigen Vegetationskarte sowie Erkenntnissen zu Vegetation-Umwelt-Beziehungen. Die vorliegende Untersuchung hat die Aufgabe, die bestehenden Erkenntnisse zu verfeinern sowie auf Teile des Reservats, die erst kürzlich zugekauft wurden, zu erweitern. Die resultierenden Ergebnisse sollen ein möglichst geschlossenes und detailliertes Bild der Vegetation des Reservates ergeben und so eine wichtige Grundlage für weitere Massnahmen zur bestmöglichen Erhaltung der Arten und Ökosysteme darstellen.

Zusätzlich zu den 48 Vegetationsaufnahmen aus dem Jahre 1997 wurden 23 weitere Aufnahmeflächen eingerichtet und hinsichtlich ihrer Artenzusammensetzung (für jede identifizierbare Art wurde die Deckung ermittelt) und der wesentlichen Umweltfaktoren (topographische Faktoren, physikalische und chemische Bodeneigenschaften) untersucht. Für 127 weitere Lokalitäten wurden nur die dominanten und leicht identifizierbaren Arten sowie die Topographie notiert, um ein verdichtetes Informationsnetz für die nachfolgende Vegetationsanalyse sowie die Kartierung zur Verfügung zu haben.

Die Numerische Vegetationsanalyse bestand aus einer Klassifikation (two-way indicator species analysis),

einer indirekten (Detrended Correspondence Analysis) sowie einer direkten Ordination (Canonical Correspondence Analysis). Die Ergebnisse standen grossteils in Einklang miteinander und legten die Unterscheidung dreier Niveaus von Vegetationstypen nahe: Biom, Komplex und Formation. Tabelle S.1 bietet eine Übersicht über alle Einheiten an. Auf dem Niveau des Bioms wurden drei Einheiten unterschieden: Wald, Feuchtflächen und Fynbos. Die Wälder sind kleinflächig, artenarm und nicht vom Feuer beeinflusst. Afromontane Forests kommen in schattigen Tälern vor, während Milkwood Scrub Forests an den niedrigeren Hängen des Reservats auftreten. Für den artenreichen Fynbos, der den Grossteil der Fläche des Reservates einnimmt, legten sowohl die Ergebnisse der Klassifikation als auch der Ordinationen eine Zweiteilung in einen mit sauren, flachgründigen Böden assoziierten und einen mit eher alkalinen Böden assoziierten Komplex nahe. Auf dem Niveau der Formation herrschen fliessende Übergänge zwischen den Einheiten vor, so dass einzelne dominante Arten, vor allem nicht zum Stockausschlag befähigte Proteaceae als Indikatoren verwendet werden mussten. Dies ist jedoch insofern problematisch, als solche sehr oft eine geringe Standortkonstanz über mehrere Intervalle zwischen Buschfeuern aufweisen.

Zum Zwecke einer möglichst exakten und detaillierten Vegetationskartierung wurde versucht, Vegetations-einheiten mittels numerischer Methoden aus Farborthophotos zu extrahieren. Ein Vegetationsindex sowie die Oberflächenstruktur wurden dazu verwendet, die Ergebnisse zeigten jedoch nur eine sehr begrenzte Verwendbarkeit zur Abgrenzung verschiedener Typen von Fynbos. Für die Abgrenzung zwischen Fynbos und Wald waren die Ergebnisse besser. Die neu zugekauften Gebiete mussten begangen und mit Hilfe der GPS-Technik kartiert werden, ebenso wie einige Zonen, die in der Kartierung von 1997 nur unzureichend erfasst worden waren. Die Ergebnisse der Begehungen wurden mit der existierenden Karte kombiniert. Gegenüber der numerischen Vegetationsanalyse wurde ein weiteres Niveau höherer Detailierung eingeführt.

Die Vegetationskarte und einige Rasterdatensätze zur Topographie wurden verwendet, um Vegetation-Umwelt-Zusammenhänge auch auf räumlicher Basis zu ermitteln. Es wurde eine Geostatistische Analyse durchgeführt um zu ermitteln, inwieweit die Verteilung der Vegetationseinheiten von der Verteilung der Umweltfaktoren bestimmt wird. Die Einheiten von jedem der drei Niveaus wurden mit verschiedenen Kombinationen der folgenden topographischen Variablen kombiniert: Meereshöhe (das DEM wurde mit Hilfe von Höhenlinien generiert), Hangneigung,

## 4 Summary

complex/variety	criteria	common species	elevation [mts]	soil depth [cm]	pH
<b>Milkwood Scrub Forest (11,0)</b>		<i>Sideroxylon inerme, Euclea racemosa, Myrsine africana, Cynanchum obtusifolium, Asparagus aethiopicus, Droguetia iners, Ehrharta erecta</i>	<b>246</b>	<b>91</b>	<b>7,2</b>
<b>Afromontane Forest (13,2)</b>		<i>Rapanea melanophloeos, Kiggelaria africana, Diospyros whyteana, Celtis africana, Chionanthus foveolatus, Droguetia iners, Asparagus scandens, Asplenium adiantum-nigrum</i>	<b>308</b>	<b>34</b>	<b>6,7</b>
<b>Thicket Complex (ND)</b>			<b>ND</b>	<b>ND</b>	<b>ND</b>
True Thicket	<3: <i>Pteris dentata</i>	<i>Euclea racemosa, Salvia africana-lutea, Myrsine africana, Nylandtia spinosa, Gymnosporia buxifolia, Leucadendron coniferum, Thamnochortus erectus, Sideroxylon inerme</i>	ND	ND	ND
<i>Pteris dentata</i> Shrubland	>2: <i>Pteris dentata</i>	<i>Pteris dentata, Leucadendron coniferum, Myrsine africana, Diospyros whyteana</i>	ND	ND	ND
<b>Wetland Complex (9,3)</b>			<b>272</b>	<b>100</b>	<b>6,8</b>
indicator: <i>Mariscus thunbergii</i>					
True Wetland	<3: <i>Pteris dentata</i>	<i>Mariscus thunbergii, Artemisia afra, Cliffortia ferruginea, psoralea arborea, Senecio halimifolius, Zantedeschia aethiopica, Gunnera perpensa, Hippia frutescens, Helichrysum cymosum ssp. cymosum, Leonotis leonurus</i>	291	100	7,1
<i>Pteris dentata</i> Fernland	>2: <i>Pteris dentata</i>	<i>Pteris dentata, Mariscus thunbergii, Kiggelaria africana, Zantedeschia aethiopica, Diospyros whyteana, Gunnera perpensa</i>	236	100	6,1
<b>Alkaline Sand Fynbos Complex / Coastal Fynbos Complex (24,9)</b>			<b>286</b>	<b>62</b>	<b>7,3</b>
Dune Asteraceous Fynbos	<2: <i>Leucadendron coniferum, Leucospermum patersonii, Protea obtusifolia, P. repens, Thamnochortus fraternus</i> ; <3: <i>Erica coccinea</i> var. yellow	<i>Metalasia muricata, Passerina vulgaris, Euclea racemosa, Erica irregularis, Ischyrolepis eleocharis, Thamnochortus erectus, Otholobium bracteolatum, Anthospermum aethiopicum</i>	255	77	7,7
Neutral Sand Proteoid Fynbos	>1: <i>Leucadendron coniferum</i> or <i>Leucospermum patersonii</i> ; <3: <i>Erica coccinea</i> var. (yellow); <2: <i>Protea obtusifolia, P. repens, Thamnochortus fraternus</i>	<i>Leucadendron coniferum, Leucospermum patersonii</i>	335	59	6,5
<i>Protea repens</i> Proteoid Fynbos	>1: <i>Protea repens; P. obtusifolia</i> < <i>P. repens</i>	<i>Protea repens, Cliffortia ilicifolia, Willdenowia teres, Phylica disticha, Diasma subulata</i> var. <i>subulata</i> , <i>Passerina vulgaris</i>	326	100	6,0

<b>Protea obtusifolia Proteoid Fynbos</b>	>1: <i>Protea obtusifolia</i> ; <2: <i>Thamnochortus fraternus</i> ; <i>P. obtusifolia</i> => <i>Erica coccinea</i> var. (yellow)	<i>Protea obtusifolia</i> , <i>Erica coccinea</i> var. (yellow), <i>Leucadendron coniferum</i> , <i>Leucospermum patersonii</i>	258	82	7,7
<b>Erica coccinea Ericoid Fynbos</b>	>2: <i>Erica coccinea</i> var. (yellow); <2: <i>Thamnochortus fraternus</i> ; <i>E. coccinea</i> var. yellow < <i>Protea obtusifolia</i> , <i>Leucadendron coniferum</i> and <i>Leucospermum patersonii</i>	<i>Erica coccinea</i> var. (yellow), <i>Erica irregularis</i> , <i>Cullumia squarrosa</i> , <i>Oedera capensis</i> , <i>Indigofera brachystachya</i>	209	30	8,0
<b>Thamnochortus fraternus Restioid Fynbos</b>	>1: <i>Thamnochortus fraternus</i>	<i>Thamnochortus fraternus</i> , <i>Erica coccinea</i> var. (yellow), <i>Protea obtusifolia</i> , <i>Leucadendron coniferum</i> , <i>Indigofera brachystachya</i>	323	2	7,3
<b>Protea repens Proteoid Fynbos (post fire regenerating)</b>	>1: <i>Aspalathus microphylla</i>	<i>Aspalathus microphylla</i> , <i>Leucospermum patersonii</i> , <i>Helichrysum patulum</i>	312	100	6,2

### Acid Sand Fynbos Complex / Mountain Fynbos Complex (35,0)

indicators: *Mimetes cucullatus*, *Leucadendron salignum*, *Erica glabella*

<b>Acid Sand Proteoid Fynbos</b>	<2: <i>Leucadendron coniferum</i> , <i>Leucospermum patersonii</i> , <i>Protea obtusifolia</i> ; <3: <i>Erica sessiliflora</i> , <i>Elegia thyrsifera</i>	<i>Mimetes cucullatus</i> , <i>Leucadendron salignum</i> , <i>Aulax umbellata</i> , <i>Protea cynaroides</i> , <i>L. xanthoconus</i> , <i>Protea longifolia</i> , <i>Penaea mucronata</i> , <i>Morella quercifolia</i> , <i>Indigofera brachystachya</i> , <i>Elegia juncea</i> , <i>Pseudopentameris macrantha</i> , <i>Bobartia indica</i> , <i>Erica glabella</i> , <i>Trichocephalus stipularis</i>	386	26	5,4
<b>Transitional Proteoid Fynbos</b>	>1: <i>Leucadendron coniferum</i> or <i>Leucospermum patersonii</i> ; <i>E. sessiliflora</i> , <i>Elegia thyrsifera</i> < <i>L. coniferum</i> , <i>L. patersonii</i>	<i>Leucadendron coniferum</i> , <i>Leucospermum patersonii</i> , <i>Protea obtusifolia</i> , <i>Mimetes cucullatus</i> , <i>Leucadendron tinctum</i> , <i>Leucadendron salignum</i> , <i>Erica glabella</i>	376	40	5,6
<b>Erica sessiliflora Ericaceous Fynbos</b>	>2: <i>Erica sessiliflora</i> ; <i>E. thyrsifera</i> , <i>Leucadendron coniferum</i> , <i>Leucospermum patersonii</i> <= <i>E. sessiliflora</i>	<i>Erica sessiliflora</i> , <i>E. glabella</i> , <i>Leucadendron coniferum</i> , <i>Mimetes cucullatus</i> , <i>Leucospermum patersonii</i> , <i>Drosera capensis</i> , <i>Cliffortia ferruginea</i> , <i>Psoralea arborea</i> , <i>Berzelia lanuginosa</i> , <i>Staavia radiata</i>	297	55	5,6
<b>Elegia thyrsifera Restioid Fynbos</b>	>2: <i>Elegia thyrsifera</i> ; <i>E. thyrsifera</i> => <i>Leucadendron coniferum</i> , <i>Leucospermum patersonii</i> ; <i>E. thyrsifera</i> > <i>Erica sessiliflora</i>	<i>Elegia thyrsifera</i> , <i>Helichrysum patulum</i> , <i>Thamnochortus erectus</i> , <i>Morella quercifolia</i> , <i>Leucospermum patersonii</i> , <i>Leucadendron coniferum</i> , <i>Erica sessiliflora</i>	ND	ND	ND
<b>Acid Sand Fynbos (post-fire regenerating)</b>	>1: <i>Aspalathus ciliaris</i>	<i>Aspalathus ciliaris</i> , <i>Pseudopentameris macrantha</i> , <i>Thesium strictum</i> , <i>Othonna quinquedentata</i> , <i>Euryops abrotanifolius</i> , <i>Mimetes cucullatus</i> , <i>Leucospermum patersonii</i> , <i>Helichrysum dasyanthum</i> , <i>Helichrysum patulum</i>	384	10	5,4

Tab. S.1: Summary of the vegetation units recognized in this study. The Forest biome is shaded green, the Wetland Biome blue and the Fynbos Biome red. The numbers in brackets added to the complex names are the average species numbers of the complexes on the 50 mts<sup>2</sup> level, the environmental data account for the average for each unit. The numbers close to the diagnostic species (column "criteria") are the pseudospecies levels of the TWINSPLAN-classification for the extended dataset (for a detailed explanation see chapters 3 and 4).

## 6 Summary

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Hangexposition, solare Einstrahlung, Abflussakkumulation und Exposition gegenüber den zur Ausbreitung von Buschfeuern beitragenden SO-Winden. Die Übereinstimmung der Vorhersagekarte mit der tatsächlichen Verbreitung der Vegetationseinheiten betrug - je nach Niveau und Faktorenkombination - zwischen 17.7 und 75.5 Prozent. Die auffälligsten Fehlinterpretationen betrafen den Komplex des Alkaline Sand Fynbos, der zu einem Teil als Milkwood Scrub Forest vorhergesagt wurde, einige in Fynbos gekleidete S-Haenge, für die ein Bewuchs mit Afromontane Forest vorgeschlagen wurde sowie den

Neutral Sand Proteoid Fynbos, für den die Vorhersage generell sehr schlecht war.

Die grösste Bedrohung für die naturnahen Ökosysteme des Reservates geht von invasiven Neophyten aus, wobei hier *Acacia cyclops* (Rooikrans) aus Australien eine grosse Rolle spielt. Um die Erhaltung der Ökosysteme zu gewährleisten ist es deshalb wichtig, Massnahmen zur Kontrolle und zur Entfernung dieser Elemente zu treffen. Darüber hinaus ist das Feuerregime zu kontrollieren und zu steuern sowie auf den besondere Schutz von Arten der Roten Liste zu achten.

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# 1 Introduction

## 1.1 Objectives and scope of the thesis

The Cape Region of South Africa is bearing an extraordinarily high diversity of vascular plants. Since almost 70 per cent of the more than 9,000 species are endemic to the region, it is sometimes considered a separate Floral Kingdom. While other kingdoms cover land areas of about 10 to 50 million square kilometres, the Cape Floral Kingdom only extends over about 90,000 square kilometres. Much research has taken place in the past two decades to improve the understanding of the structures and processes relevant for the conservation of this hot spot of biodiversity. There are nevertheless still unsolved problems. Cowling et al. (1997a: 123) listed some possible research fields for the future. Some of them are related to Global Climate Change, others deal with the control of invasive alien plants or with sustainable harvesting techniques. From a geographical point of view, one statement in that list is of special interest:

- "There is an inadequate understanding of the causal determinants of vegetation boundaries at all spatial scales. The results of such studies are an essential input for mechanistic models aimed at predicting the impact of global change on vegetation and species distributions."

The master goal of this thesis is to approach a solution to some aspects of this question.

For the reason that it was - within the given scope - impossible to investigate the whole Cape Region, a research site had to be found. This area required certain features to be suitable for the the studies:

- The site should not be too large (maximum 15 - 20 square kilometres)
- It should be in a near-natural condition (a nature reserve would be best)
- It should contain different vegetation types
- The flora should be well documented
- Color or infrared aerial images or high resolution satellite images should be easily available

The privately owned Grootbos Nature Reserve (Fig. 1.1) was chosen, since it fulfills these criteria fairly well. It has a surface of 17 square kilometres and is nearly completely covered with near-pristine Fynbos vegetation of different types (the site will be described in detail later). A complete list of the flora was available, as well as color orthophotos. The major vegetation units had already been mapped on GIS. Fire history was also available as a spatial dataset. 48 vegetation samples were taken in the autumn and winter of 1997, so that a database was already existing, on which new research could be based. However, the property had been extended since those activities took place, so that more exploration work was necessary.

The following tasks were included in the analysis:

- to establish, update resp. fine-tune meaningful vegetation units for the research area. The existing samples should be supplemented by new ones, and the total dataset should be used for a comprehensive numerical vegetation analysis
- to map the spatial distribution of the vegetation units as exact as possible, supported by numerical interpretation of the aerial images
- to investigate the relationships of the vegetation and the environmental controls like topographical and soil variables

Before starting with the detailed descriptions and discussions, it may be useful to give a short introduction to the major geographical, physical, biological and also historical features of the research site, Grootbos Nature Reserve.

## 1.2 Grootbos Nature Reserve - an overview

Grootbos Nature Reserve is located between the village of Stanford and the town of Gansbaai in the Overberg Province of the Western Cape Region of South Africa, about 150 road kilometres SE of Cape Town. The coordinates of the lodges are 34°32'30" S and 19°24'50" E (Fig. 1.1).

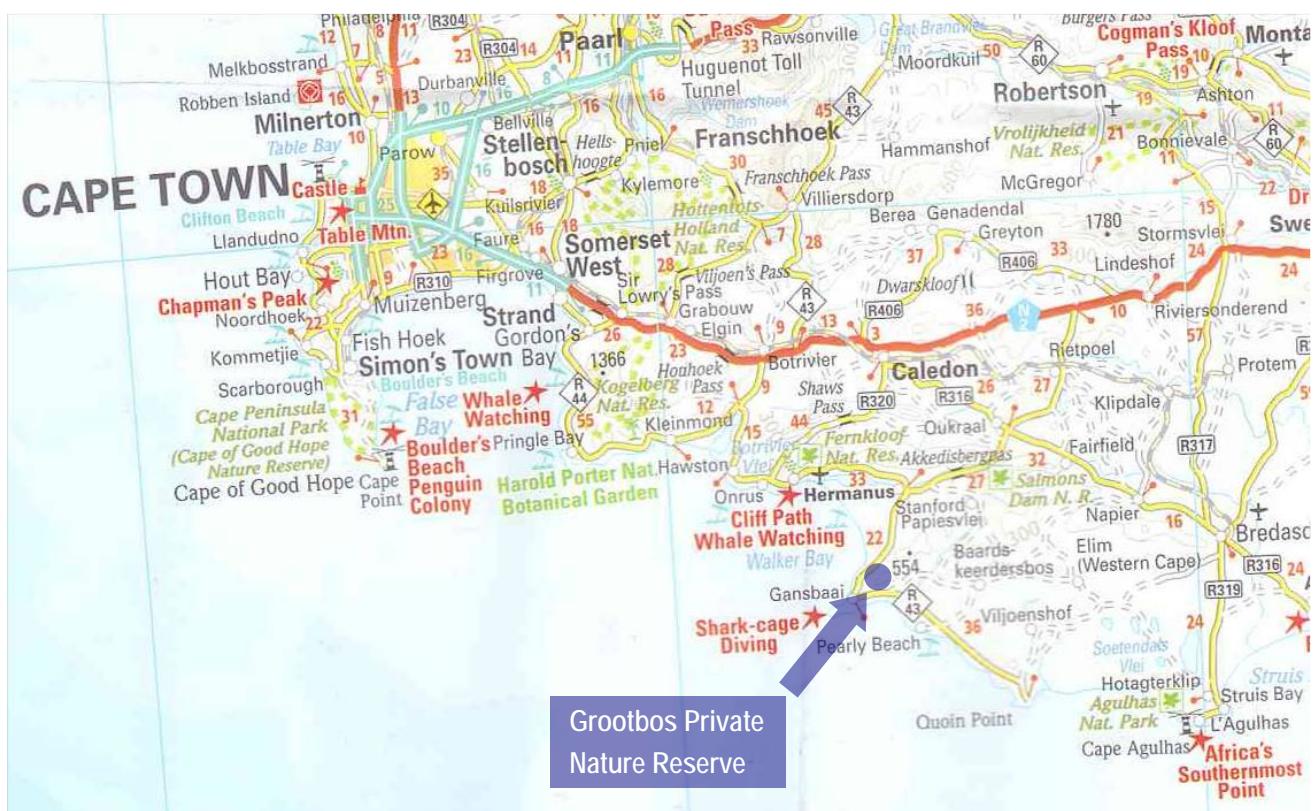
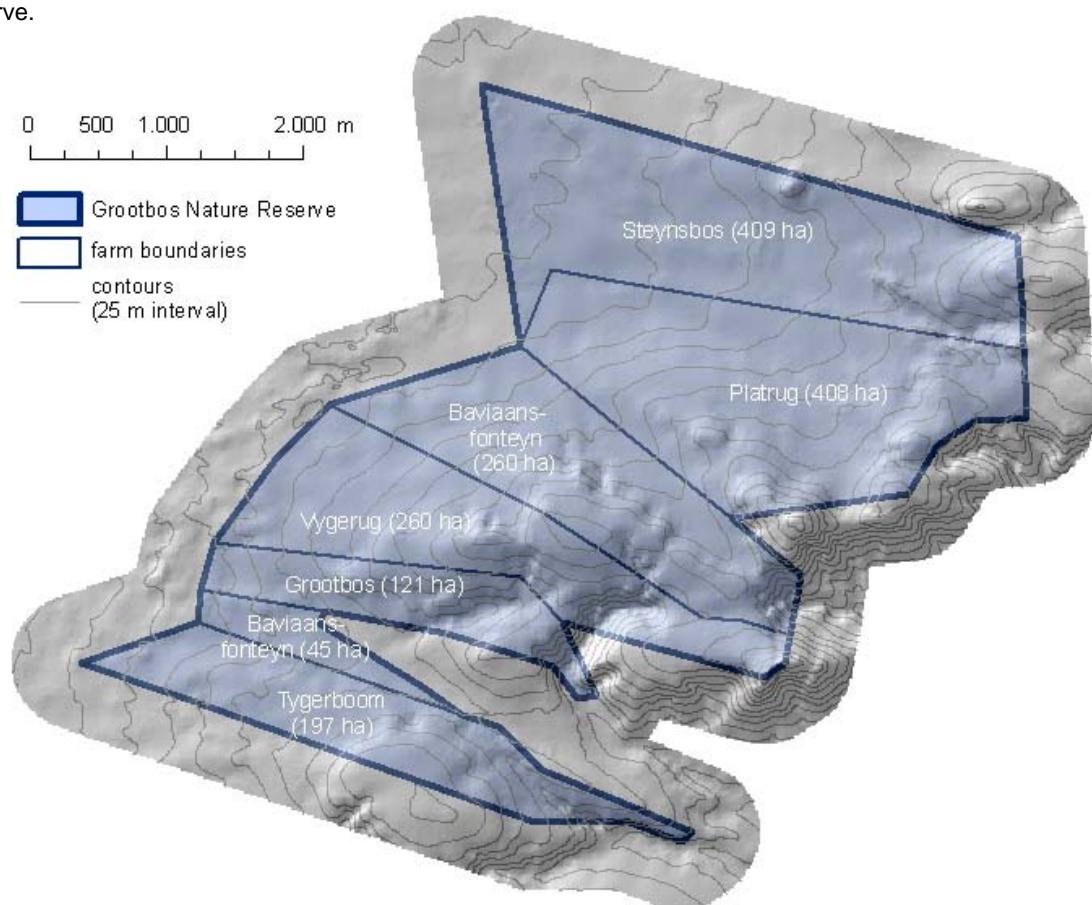


Fig. 1.1 (top): Grootbos Nature Reserve is located on the slopes above the Walker Bay, SE of Cape Town (map reproduced from the "Reise-know-how" map "South Africa").

Fig. 1.2 (bottom): The farms making up the reserve.



The reserve consists of seven formerly separate farms (Fig. 1.2), covering an area of 1700 ha altogether, including about 640 ha of recently bought properties (Steynsbos, Baviaansfonteyn and Tygerboom) not included in the vegetation analysis of 1997.

The landscape is sloping, with a maximum elevation of about 475 m along the slopes of Swartkransberg (Fig. 1.3 - 1.6). The underlying rock type of the more elevated hills is quartzitic sandstone, part of the Table Mountain Sandstone formation. On the lower slopes, deposits of sandy aeolian material overlay the bedrock. Limestone is exposed in some places (Grootbos Nature Reserve 2002).

The climate is characterized by a strong seasonality of the precipitation. May to August are the wettest months (most precipitation is carried by NW winds), whilst the SE winds prevailing during the summer months are dry. There has been no long-term precipitation record at Grootbos. The mean annual sum from 1996 to 1998 is 730 mm. The mean maximum daily temperatures fluctuate between 25 degrees centigrade in February and 14 degrees centigrade in July (Grootbos Nature Reserve 2002). The reserve is absolutely frost-free.

Although human activities in the region have been recorded for the last 250,000 years, most anthropogenic influences on the natural ecosystems have taken place in the previous hundred years, with the import of advanced agricultural techniques. Until 1991, some areas of Grootbos were grazed and burned artificially, causing the local extinction of some plant species. Commercial flower picking took place until recently, removing several tons of material per year. Today Grootbos Nature Reserve is only used for recreation. The influences of these activities, however, are concentrated on linear structures such as roads, horse trails and hiking paths, which are not supposed to cause ecologically significant fragmentation. The spatial extent of the two five star lodges (Garden Lodge and Forest Lodge) and a housing facility on Steynsbos is limited (for a map of all major infrastructures please consult App. 4).

All in all, the majority of the ecosystems on the reserve may be considered as near-natural.

The vegetation - largely fynbos shrubland - is composed of 653 native species of vascular plants, but more are still occasionally found. 51 species are included in the read data list of threatened species, and two species (*Erica magnisylvae* and *Cliffortia anthospermoidea*) are endemic to the reserve. Privett (unpublished) has assigned the 48 vegetation samples to eight plant communities and related them to the major environmental variables (the diagnostic species are put into brackets):

- Milkwood Forest (*Sideroxylon inerme*): calcium-rich, sandy soils
- Afromontane Forest (*Diospyros whyteana*): fire-protected ravines, on sandstone
- Wetland (*Artemisia afra*): rich soils in seepage zones
- Acid Sand Proteoid Fynbos (*Mimetes cucullatus*, *Leucadendron salignum*): shrubland at higher altitudes, on sandstone
- Dune Asteraceous Fynbos (*Passerina vulgaris*, *Euclea racemosa*): low shrubland on deep calcareous soils
- Limestone Fynbos (*Protea obtusifolia*, *Thamnochortus fraternus*): shrubland on limestone deposits overlaying sandstone
- Protea repens Proteoid Fynbos (*Protea repens*): medium height shrubland
- Neutral Sand Proteoid Fynbos (*Leucospermum patersonii*, *Leucadendron coniferum*): medium height shrubland on shallow sands overlaying sandstone

All of the fynbos on the reserve has burned since 1988.

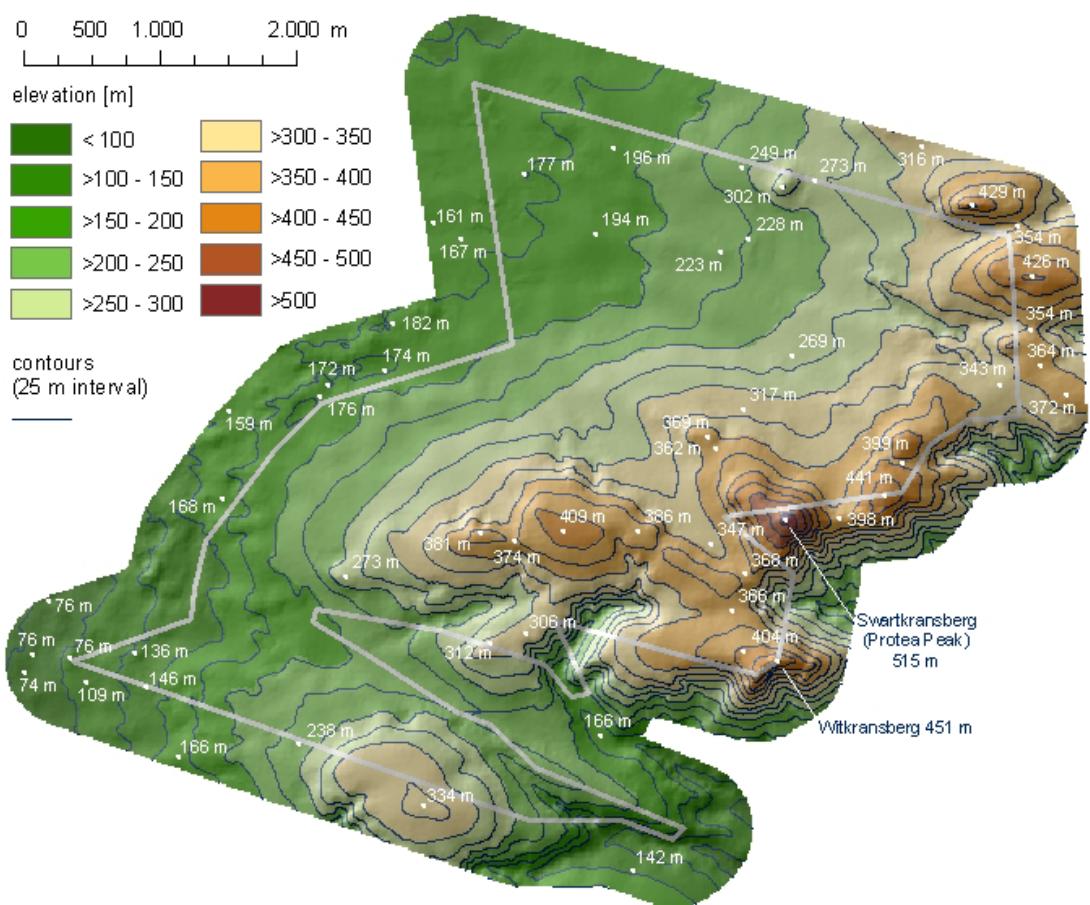
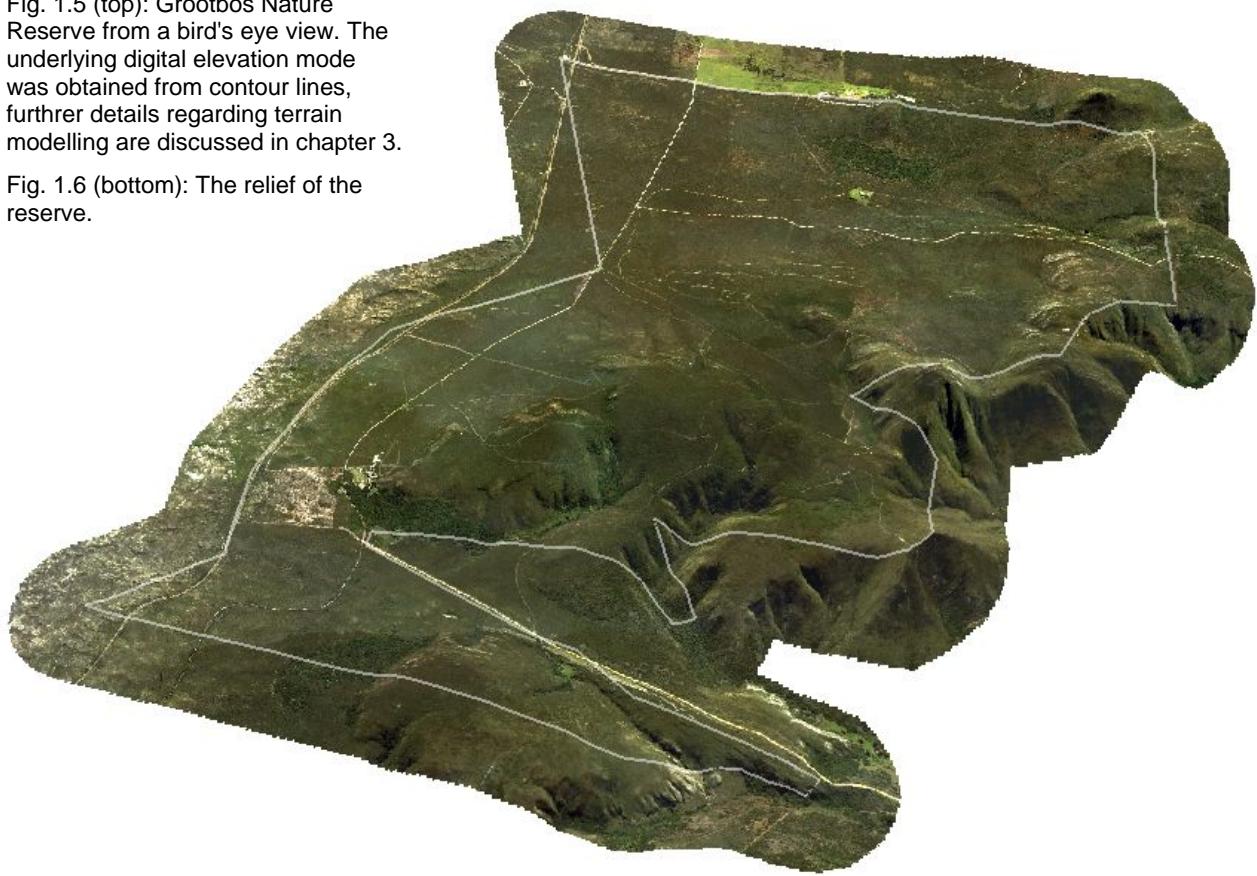


Fig. 1.3 (top): The facilities of the Garden Lodge, Walker Bay in the background. The visible dunes belong to the Walker Bay Nature Reserve (10/2004).

Fig. 1.4 (bottom): The Witkransberg (451 m) is one of the highest points of the reserve (11/2004).

Fig. 1.5 (top): Grootbos Nature Reserve from a bird's eye view. The underlying digital elevation mode was obtained from contour lines, furthrer details regarding terrain modelling are discussed in chapter 3.

Fig. 1.6 (bottom): The relief of the reserve.



## 1.3 Regional settings

### 1.3.1 A historical approach

Hominids are known to have inhabited Southern Africa for the last three million years (Hoffman 1997: 507). For the southernmost portion of the continent, evidence of human settlements obtained from caves dates back a couple of hundred thousand years. Research is going on in Klipgat Cave near De Kelders (about five kilometers away from Grootbos Nature Reserve), promising further knowledge of early human inhabitation of the Stanford-Gansbaai-area. The San (also known as bushmen) were predominantly hunters and gatherers, ways of living supporting relatively low population densities. Their influence on the natural ecosystems was therefore limited. The Khoi-Khoi (called hottentots by the colonialists) had moved on to extensive pastoralism when the first Europeans arrived at the Cape.

The S tip of Africa had some strategic importance since the trade between the European countries and Asia had come up and European ships were sailing round Southern Africa. The names of some places bring to mind Portugese explorers and traders (Cape Agulhas, Natal), who frequently passed by in the late 15th and particularly the 16th century, but they never assigned any importance to the land areas close to the

S Coast of Africa (Thompson 1990: 31f). The Dutch, one century later, did also not consider the land worthy of colonization. However, the way from Europe to Asia was far and the travel time long. The VOC (United East-Indian Company) decided to install a base for reloading the ships with fresh water, fruits and vegetables and for the recuperation of sick employees (Thompson 1990: 33). The Cape Peninsula and the arable lands N and NE of it were chosen (Fig. 1.7), and later on a fort was built at the place of today's Cape Town. Jan Van Riebeeck was in charge of organizing this small-scale colonization, which was started in 1652. The relationship with the Khoi-Khoi was peaceful in the beginning, both parties taking profit from trading activities. Later on, the European settlers (who were still small in number) claimed more and more resources, including fresh water, which led to tensions and finally warfare with groups of the indigenous ethnicity. As people were released from the VOC and hugenottes from France emigrated to the Cape, the colonized area was extended towards the end of the 17th century. Stellenbosch, the second oldest town of today's South Africa, was founded by the governor Simon van der Stel. But still only the arable lands in the vicinity of Cape Town were explored and cultivated in order to produce crops, fruits and wine. Part of the agricultural and domestic work was done

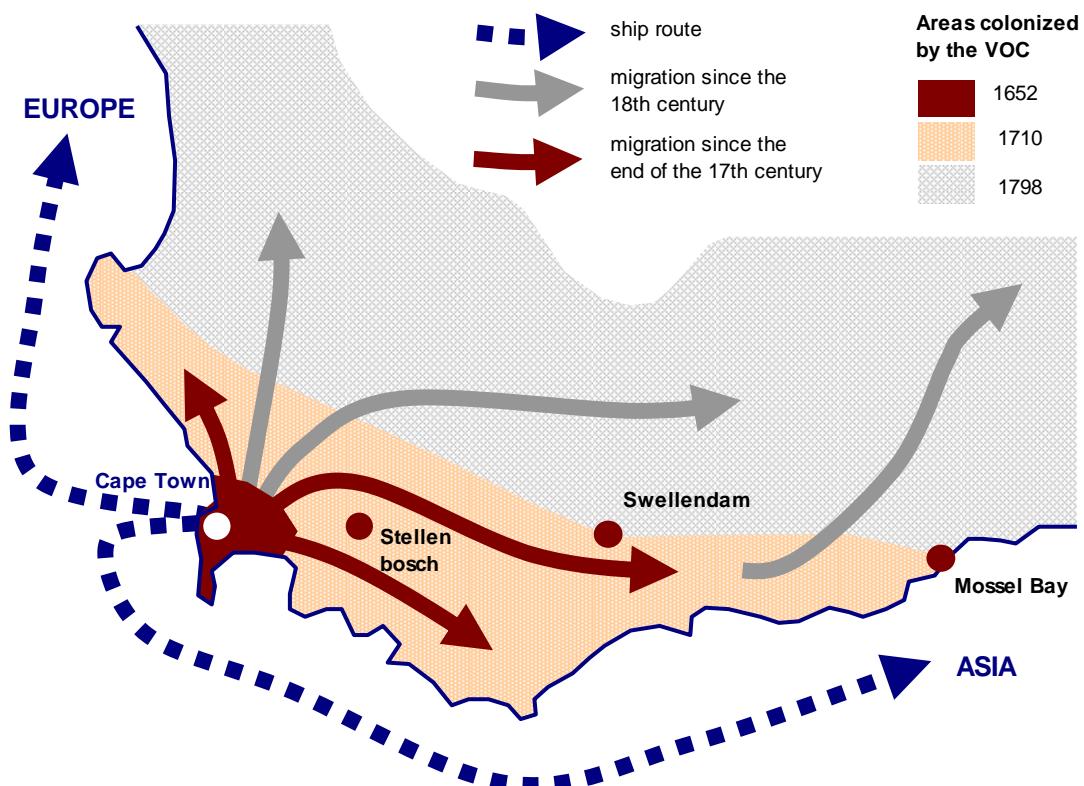


Fig. 1.7: The colonization of the Cape region of South Africa by the VOC and settlers of European origin. Adapted from Thompson (1990).

by slaves. They were most often imported from the S- and SE-Asian region, a certain number of them Islamic. Today, their descendants contribute to the ethnic pluralism of the country and are known as Malay people.

The Khoi-Khoi-people had to choose whether to leave or to work for the new settlers. A large number of them died due to introduced diseases, like the small pox (Thompson 1990: 37ff).

Not all Europeans living in the Cape Colony were able to earn a livelihood from the growth of crops, fruit or wine any more, since most labour was done by slaves and the land was limited. Most farmers were already raising cattle and sheep as a sideline. Therefore, a number of young people chose a new lifestyle, concentrated on extensive, semi-nomadic pastoralism. The vast, semi-arid and arid land areas N of the escarpment were explored, but the so-called "trekboeren" also expanded eastwards, beyond today's Port Elizabeth (Thompson 1990: 46). The Khoi-Khoi were not able to resist, as they had already been weakened by wars, suppression and introduced diseases.

The economy of the trekboeren was largely, but not entirely, based on subsistence (Thompson 1999). The road infrastructure was poor, and it took several weeks to go to Cape Town and back. The social stratification was far less developed than in the core region. Concentrated settlements with administrative function

existed, like Swellendam, but they only consisted of few houses and their function as centers was limited. The social structure of the farmers was characterized by large families. They could not afford a larger number of employees, but some of them owned a slave.

By 1710 the colonized lands extended to Mossel Bay in the E and to today's West Coast National Park in the N (Fig. 1.7). By the end of the 18th century, the frontier had shifted again, so that the area under the control of the VOC corresponded approximately to the Western and Eastern Cape Provinces of today. At the same time (1795) the British contested the role of the Dutch at the Cape and took over a lot of administrative power, partly by violent means. The way of thinking and acting of the - from today's view - more open-minded British people, guided by the protestant ethics and a rather critical view on racial discrimination and slavery, contrasted with the traditional-European Dutch farmers (Afrikaners). Tensions between the farmers and the British authorities led to an extended migration of the former towards NE, a movement known as the Great Trek, leaded by the so-called Voortrekkers. Since these activities did not touch the research area any more, a detailed discussion would go beyond the given scope. More information is provided by Thompson (1990) and Davenport & Saunders (2000).

The situation prevailing in today's Cape Provinces of

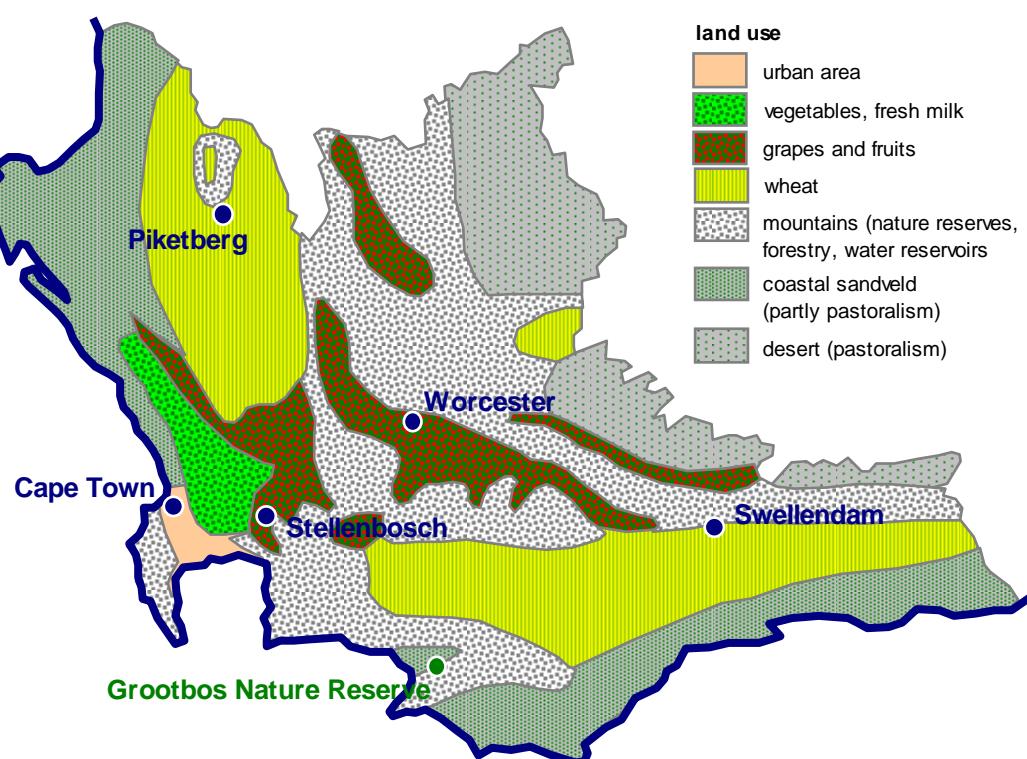


Fig. 1.8: The general land use patterns in the SW corner of South Africa. Adapted from Wiese (1999).

South Africa at the end of the 18th century appeared as highly persistent. Afrikaans, originating from Dutch but including elements of other languages, too, became one of the most-spoken languages in the country. White farmers owned the majority of the land, while indigenous groups were limited to unfavorable sites. Under the apartheid regime, these structures were retained or even accentuated. Laws ruling the possession of land were introduced, clearly favoring the people of European origin (Wiese 1999: 188).

### 1.3.2 Economic activities and social structures in the SW corner of the new South Africa

Today, the economically most important forms of agriculture of the SW corner of the country are the intensive cultures of fruits and grapes (Wiese 2000: 200, Fig. 1.8). They are however restricted to topographically and climatically suitable habitats, centered around Stellenbosch, Franschhoek, Paarl and the Ceres Valley further N. The Agulhas Plain further E is largely covered by wheat farms. The dominant form of agriculture in the coastal belt between Hermanus and the Cape Agulhas, however, is still sheep- and particularly cattle-farming, as it has been since the 18th century. However, the orientation has changed from extensive, subsistent economy to market



oriented herding (Wiese 1999: 196, 200), in places where it is supported by the topography and the soils. Less favorable areas were abandoned (Fig. 1.9) and served for other purposes. Some elderly people used them as residences, or they were retained as status symbols. With the collapse of the apartheid regime the call for a land reform was heard from the public, the realization of which has already begun (Wiese 1999, 188f). The land of the white farmers was competed for by indigenous groups and the state, and the crime against white farmers increased drastically. Some areas were recolonized by the natural vegetation. While cattle farming still plays a role in some of the flat portions of the area, it is competed for or at least joined by other economic activities. One of the traditional ones being the fisheries, which are performed at different scales and different levels of market-orientation.

Tourism is an increasing branch, particularly along the coast line. It is not primarily the scenery, but the marine life attracting tourists from all over the world: Hermanus is well-known for whale-watching and Gansbaai is often mentioned as the world's best place for a land-based observation of these animals. Boat-based whale-watching (Fig. 1.10) or shark cage-diving are prospering activities, providing jobs for a certain number of people. However, all these activities are of seasonal character, mainly limited to the spring. Grootbos Nature Reserve itself, the only lodge of its type along the S coast of Africa, plays an important role for tourism in the region and provides jobs for almost 100 people (status: end of 2004). Linked to the reserve, a life skills and gardening school (Green Futures) was set up in order to provide unemployed people of formerly suppressed groups living in the surrounding towns and villages a chance for education. Further social engagement is planned by the management of the Reserve, the role of which goes therefore far beyond that of a Nature Reserve. A major employer is also the Flower Valley company bordering Grootbos Nature Reserve, specialized in commercial flower harvesting.

Those rather selective developments and initiatives can not hide the fact that many of the social and economical stuctures of the apartheid period persist. All villages and towns are bipolar, principally showing similar features as the large cities like Cape Town or Johannesburg. One part, predominantly inhabited by white-skinned people, shows a regular pattern and is often characterized by its colonial heritage (Stanford),

Fig. 1.9 (top): Mosaic of pastures and fynbos shrubland SE of Grootbos Nature Reserve (view from Witkraalberg, 10/2004).

Fig. 1.10 (bottom): Boat-based whale-watching (*Eubalaena australis*) near Franskraal (10/2004).

and also by indicators of globalization like shopping centers (Hermanus, Gansbaai) and fast-food restaurants. The other part, the so-called township, is exclusively inhabited by people with dark-coloured skin. Unemployment is high, leading to a certain importance of the informal economy.

The impacts of human activities - particularly agriculture, but also urbanization, forestry and indirect effects - on the natural ecosystems are discussed in chapters 2 (for the entire Fynbos Biome) and 5 (for Grootbos Nature Reserve in particular).

## 2 Ecological and biogeographical settings

### 2.1 The Fynbos Biome in a global context

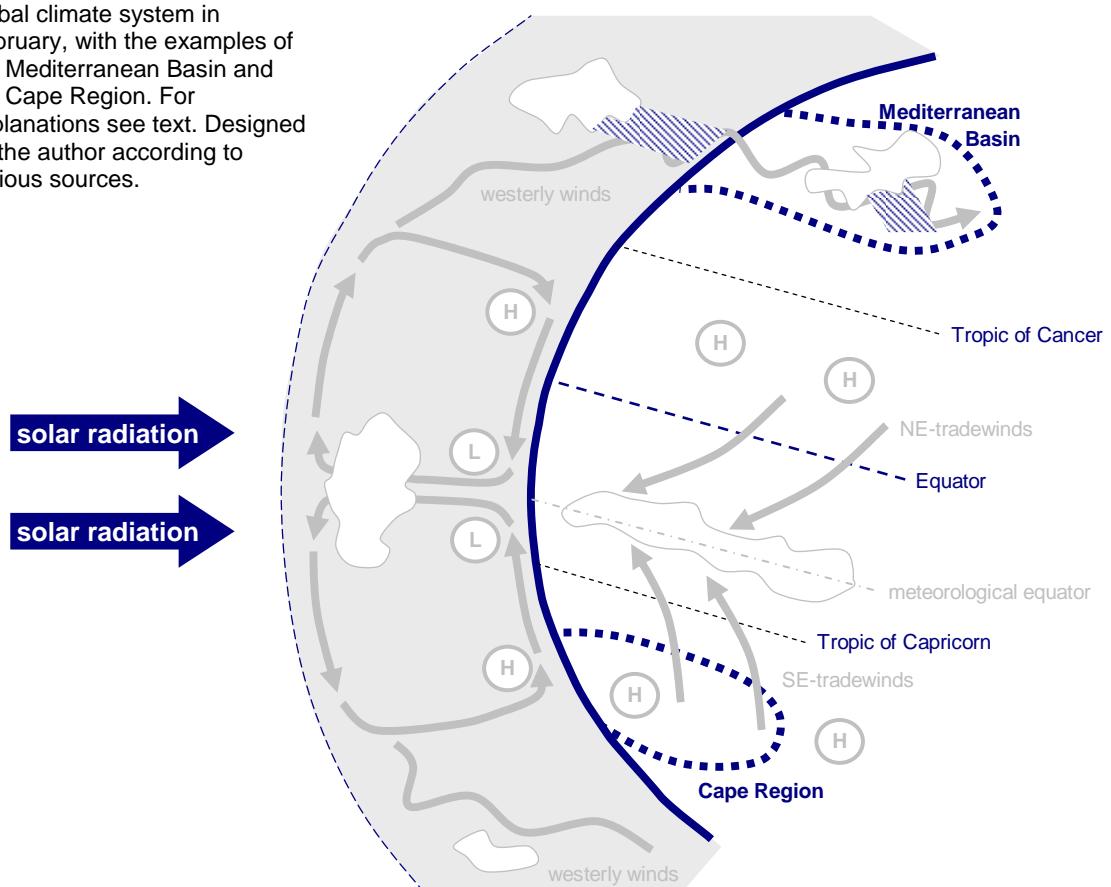
#### 2.1.1 The mediterranean climate within the system of global circulation

To gain a deeper understanding of the climate of the Fynbos Biome and its driving forces, it might be helpful to have a look to the inner tropics, to the meteorological equator. Solar irradiation is intense there, putting a huge amount of energy into the atmosphere. This energy is used to heat and to lift up the air masses to the higher layers of the troposphere. Air cools down and vapor condenses causing considerable amounts of precipitation, fundamental for the ecology of the tropical rain forests. As more and more air is constantly raising, and air can not penetrate the stratosphere, pushing aside towards N and S takes

place in the upper troposphere. These intense air flows, called jet streams, are, on one hand, the main suppliers of energy to the Arctic regions. On the other hand, air is removed on the way to the Arctic in two ways (Kaser 2001, Kerschner 2001):

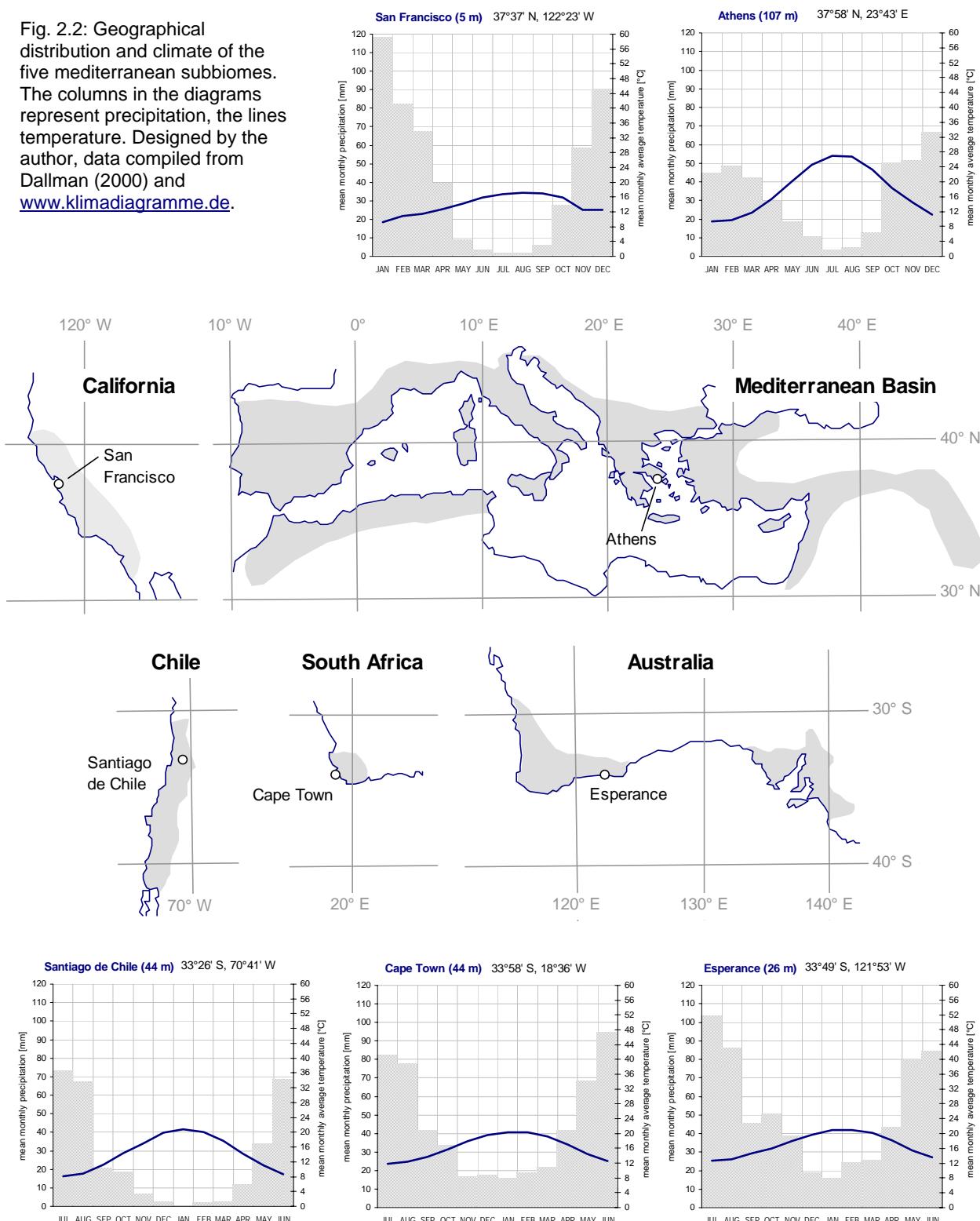
In the lower troposphere of the inner tropics, a low pressure area is created by the uplift of the air masses. As a consequence, air is pulled towards the meteorological equator, causing air flows known as tradewinds. These processes induce a downward movement of high-tropospheric air masses around the tropic circles, causing extremely persistent high pressure cells in the lower troposphere. As air is heated when it moves downwards, vapor can not condense and precipitation is rare, favoring the presence of deserts like the Sahara or the Kalahari. The tradewinds transport dry air masses towards the meteorological

Fig. 2.1: Schematic view of the Mediterranean Biome in the global climate system in February, with the examples of the Mediterranean Basin and the Cape Region. For explanations see text. Designed by the author according to various sources.



## 18 Ecological and biogeographical settings

Fig. 2.2: Geographical distribution and climate of the five mediterranean subbiomes. The columns in the diagrams represent precipitation, the lines temperature. Designed by the author, data compiled from Dallman (2000) and [www.klimadiagramme.de](http://www.klimadiagramme.de).



equator, only providing considerable amounts of precipitation when being forced to rise up along mountain ranges. Closed cycles of air flow - the so-called Hadley cells - are generated N and S of the meteorological equator.

The remaining air of the jet streams continues moving towards the poles, but with increasing absolute latitude they are increasingly forced eastwards by the Coriolis

diversion. In the mid latitudes, they are generally directed eastwards. Actually, they oscillate from NW to SW winds, often forced into cyclonal systems, providing a lot of moist air and thus precipitation to the continents. This is especially true for regions situated near to the E edge or very close to the W edge of a large water body like an ocean, favoring moist-temperate ecosystems.

But what climate and what types of ecosystems are located in between the extremely dry deserts around the tropic circles, often completely devoid of vegetation, and the moist temperate forests of the oceanic mid-latitudes? Is it just a transition or does it show its own character? To answer this question it has to be considered that the meteorological equator is moving some degrees of latitude southwards in the southern summer and northwards in the northern summer. Fig. 2.1 outlines the major constellations and processes. The high pressure cells around the tropic circles and the zones of W winds move N and S, too. As a consequence, regions around 30 - 40 degrees N or S latitude are mainly influenced by the high pressure cells in summer and by the W winds during winter. In regions situated close to an ocean, the W winds provide a lot of precipitation, so that pronounced hygric seasons are present. They are superimposed by thermic seasons: the summers are hot, and the winters are temperate. Five regions all over the world - all of them situated at the W or S edge of continents, roughly between 30 and 45 degrees absolute latitude - share these climatic patterns, showing converging vegetation patterns as a response to the characteristic climate: The Mediterranean Basin, parts of California, Central Chile, parts of SW and S Australia and the Cape Region of South Africa. The climate is called mediterranean, and the whole biome may be referred to as Mediterranean Biome. However, pronounced variations in the fine-tuning of the climate and the vegetation are present between, but also within, the five subbiomes. The Cape Region is maybe most atypical. Fig. 2.2 shows the distribution and the climate of the subbiomes.

The Mediterranean Biome is characterized by hot, dry summers and temperate, moist winters. The similar climatic settings are expressed in converging traits of the vegetation of the five subbiomes (Mediterranean Basin, California, Central Chile, SW and S Australia, Cape Region of South Africa).

### 2.1.2 Plant adaptations and strategies in the Mediterranean Biome

Water is fundamental for the maintenance of all life processes. With few exceptions, higher plants can not tolerate drying up completely. But in the mediterranean climate, there is a pronounced lack of water during the summer months. If there is precipitation at all it is supplied by short, heavy rainfalls, so that the water is quickly evaporated or it runs off. The moisture status of the soil is very poor during average summers, and water is a major limiting factor, except where rivers or lakes cause high levels of groundwater. During winter the soils usually contain sufficient moisture to ensure the life processes of plants (Breckle 2002, Dallman 2003).

The Mediterranean Biome shares its pronounced hygric seasonality with the regions around 10 - 20 degrees N and S latitude, respectively, but there is an important difference, fundamental for plant life: In the outer tropics precipitation takes place mainly during summer, when the temperatures are favorable for biological processes. The consequence are winter-deciduous forests - production takes place in summer, while the transpiration is drastically reduced by dropping the leaves during winter. In the Mediterranean Biome, the case is more complicated (Breckle 2002: 293):

- The main ecological challenge for plant life in the mediterranean biome is the temporal coincidence between favorable temperatures and lacking water supply respectively unfavorable temperatures and sufficient water supply.

The temperatures during winter time are usually high enough for some photosynthetic activity, but nevertheless, most of the mediterranean plant species (excluded those of habitats with sufficient groundwater supply) have developed anatomical and morphological adaptations for the mediterranean climate conditions (e.g. Erschbamer 2002). Some of these adaptations are typically mediterranean, but some of them occur in other biomes as well:

- hard evergreen leaves: leaves with a high proportion of sclerenchymatic tissue retain their shape during periods with low turgescence - fading is prevented or at least delayed.
- hairy leaves can help to reduce heat absorption, but also transpiration by reducing turbulent air exchange.
- small leaves reduce the area for transpiration. They are also less susceptible to extreme heating, as turbulent flow is promoted. This turbulent flow, on the other hand, can also increase transpiration.
- small stomata can reduce transpiration, balanced by a high density of stomata
- a deep and well developed root system helps to exploit the little amount of moisture in the soil, especially in deeper layers
- compact growth forms provide some kind of shelter as turbulent flow is reduced and moisture can not escape easily from the canopy. The most extreme forms are cushion plants. They are not only typical of the Mediterranean Biome, but also of the deserts. As the cushions can also store heat and nutrients, this life form is favorable in cold environments, too.
- succulence helps to endure drought periods by storing water in the leaves or in the stem. This

adaptation is not typical for the Mediterranean Biome, but for the adjacent hot deserts.

Most plants have developed life strategies representing a combination of some of the adaptations described above (Fig. 2.3):

Most characteristic is sclerophyll (Fig. 2.4), applied by shrubs and trees and including not only the name-giving hard leaves, but also small stomata and an extensive root system. The leaves may be somewhat reduced or hairy, and a tendency towards a compact growth form may be present. The strategy allows the plant to extend photosynthesis far into the dry season, albeit on a reduced level forced by the reduction of transpiration. The highest photosynthetic rates are

and the depleting water status. The consequence is the drying up of the leaves, which are shed when there is no more water supply from the soil. Malacophyll is widely applied by mediterranean plants, but it is also a frequent adaptation in the temperate and the hot deserts. Some species can develop and shed leaves several times a year, reacting spontaneously to precipitation events.

Sclerophyll is a strategy to tolerate drought stress, malacophyll partly to avoid it. But malacophyllous shrubs still survive the summer with organs above the soil surface - like sclerophyllous plants, they are phanerophytes or sometimes chamaephytes. A large group of plants has not developed specific morphological adaptations to cope with drought, but

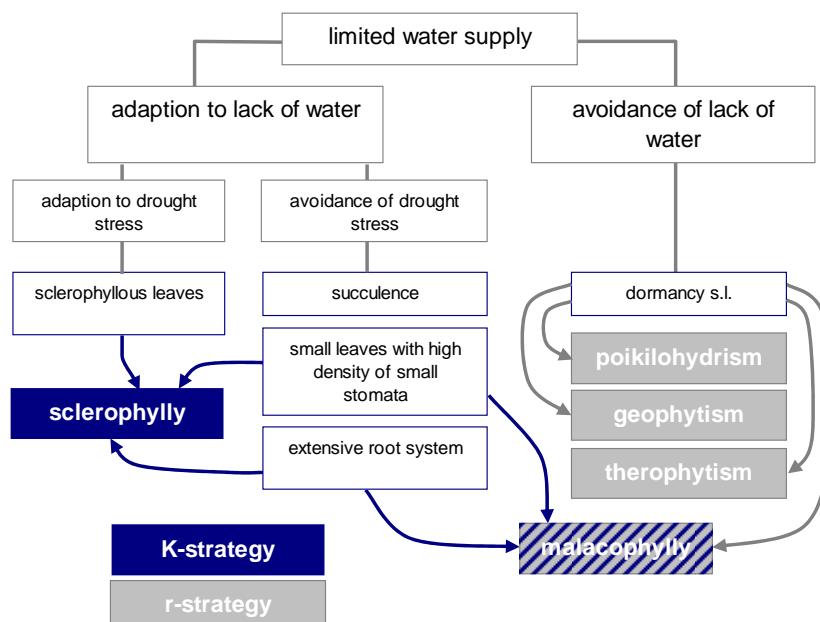


Fig. 2.3: The most important adaptations and strategies of plants to the mediterranean climate. Designed by the author according to different sources.

usually maintained during spring when the soil still contains sufficient water and temperatures are favorable. Sclerophyllous shrubs and trees have evolved convergently in all five mediterranean subbiomes and dominate most natural ecosystems there. Along gradients towards better summer water supply they lose importance because sclerophyllous leaves are expensive for the plant and only economic if pronounced drought stress is present (Breckle 2002: 260ff).

Another combination of adaptations is called malacophyll (Fig. 2.5) The leaves of malacophyllous plants (mainly shrubs) are softer and deciduous. Furthermore, they are often hairy in order to reduce transpiration. As soon as temperatures are favorable, the plant tries to achieve as high a photosynthetic rate as possible, neglecting the reduction of transpiration

they apply a very useful strategy instead: They complete their life and reproductive cycles during spring, when temperatures are favorable and the soil still contains some moisture. Once the soil dries out, they die back below the soil surface and survive as tubers or rhizomes or they die completely and only survive as seeds until the conditions are favorable again. Such plants are called geophytes and therophytes (annuals), respectively (Fig. 2.6). They are typical both of mediterranean and of desert biomes. In the latter they run their life cycle not periodically, but rather episodically after rain events. They are titled as ephemeroid (surviving as rhizome or tuber) or ephemeral plants (surviving as seed), respectively. Geophytes and Therophytes thrive best if the soil is nutrient-rich and if a lot of sunlight is available. For this reason I will come back to them when discussing the role of fire.



Fig. 2.4: The sclerophyllous tree *Quercus agrifolia* from the mediterranean subbiome in California (09/2003).



Fig. 2.5: The malacophyllous shrub *Artemisia tridentata* is concentrated in the Great Basin, but is also present in parts of the mediterranean subbiome of California (09/2003).



Fig. 2.6: The geophyte *Asphodelus fistulosus* is present all over the mediterranean Basin, but also, like in the picture from Morocco, in the adjacent deserts (03/2004).

Mediterranean Basin, sclerophyllous forests with *Quercus ilex* the dominant species are considered the natural vegetation of eu-mediterranean habitats. In California open woodlands (Fig. 2.6) dominated by sclerophyllous oaks (*Quercus agrifolia*, *Q. chrysolepis* and *Q. wislizenii*) and by some semi-deciduous (*Q. engelmannii*) or winter-deciduous oaks (*Q. douglasii*), are relatively abundant and considered as near-natural, although it is not clear to what extent the open character of these forests has been induced by grazing activities. The mediterranean parts of Australia contain open woodlands made up of several evergreen species of the genera *Eucalyptus*, *Acacia*, *Banksia* and *Hakea*. In Central Chile, moist, S-facing slopes support scrub forests, but in the Cape Region, forest-like ecosystems are rare (Dallman 2003). In short, there is no typical forest type for the Mediterranean Biome, which can be tracked over all five subregions. But what then is the connecting feature of the vegetation over the continents? In fact, it is the shrubland widespread in all the mediterranean subbiomes, slightly different in structure from region to region, but of similar characteristics. It is called macchia in the Mediterranean Basin (including the lower, malacophyllous units regionally known as phrygana, garrigue or batha, Fig. 2.7), chaparral in California (Fig. 2.8), matorral in Chile, kwongan in Australia and fynbos in the Cape Region.

But why are these shrublands so abundant, when tree growth would be allowed by the climatic conditions? In the Mediterranean Basin, they are often considered as successional periods from abandoned agricultural and grazing land to forest. In Australia and especially in the Cape Region, the low vegetation is attributed to poor soils. However, the more or less constant, or at least seasonal, climatic and edaphic variables are complemented by periodic and episodic factors called disturbances, reshaping the ecosystems within short time periods (e.g. Van Wilgen et al. 1987). One major disturbance factor is present all over the mediterranean subbiomes of the globe, supposed to suppress forest and to promote shublands: FIRE. Only in Central Chile is the influence of fire rather limited (Dallman 2003).

Up to now, only discussed morphological adaptations on the meso- and microscale were discussed, mainly leaves, roots and stomata. But which vegetation types are shaped by these sclerophyllous, malacophyllous and annual elements? Do these plants build up forests, scrublands, or open forests? Due to the strong human influence prevailing in the mediterranean areas since millennia or at least centuries, it is not easy to reconstruct the natural conditions. At least for the



Fig. 2.7: Garrigue in the Grand Canyon of Cassibile (Sicily, Italy, 06/2003).

Fig. 2.8: Coastal chaparral in Marin County close to San Francisco. Photo by Elisabeth Bacher (09/2003).

### 2.1.3 Fire and mediterranean ecosystems

During long, dry summers biomass and especially litter become extremely dry, so that the matter burns easily once it is ignited. Nowadays the source of ignition is frequently human activity, but natural fires are usually ignited by lightning - not necessarily occurring more frequent in the Mediterranean Biome than elsewhere. According to Schulze (1997a: 34), far more lightning strikes are being recorded along the E Coast of South Africa than in the mediterranean part. But in the moist climate of the E Coast, fires can not ignite or they extinguish quickly, while in the mediterranean area they can spread easily during the dry season.

By humans, wildfires are usually considered as negative things and as a threat - no wonder, when remembering that they destroy a large number of buildings every year and frequently cause injury and death in S California. Irrespective of that, fire in mediterranean ecosystems should be considered as natural periodical

process, like floods in riverine forests, being important for the maintenance of the ecosystem features, including biodiversity. The natural frequency differs considerably from region to region and strongly depends on the local conditions, so that it is impossible to provide confident averages. In general, a natural return interval of a decade up to a few decades can be considered as usual. Also the mode of fire-induced succession is subject to change from subbime to subbiome. As the general succession patterns for the chaparral are well established and contain many characteristics also present in the other subbiomes, it should be presented here as basis for the discussion of fire ecology in the fynbos in chapter 5. Schoenherr (1992: 344f) described a typical succession between two fire events in the Lower Chaparral of California:

The fire destroys most of the above-surface biomass, the mineral nutrients are deposited on and in the soil. In the following spring, geophytes and therophytes germinate and complete their life and reproduction cycle very quickly, favored by the excellent nutrient supply and availability of sunlight. The small-leaved sclerophyllous shrub *Adenostoma fasciculatum* (Rosaceae), which is often quite abundant before the fire event, has the ability to resprout after fires. But it is growing very slowly, so that it can not come to dominance in the first years. Instead, seeds of the genus *Ceanothus* (a sclerophyllous shrub, distributed all over the chaparral with more than 40 species) germinate soon - *Ceanothus* gains dominance over the next years and suppresses *Adenostoma*. But the individuals of that fast-growing Rhamnaceae are rather short living and begin to die about 10 years after the fire. They can not reproduce, because they do not have the ability to resprout by suckers, and seeds remain dormant since they can only germinate after fire events. Now, *Adenostoma fasciculatum* has free way to gain dominance. It forms dense canopies, so that it is difficult for other species to resist and the biodiversity decreases, until a fire destroys the stand of *Adenostoma* and the succession can begin again. Fig. 2.9 summarizes the major stages of succession.

According to Breckle (2002: 266), *Adenostoma* attains its densest cover after 22 - 40 years and almost ceases growth after 60 years. The long-term character of chaparral remains unchanged with a fire frequency of twelve years. With a frequency of less than two years, non-resprouting shrubs can not survive because their seedlings are killed by the fire.

If no fire occurs for some decades larger shrubs and trees invade the chaparral so that, without any fires, most of the chaparral vegetation would disappear and be replaced by forest or woodland. Without fire,

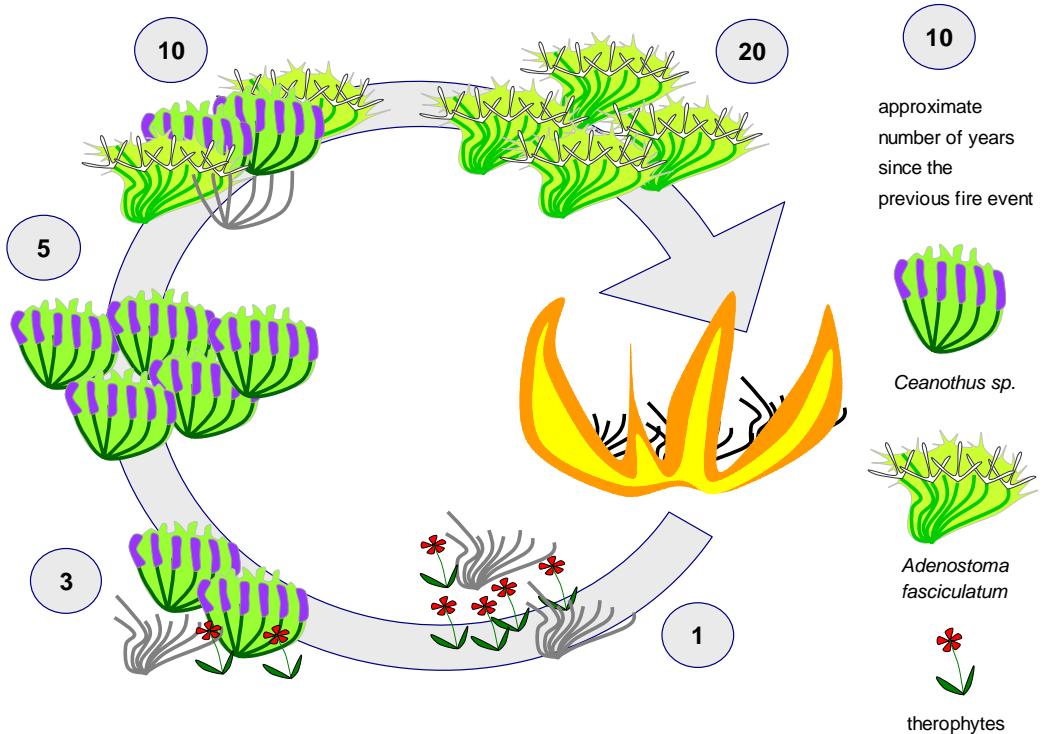


Fig. 2.9:  
Succession  
between two fire  
events in the  
chaparral of  
California.  
Designed by the  
author  
according to  
Schoenherr  
(1992).

chaparral could only persist at extremely exposed sites with poor soil development (Schoenherr 1992).

It is important to emphasize that natural fires are usually of a limited spatial extent, because only a relatively small amount of litter can accumulate during the average return period, and because the probability is high that recently burned areas without litter are around, stopping the spread of the fire. Natural chaparral ecosystems are usually mosaics of different succession stages after fires, and the same is true for fynbos. Over many decades humans have tried to suppress fire but with unplanned long-term consequences: huge amounts of litter was accumulated and the fires escaping human control were often disastrous, endangering human life and property (Schoenherr 1992: 342, Dallman 2000: 10).

## 2.2 The Cape Flora - endemism, diversity and composition

### 2.2.1 Diversity and endemism - facts and models

Comprising of about 9000 species of vascular plants in about 90,000 km<sup>2</sup>, including more than 6000 endemics, the regional diversity of the Cape Floristic Region is extraordinarily high for an extratropical region of its size (Goldblatt & Manning 2002: 281). The level of endemism is more comparable to an isolated island than to a part of a large continent. The determinants for those patterns are manifold - including ecological variables and geographical settings, but also historical aspects and reproductive traits of the floristic elements. Since Grootbos is located in the core of the Cape Floristic Region (Fig. 2.10), most characteristics can be applied to the reserve.

Fig. 2.10: The approximate extent of the Cape Floristic Region (cover of the Fynbos Biome). Adapted from Cowling et al. (1997a).

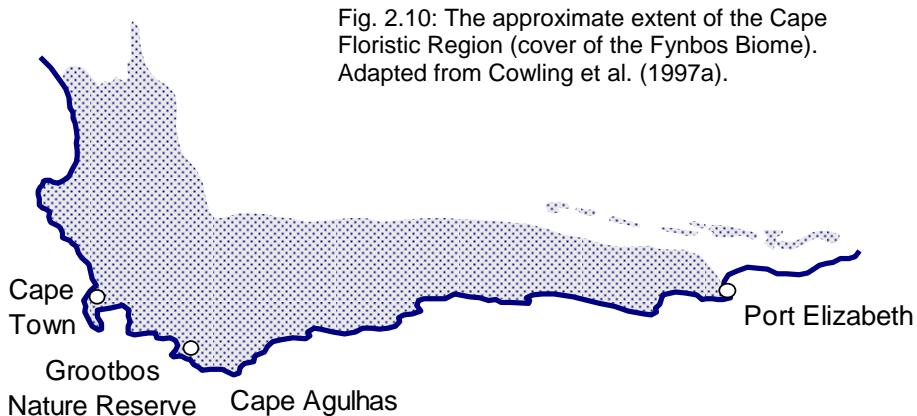




Fig: 2.11a and b: Two closely related endemics to the Cape Floristic region: *Protea eximia* (Van Staden Flower Reserve) and *Protea cynaroides* (Tsitsikamma National Park, 11/2004).

The Cape Region of South Africa is often recognized as one of the six floral kingdoms, appreciating its unique status and the steep floristic gradient towards neighbouring regions. Goldblatt & Manning (2002: 281) reject the concept of floristic kingdoms and use the more neutral term Cape Floristic Region. Its extent roughly coincides with the Fynbos Biome. The striking characteristics of the Cape Floristic region can be summarized as following (data compiled from Goldblatt & Manning 2000, compare also Tab. 2.2):

- high regional biodiversity: 9004 species of vascular plants have been recognized, including 112 ferns and 8892 flowering plants. Such a level of species richness is comparable to some tropical areas of a similar size, but is unique among extratropical ecosystems.
- high concentration of biodiversity: 77.4 % of the flora represent the twenty largest families, and 21 % are assigned to the ten largest genera. The largest genus, *Erica*, comprises 658 species, 7.3 per cent of the species of the Cape Flora.

- high endemism at the species level: 6208 flowering plant species or 68.7 % are endemic to the Cape Floristic Region. The same is true for 160 of the 942 genera (16.3 %), which is a rather moderate value.

The rate of endemism is second only to some extremely isolated islands, but it is much higher than for the other areas with mediterranean climate. Indeed, the geographical settings of the Cape Floristic Region have much in common with an island, at least in the ecological sense (Goldblatt & Manning 2002: 295). It is surrounded by semi-arid regions with strikingly different life conditions. In general, the substrate is very poor, whereas in adjacent regions other geological formations provide richer soils with a higher nutrient status. The nearest region with comparable conditions is SW Australia, and, indeed, there are strong floristic connections between the two subcontinents, although they have been separated since the Jurassic.

Much more debated than endemism is the huge field of biodiversity, which will be focused on in this section. Biodiversity is a popular expression today, and it is a highly political topic too. In fact, the term has different meanings - species diversity, ecosystem diversity, functional diversity or structural diversity are only some of them. This section will specifically deal with species diversity of fynbos ecosystems, which is also no unambiguous term. Three types of species diversity can be characterized (Cowling et al. 1997c: 448):

- alpha-diversity means the number of species within a certain ecosystem at the community level
- beta-diversity describes the shift of species composition among community-level ecosystems with different environmental properties
- gamma-diversity accounts for the shift of species among community-level ecosystems with similar environmental properties but different geographical location

Alpha-diversity is the most easy one to be expressed quantitatively, with a single number. The mean value for fynbos communities is 15.9 for 1 m<sup>2</sup> and 65.7 for 1000 m<sup>2</sup>, respectively, without significant variations throughout the biome (Cowling et al. 1997a: 117). Compared with other biomes on the global scale, the species richness at fynbos sites is moderate. It is doubled by tropical rainforests, but also exceeded by certain European grasslands and grazed woodlands of the Mediterranean Basin (Israel). Compared with mediterranean-type ecosystems of the other continents, fynbos does not show an extraordinarily high alpha-diversity. It doubles the values for the chaparral, but it does not differ significantly from SW

Australia. Little data is available for the matorral, but it seems that alpha-diversity is equal or even slightly higher there than in the fynbos (Cowling et al. 1997c: 466).

Alpha-diversity (or local richness) is determined by an array of controls. The number of niches (the environmental heterogeneity) of the considered site is one of the major determinants. Heterogeneity is strongly influenced by the complexity of the spatial - especially vertical - structure of the ecosystems, which in its turn is determined by the favorableness of the environmental conditions and the amount of available energy. In fire-prone ecosystems like the fynbos, the temporal heterogeneity is also of major importance. Each stage of succession after a fire provides niches for certain different species.

Alpha-diversity is not determined by the habitat alone, but also by external factors: There is a clear interrelation between species richness on a regional scale and local richness (Cowling et al. 1997c: 464). In areas with high regional richness the pool of potential invaders into a certain community-scale habitat is larger, promoting the probability of immigration of new species, especially in cases of disturbances like fires.

Beta- and gamma-diversity are more problematic to quantify than alpha-diversity, but both express the unusually high diversity of the Cape Floristic Region. Cowling et al. (1997c) used the concept of regional diversity for a comparative study all over Southern Africa, using just the total sum of species for quadrats of 1.41 to 2680 km<sup>2</sup> for the fynbos, comprising of 173 to 2256 species. The authors tried to investigate the correlations between regional diversity and an array of control factors.

Unsurprisingly there is a positive correlation between area and species richness. But area should be considered as surrogate for other factors, especially heterogeneity, rather than as primary control. In regions with homogeneously dispersed resources the species-area curve levels off quite early. In contrast, the Fynbos Biome shows highly heterogeneous patterns of environmental controls like precipitation, soil, slope and aspect, all of them connected to the rather mountainous terrain. The species-area curve hardly levels off because new combinations of resources are always explored when the investigated area is expanded (Cowling et al. 1997c: 453). The consequence is an extraordinary high regional species richness.

The variable of heterogeneity can therefore be used to explain the high regional diversity of the Fynbos Biome compared to adjacent biomes, like savanna or succulent karoo. But in comparison with the mediterranean biomes of the other continents this argument fails (Goldblatt & Manning 2002: 296f).

Normalized to the area, the regional richness is significantly lower in all of them despite similar or even higher environmental heterogeneity. SW Australia, with substrates similar to the Fynbos Biome, shows the highest values despite the lowest environmental heterogeneity.

Favorableness of the environment and availability of energy show no substantial correlation to regional diversity in the fynbos, in contrast to adjacent biomes of Southern Africa. The same is true for the seasonality of the climate and for the irregularity between different years. In the Chaparral, regional diversity can particularly be related to energy availability, but less to heterogeneity like in the fynbos (Cowling et al. 1997c: 458).

In many cases, overlapping areals of species with different centres of distribution cause comparatively high diversity at ecotones, as described by Schoenherr (1992: 358f) for the Desert Chaparral. Also valid for some areas situated within the transition zone between the fynbos and the ecosystems of the E Coast, so-called edge-effects can not be a reason for the high diversity of the biogeographically very homogeneous core of the Fynbos Biome.

There is considerable evidence showing that speciation history plays a major role as determinant for regional species richness in the Cape Floristic Region. The Fynbos Biome provides very old environments where speciation has been able to take place over a long time without significant disturbance. The few records available from the Pleistocene indicate only minor climatic variations compared with the other mediterranean biomes. The highly seasonal climate may have been present since the late Tertiary, while the majority of the substrate is several 100 millions of years old. Due to the sclerophyllous leaf habit induced because of millions of years of poor nutrition, the taxa were preadapted to the advent of the mediterranean climate (Goldblatt & Manning 2002: 284f). Biological lineages adapted to the environmental conditions could evolve into a lot of different taxa by an adaptive radiation, preserving their traits of adaptation, leading not only to high species numbers, but also to the concentration of diversity to those preadapted lineages (compare beginning of this section and Tab. 2.2). Therefore, most endemics are neoendemics. One of the characteristics of these is the high number of species per genus or family, which is especially true for the Ericaceae. Paleoendemics and -subendemics are present in the Cape Floristic Region as well. They are usually endemic or subendemic at the family level, like Bruniaceae, Grubbiaceae or Penaeaceae, comprising of only a small number of species. They represent groups adapted to ancient conditions and some of them are therefore centered in rather moist habitats.



Fig. 2.12: *Berzelia intermedia*, a paleoendemic member of the Bruniaceae family (Tsitsikamma National Park, 11/2004).

In ecologically comparative, but younger ecosystems (California, Mediterranean Basin), species diversity is lower, indicating that regional diversity is not converging in geographically distant, but ecologically similar habitats. No evidence exists that diversity would approach a threshold after a certain period of development (Cowling et al. 1997c: 450). This is also indicated by the steady worldwide increase of the Angiosperm richness since the Cretaceous.

The speciation history is associated with the ability of the species pool to rapid genetic change. In the fynbos, most plants are reseeders, allowing rapid evolution connected to the short turnover of generations induced by frequent fire events (Goldblatt & Manning 2002: 297ff). The SW Australian mediterranean flora and vegetation have quite similar ecological and reproductive features like the South African, so that the lower regional diversity can largely be assigned to the less pronounced environmental heterogeneity. In the Matorral, in contrast, most shrubs are resprouters - the consequence is much slower evolution, so that beta-diversity is very low and Central Chile is one of the species-poorest mediterranean biomes. California lies somewhere in between mediterranean Central Chile and the Fynbos Biome. The difference in speciation between reseeders and resprouters can be observed beautifully between the genera *Adenostoma* (Rosaceae) and *Ceanothus* (Rhamnaceae). The former is a resprouter and has only one species in the Chaparral, the latter is a reseeder and has more than 40 species -

both deriving from the same ancient group, the Madro-Tertiary flora (Graham 2000, Ornduff 1974). Wisheu et al. (2000: 950) also underlined the connection between the abundance of reseeders and species richness, mentioning low risk of extinction and short generation times as some of the major driving forces. The authors suggested a connection of the strategy of reseeding with nutrient-poor soils based on data from the fynbos and the Australian kwongan because it may not be worthwhile for a plant to invest in a lignotuber or a similar storage organ deep in the soil because the majority of the nutrients after a fire are available near to the soil surface.

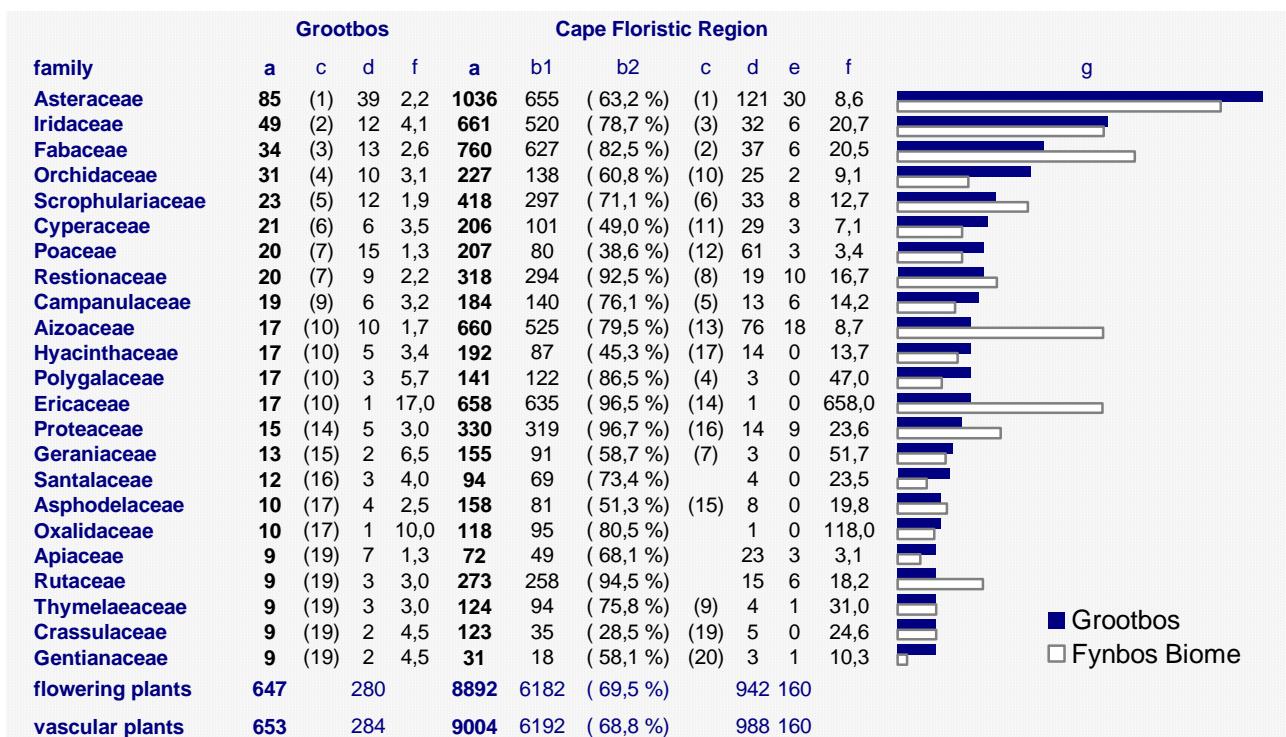
The potential for evolution among reseeders may also differ considerably (Goldblatt & Manning 2002: 298). An important set of determinants are the features of the seeds. Species with large, heavy seeds without adaptations for dispersal have a higher potential to rapid diversification than species with smaller, easily dispersed seeds: genetic isolation is facilitated if alleles remain spatially separated once they are established, and are not intermixed again. A striking example of this effect in the fynbos are the genera *Nylandtia* (berry fruits, 2 species) and *Muraltia* (dry fruits, more than 100 species), both representing the Polygalaceae.

In the previous decades an array of mathematical relationships has been established to predict the species richness as a function of area. As discussed above, area is only a surrogate for other controls, so that different relationships are valid for ecologically distinct regions. Models including environmental factors, such as variables of favourableness or seasonality exist as well, but for the SW Fynbos the highest values for  $R^2$  have been achieved with simple models (Cowling et al. 1997c: 455).

Tab. 2.1 illustrates different models applied to the area of Grootbos Nature Reserve ( $17 \text{ km}^2$ ). The different models show a wide range of results, between 187 and 559 species, with an average of 410 species. Unfortunately, Cowling et al. (1997c) did not mention the expected errors of the models. The real number of vascular plant species on Grootbos Nature Reserve is located beyond the upper limit of the predicted range of values: 653 indigenous species have been recorded, including 6 ferns and 647 flowering plants (compare App. 1.1).

model	n	area range [ $\text{km}^2$ ]	S	$R^2$	reference
$\log S = 2.69 + 0.25 \log A$	8	0.27 - 471	559	93	Kruger & Taylor (1979)
$\log S = 2.58 + 0.253 \log A$	19	0.20 - 1609.3	435	90	Cowling et al. (1992)
$\log S = 2.21 + 0.27 \log A$	15	1.41 - 4800	187	90	Cowling et al. (1992)
$\log S = 2.61 + 0.227 \log A$	11	no data	460	90	Cowling et al. (1997c)

Tab. 2.1: Prediction of the species diversity of Grootbos Nature Reserve according to different area-species models ( $A = \text{area in } \text{km}^2$ ,  $n = \text{sample size}$ ,  $S = \text{number of species}$ ). Data compiled from Cowling (1997c).



Tab. 2.2: The quantitatively most important families of the Cape Floristic Region and of Grootbos Nature Reserve (a = number of species, b1 = number of endemic species, b2 = percentage of endemic species, c = ranking according to the number of species, d = number of genera, e = number of endemic genera, f = ranking according to number of genera, g = percentage of the species within each family compared with the total species number). There are no endemic genera at Grootbos, the only endemic species is *Erica magnisylvae* - data compiled from the Grootbos species list (App. 1.1) and Goldblatt & Manning (2000).

## 2.2.2 The Cape Flora and the Grootbos flora - a comparison

The Cape Floristic Region not only shows unique features regarding endemism and species diversity, but also composition of its flora (Tab. 2.2). An extraordinarily high proportion of the Cape Flora is concentrated in 20 families. The dominance of Asteraceae and the third position of Fabaceae, both belonging to the most diverse families worldwide, are predictable, as well as the sixth place of the Scrophulariaceae. But there are hardly any other floristic regions in the world where families like Iridaceae, Aizoaceae, Orchidaceae, Restionaceae, Ericaceae and Proteaceae could develop a diversity comparable to the Cape - adjacent desert ecosystems may be excluded in the case of Aizoaceae, and Australia for Proteaceae and Restionaceae (Goldblatt & Manning 2002: 282). All of these families, Orchidaceae excluded, show rates of endemism of at least about 80 per cent, Proteaceae and Ericaceae even show 97 per cent each - indicating that they could evolve over a long time without a lot of exchange with adjacent regions. Conspicuous is the extremely low number of genera of Ericaceae - maybe explained by a relatively recent advent in the Cape Floristic Region (Goldblatt & Manning 2002: 288).

Compared to other floristic regions, the families show relatively even patterns all over the Cape, in contrast to the species. It may be useful to compare the bulk of the Cape Flora with the flora of Grootbos, regarding the importance of the dominant families (tab 2.2). The Asteraceae are the most diverse family both at Grootbos and in the Cape Floristic Region. Its proportion of the total species richness is even slightly higher on the reserve, probably due to the high proportion of Dune Asteraceous Fynbos. Most of the families represented by small, temporarily inconspicuous species (Iridaceae, Hyacinthaceae, Campanulaceae and Orchidaceae) are overrepresented on the reserve as well. The reason, however, may not be because of ecological nature, but rather because of the intense sampling efforts of H. Lutzeyer during the previous years, which was concentrated on such taxa. Poaceae, Cyperaceae, Polygalaceae and Gentianaceae show similar patterns, but for less clear reasons. Fabaceae, Scrophulariaceae, and Rutaceae are underrepresented on the reserve, as well as are all of the diagnostic families of the fynbos - Proteaceae, Restionaceae and Ericaceae. The reason may be due to the limited distribution of mountain fynbos on Grootbos Nature Reserve (for a detailed account of this phenomenon please consult chapters 4 and 5). The Ericaceae, however, contribute one of two endemic

species, *Erica magnisyphae*, to the reserve. The second endemic is *Cliffortia anthospermoides* (Rosaceae).

The Aizoaceae, one of the most abundant families of succulents in the Cape Floristic Region, have a comparatively clear higher diversity throughout the Biome than on the reserve, probably connected to the distant locations from its centre of distribution, the arid biomes of Southern Africa, and the different environmental conditions there. Towards the interior a significant increase of the abundance of these families can be expected. The second family of succulents, however, the Crassulaceae, is only slightly underrepresented on the reserve.

Overinterpretation of the diagram in Tab. 2.2 should be avoided as it may contain a lot of noise. Since new species are continuously discovered both on Grootbos Nature Reserve, (a publication on this issue is planned) and in the remaining Fynbos Biome, the account above is prone to rapid outdated, but the broad patterns are not supposed to lose their validity.

## 2.3 Fynbos structure and function

### 2.3.1 Geography and environment of the Fynbos Biome

After discussing the general climatic settings and fire patterns in the Mediterranean Biome and presenting the uniqueness of the Cape Floristic Region, it is time to introduce the ecology of the shrubland dominating the subbiome in the Cape Region of South Africa and covering the vast majority of Grootbos Nature Reserve: the fynbos. Figure 2.13 shows the geographical range of the Fynbos Biome.

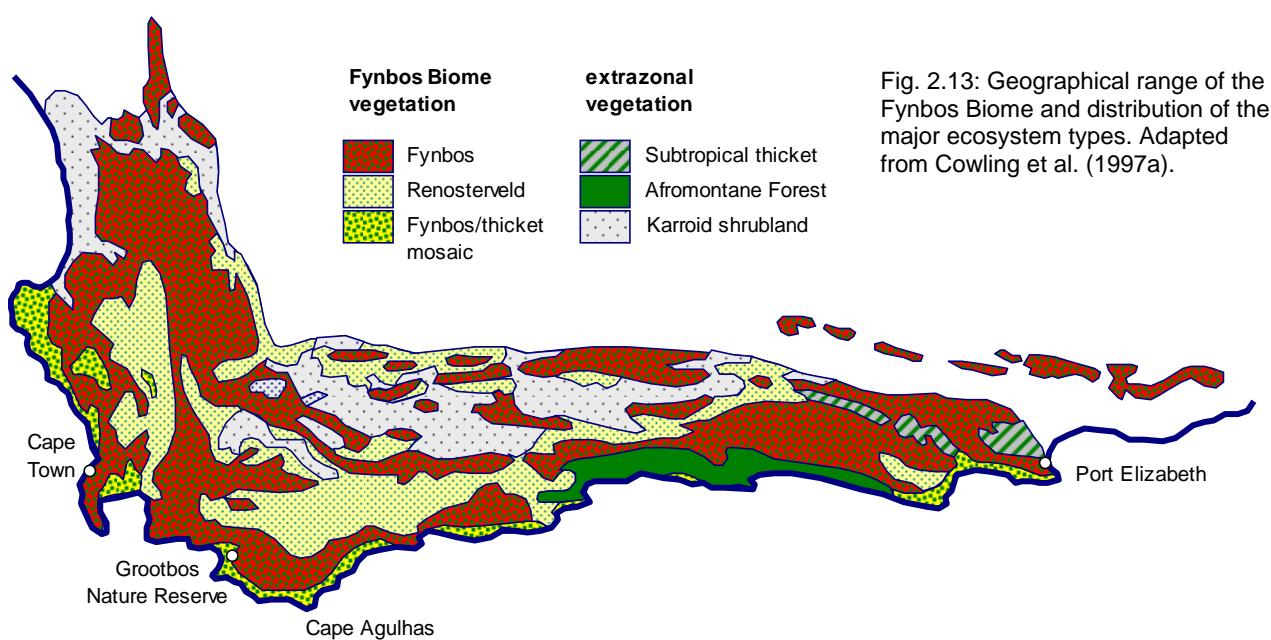
The environmental conditions are anything but constant throughout the biome. Precipitation varies from 210 mm in the driest habitats of the interior to

3000 mm in some coastal mountain regions. Along parts of the coast the ecological importance of fog precipitation should not be neglected. In the W part of the biome there is a clear winter maximum of precipitation, associated with the mediterranean climate. However, the summer drought is less pronounced than in most of the other mediterranean subbiomes (compare diagram in Fig. 2.2, Cowling et al. 1997a: 99f, Schultze 1997). Towards E, the share of summer precipitation increases.

The substrate is highly diverse in terms of grain size and drainage conditions. Concerning nutrient status it is markedly poor. This is particularly true for the old, nutrient-depleted quartzitic sandstones of the Table Mountain formation and adjacent groups as well as for the sands deriving from them. Only limestone deposits near to the coast as well as carbonaceous dunes provide more nutrients to the plants (Cowling et al. 1997a).

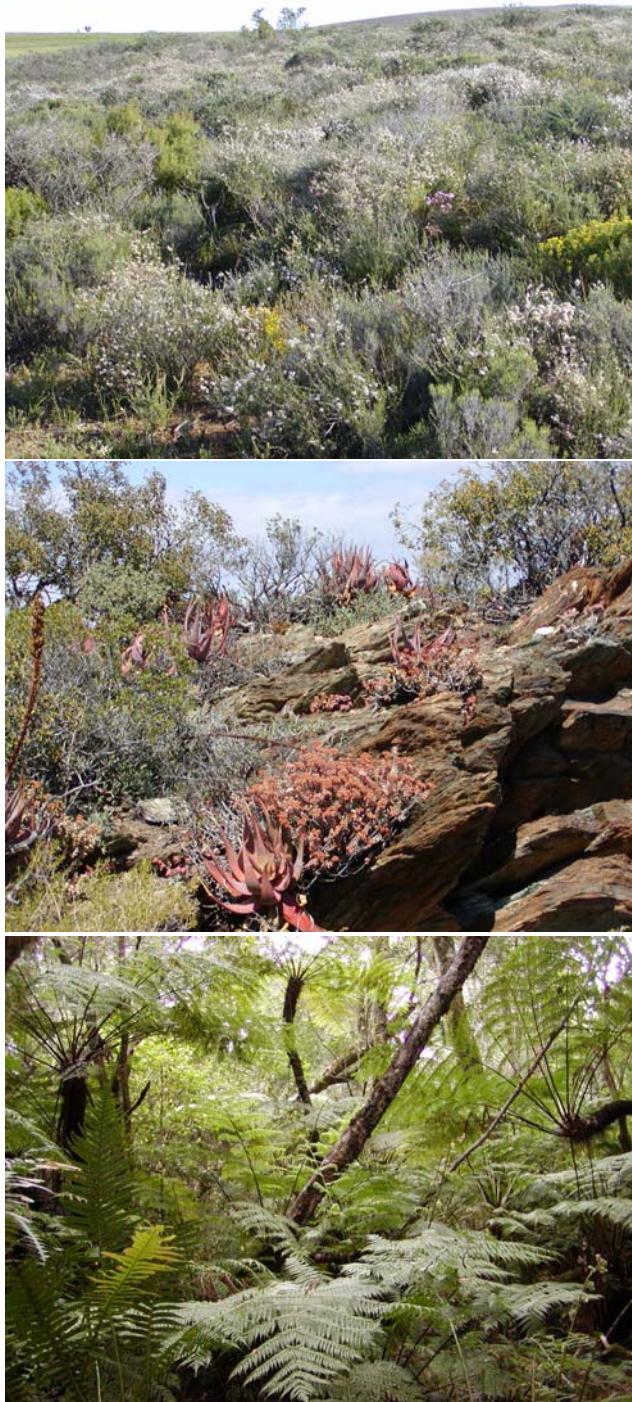
The fine-tuned combination of environmental controls determines the type of ecosystem predominating at each location within the biome. Adjacent to or intermixed with fynbos, other types characterized by distinctive features are also present within the Fynbos Biome (Cowling et al. 1997a):

- renosterveld (zonal, Fig. 2.14): a low, fire-prone asteraceous shrubland characterized by the Asteraceae *Elytropappus rhinocerotis* (renosterbos, rhinoceros bush) and Poaceae as undergrowth
- karroid shrubland (zonal, Fig. 2.15) with a high abundance of succulent elements
- strandveld (zonal): a thicket composed of subtropical shrubs and fynbos elements
- subtropical thicket (extrazonal), mainly



- composed of shrubby resprouters
- afromontane forest (extrazonal, Fig. 2.16): forest patches of varying floristic composition

Renosterveld and karroid shrubland are concentrated in interior regions with little precipitation, the subtropical thicket mosaic to the E edge of the biome. Strandveld and afromontane forest range over much of the Fynbos Biome, especially near to the coast. Since both are present on Grootbos Nature Reserve (the strandveld not in its typical formation), they should be discussed in more detail, but preferably in connection with fire ecology rather than now.



The term fynbos literally means "fine bush". Cowling et al. (1997a: 101) provided a comprehensive definition based on some important characteristics, the major points of which can be summarized as follows:

Fynbos is ...

- an evergreen, fire-prone shrubland
- structurally characterized by the common occurrence of overstorey proteoid shrubs, high cover of ericoid shrubs, mainly Ericaceae, and the universal presence of restioids
- largely confined to sandy, infertile soils

Fynbos has also been described as heath, and indeed, its structural and ecological features are quite similar to high-altitude heathlands of tropical Africa. Similarities to shrublands of the other subbiomes, like macchia, chaparral or matorral are obvious, but there are also unique features of fynbos vegetation, differentiating it to some extent from its counterparts on the other continents. It shares some of these unique features with the kwongan vegetation of the Mediterranean Biome of Australia.

### 2.3.2 The main structural elements of fynbos vegetation

The most important structures and processes shaping fynbos vegetation will now be described in more detail. Fundamental features of the ecosystems are the life forms lending fynbos vegetation its character. Remembering the life strategies of mediterranean plants it may be useful to become familiar with the major life forms of the fynbos described by Cowling et al. (1997a: 103):

- proteoids are shrubs, 1.5 - 5 m high, with sclerophyllous, small- to medium-sized, isobilateral leaves. The group is characterized by a high percentage of reseeders (more than 80 per cent) and large seeds exceeding 5 mg. Among the families Proteaceae are dominant.
- ericoids are dwarf- to mid-tall shrubs, 0.5 - 2 m high, with fine, rolled, but sclerophyllous leaves. More than 60 per cent of the species are reseeders, and, in contrast to the proteoids, they have fine seeds (less than 1 mg). Besides the Ericaceae, the Asteraceae, Fabaceae, Rutaceae, Proteaceae and several other families can also

Fig. 2.14: Renosterveld (Darling Renosterveld Reserve, 09/2004).

Fig. 2.15: Karroid shrubland with representatives of the genera *Aloe* and *Crassula* (Worcester, 09/2004).

Fig. 2.16: Interior of the large Afromontane Forest near to Knysna, with tree ferns *Cyathaea capensis* (11/2004).

form ericoids.

- restioids are dwarf- to mid-size evergreen graminoids. More than 80 per cent are resprouters. Restionaceae are dominant, but some Poaceae and Cyperaceae also appear as restioids.
- geophytes are evergreen or deciduous herbs with below-ground storage organs. All of them have the ability to resprout. Monocots like Iridaceae, Liliaceae, Orchidaceae and Amaryllidaceae are typical geophytes of the fynbos.
- fire ephemerals are forbs or dwarf to low shrubs (0.5 - 1 m), more than 80 per cent reseeding. Asteraceae are the most abundant, followed by Scrophulariaceae, Fabaceae, Poaceae and the Mesembryanthemoideae subfamily of the Aizoaceae.
- obligate resprouters appear as low to tall shrubs with sclerophyllous, small- to medium-sized, dorsiventral leaves. They are most frequently represented by Anacardiaceae, Celastraceae and Ebenaceae.

Fig. 2.17 shows the numbers of species assigned to each life form. The structurally dominant proteoids are much less diverse than the other life forms. Ericoids, with 3000 species, are by far the richest group, while obligate resprouters, actually elements of the subtropical thickets, are only represented by 102 species.

The structure of fynbos is based on the same principles over most of its spatial extent. There is a certain overstorey of proteoid shrubs, while the lower layers are mainly ericoid and restioid. Depending on the detailed ecological conditions (mainly precipitation, substrate and fire incidence, Fig. 2.18), the coverage and height of the proteoid shrubs and the composition and structure of the lower layers shift. Less obvious, the floristic composition of the ecosystems varies to a much greater extent between different habitats than

the structure, this being related to the high regional diversity discussed above. According to the predominant life forms different structural types of fynbos can be distinguished (Cowling et al. 1997a: 102).

**Proteoid fynbos** (Fig. 2.19) is most frequently related to deep, well-drained soils of the lower slopes (up to 950 m). The substrates vary over a wide range from colluvial sands to limestone and determine the prevailing subtype of proteoid fynbos. The major genera of the overstorey are *Leucadendron* and *Protea*, with a high spatial species turnover. Also on Grootbos Nature Reserve, several compositions of the subtype are present (compare chapter 1 and Privett et al., unpublished). In general, proteoid fynbos may be described as low to tall, open to closed shrubland. Its major feature is a cover of the proteoid overstorey of at least 10 per cent, with a height of 1.5 meters or more. Only some communities in the coastal forelands are lower.

**Ericoid fynbos** (Fig. 2.20) has its core distribution in finer-grained soils of the upper slopes less susceptible to drought and usually moist for the majority of the year. These conditions prevail on the S-facing slopes of the coastal mountains, with precipitation averaging above 1500 mm per year. Ericoid fynbos can be described as low- to mid-high, closed, leptophyllous shrubland, mainly consisting of ericaceous ericoids and with a high abundance of restioids. The relatively moist conditions enable the presence of paleoendemic families like Bruniaceae and Peneaceae. Nevertheless, Ericaceae are absolutely dominant, followed by Restionaceae.

**Restioid fynbos** (Fig. 2.21) frequently occurs on coarse, drought-prone substrates of N-facing slopes, and also on poor-drained habitats with fine substrate, where shrubs can not compete successfully with restioid grasses. Restioid fynbos has the lowest shrub cover (less than 30 per cent), but the highest cover of restioids (at least 60 per cent) throughout the fynbos. The height of the canopy, which can be mid-dense, but

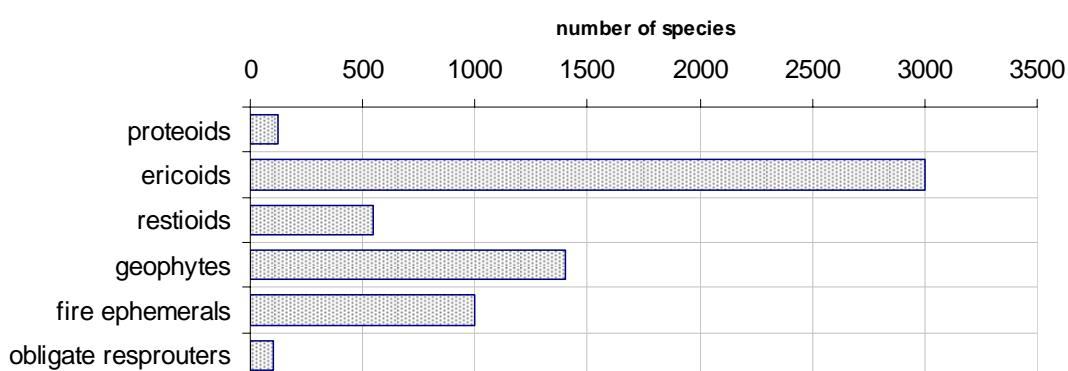


Fig. 2.17: Species numbers of the major life forms in the fynbos. Data compiled from Cowling et al. (1997a).

also closed, varies from dwarf to tall.

**Asteraceous fynbos** predominates in the driest habitats all over the fynbos biome along the transition to renosterbos and karroid shrubland. Precipitation ranges from 450 to 950 mm per year and the soils are shallow, usually not exceeding a depth of 0.4 m. The subtype may also be dominant on calcareous dunes of the coastal lowlands (like it is at Grootbos) with an annual precipitation of less than 550 mm. Asteraceous fynbos has a low total cover and can be described as low- to mid-tall, open to mid-dense leptophyllous shrubland. Non-ericaceous ericoids have a high cover, and the grass cover can be considerable. The floristic composition is diverse, including *Elytropappus rhinocerotis* as an element from the renosterbos (in the internal regions) and certain resprouting shrubs from the subtropical thicket in the coastal regions.

**Grassy fynbos** is concentrated at the transition to the easternmost parts of the Fynbos Biome with a high proportion of summer rain. As the name suggests, the grass cover is high, intermixed with non-proteoid small-leaved shrubs and forbs. Closed-scrub fynbos with its high cover of shrubs with mesophyllous leaves is largely confined to riparian habitats.

## 2.4 Fynbos and fire

Like in the other mediterranean biomes, biomass and litter dry out during summer and become susceptible to ignition. The flammability of leaf biomass primarily depends on the surface/area-ratio, the abundance of sclerenchymatic tissue and the presence of etheric oils.

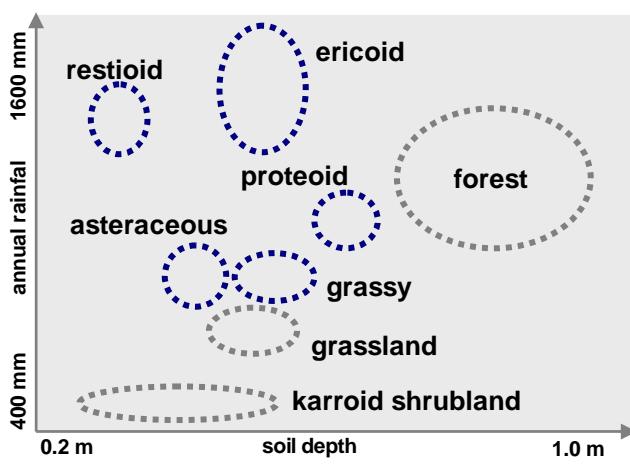


Fig. 2.18: Ecogram illustrating the prevalence of the major ecosystem types of the mountains of the Fynbos Biome along environmental gradients. Data adapted and generalized from Cowling et al. 1997a.



Fig. 2.19: Proteoid Fynbos at Du Toits Kloof Pass with *Protea nerifolia* (09/2004).

Fig. 2.20: Ericaceous Ericoid Fynbos in the Jonkershoek Mountains (09/2004).

Fig. 2.21: Restioid Fynbos on limestone with *Thamnochortus fraternus* at Cape Agulhas (11/2004).

In general, leaves of Fynbos shrubs are more susceptible to fire than most trees of the region (Bond 1997: 423).

The probability of a Fynbos ecosystem being hit by a fire event is most closely related to the accumulation of litter. In roughly the first four years after a fire proteoid fynbos can hardly burn because the litter accumulation takes place too slowly (Bond 1997: 426, Van Wilgen 1987: 8). In grasslands and savannas, the situation is quite different. Fynbos experiences a natural fire interval averaging between 11 and 15 years. Few stands remaining fire-free for more than 40 years (Van Wilgen 1987: 8). Polakow & Dunne (1999) underlined that the fire interval is partly determined by stochasticity. Although lightning is comparatively rare in the Fynbos Biome (Schultze 1997: 34f), it is considered as a major natural source of ignition. Van Wilgen (1987: 6) also mentioned rolling rocks as a source. For the Cederberg region events like rockfalls were estimated to only account for about five per cent of all ignitions, except in the case of earthquakes when the rate can rise up to 23 per cent (Bond 1997: 424). The spread of fires is largely connected to the SE tradewinds which prevail during the main fire season (Privett, pers.comm., Privett et al., unpublished: 13).

Many of the trees and shrubs in savannas can survive fires because they are protected by thick bark, or because they can resprout from suckers. In the fynbos, taxa like *Cliffortia* or *Euclea racemosa* (obligate resprouters of subtropical origin) have the ability to resprout from root suckers. Others, like *Protea nitida*, have persistent bud banks protected by bark or can survive if the apices are not damaged by fire (*Leucospermum conocephalum*, *Mimetes fimbriifolius*). Surviving above-surface organs bear the advantage that the plants can keep their position in the canopy after fire events and do not have to regrow (Bond 1997: 428).

Most of the proteoid shrubs in the fynbos neither have the ability to survive fires above the surface, nor are they resprouters. Instead, their generative reproduction is strongly associated with fire events. Some of them are serotinous - they store seeds of at least two generations in their canopy to release after they are burned and killed (Le Maitre 1987). Serotiny is strongly associated with shallow, infertile and rocky soils in fire-prone environments, where the soil does not provide favorable conditions for storing the seeds. It is largely restricted to taxa with big inflorescences with the ability to store numerous large seeds. For this reason serotiny is most common among members of the Proteaceae family (Fig. 2.22) and rarely occurs in other families native to the Fynbos Biome (it is also widespread among conifers). The majority of the species builds up a seed bank in the soil, with hard



Fig. 2.22: *Protea repens* is one of the most common serotinous obligate reseeders, occurring throughout almost the whole fynbos biome including Grootbos Nature Reserve and like in the photo, in the Van Staden Flower Reserve 50 km west of Port Elizabeth (11/2004).

seed coats enabling germination only after breakdown of the coats by heat (fire), mechanic stress like passage through the gut of an animal or by steps of animals (Bond 1997: 430). Germination of the seeds can also be induced by smoke or by the favorable nutrient status of the soil after a fire event. In general, the reproduction success is proportional to the number of produced seeds (Goldblatt & Manning 2002).

There are further adaptations of reproduction to frequent fire events. The Amaryllidaceae *Cyrtanthus* flowers only after fires, persisting vegetatively in between. Many other monocotyledonous geo- and therophytes and proteoid shrubs show similar adaptations. In general, geo- and therophytes thrive better after autumn fires than after spring fires (Bond 1997: 434). Proteoid shrubs also show stronger regrowth after autumn fires as in winter the conditions for germination are better (there would be loss of seeds during summer). Most natural fires occur in summer (Van Wilgen 1987: 9) but fires in other seasons are not uncommon. Not only seasonality, but also frequency and intensity of fires strongly determine which species can gain dominance afterwards and which are at a disadvantage. If the frequency is too high some species can not mature and produce new seeds during the interval. If the frequency is too low it might be that some species produce too many seeds, so that crowding takes place after the fire. High intensity fires destroy small seeds buried only a few centimeters under the soil surface, while they induce coat-breaking and germination of large, deeply buried



Fig. 2.23: Patches of Afromontane Forest, like here in the Swartboskloof (Jonkershoek National Park) are largely restricted to fire-protected ravines (09/2004).

seeds. Low intensity fires do not affect the latter, but they enable germination of small seeds only slightly buried below the soil surface. Fire size can also play a major role if one considers the recolonization of stands from adjacent stands as important (Van Wilgen 1987: 11). The vast majority of fires occupy small areas of less than 1,000 ha, but the majority of burned areas can be assigned to large fires. However, few fire events exceed an area of 35,000 ha. Since the introduction of prescribed fires as a management tool in the previous decades the average fire frequency as well as the size of the burned areas have decreased considerably.

Fire is not only important for the regeneration of species, but also for the maintenance of the equilibrium of the ecosystems. Decomposition is very slow, leading to a permanent surplus of production. Litter removal is largely connected to fire events (Van Wilgen 1987: 7).

Fynbos shows quite unique features concerning its fire ecology, differing from adjacent ecosystem types like strandveld, which is fairly common on calcareous dunes near the coast. Many of the shrubs are no typical Fynbos elements but originate from other subtropical regions. They either form true thickets or are intermixed with fynbos elements. The non-fynbos elements are characterized by fleshy, ornithophilous fruits and by less flammable properties. Their reproduction is not positively associated with fire events but takes place mainly in between (Cowling 1987: 3).

If, for some reason, fires are excluded for some time, fynbos has to compete with other vegetation types, especially afromontane forest, which has its focus of distribution outside the Fynbos Biome, especially in the

mountains along the E Coast where moisture is available all-year-round and fire is less common. There is no climatic barrier between fynbos and forest - the climate would allow the development of forest in the Fynbos Biome (Cowling 1997a: 105). However, forest patches can only develop in moist ravines (Fig. 2.24) or on outcrops. Tree seeds are frequently transported to the fynbos by birds where they can germinate. It seems that the seedlings of forest trees only survive in fynbos environments if fire does not occur until the seedling has developed protection mechanisms (for example, a thick bark). As leaves of forest trees are less susceptible to fire, a tree can be considered as a small island protected from the fire which also shelters seedlings of other trees. That means that once one tree has established it may initialize a positive feedback leading to a forest patch. On the territory of Grootbos some patches of afromontane forest do exist (see chapters 4 and 5).

Human-induced fires never played the role they played in grasslands and savannas but human activities have become a major source of fire in the fynbos. Some sites were frequently burned to enable sheep and cattle grazing. Compared with California and Australia the importance of fire for conservation issues was recognized quite early (Bond 1997: 438f). Burning has been applied in fynbos management since the 1970s. In the mid 1990s most fynbos ecosystems were managed under a natural burning regime: fires ignited by lightning were allowed to burn but human-induced fires were fought.

A common management tool is also the controlled ignition of so-called prescribed fires which is applied in order to decrease the amount of litter before too much accumulates - a technique that is also applied in California today (Schoenherr 1992: 342). Prescribed fires are directed so as to protect human structures but are not necessarily aimed at conservation issues.



Fig. 2.24: Fire break in the Jonkershoek National Park (09/2004).

Grootbos applies a combination of different fire management techniques (Grootbos Nature Reserve 2002): the whole reserve is divided into a number of blocks representing portions with similar vegetation age - that means, a similar period since the last fire event. The blocks are divided by roads, which require a certain minimum width and which have to be cleared periodically to serve as a barrier for fire. Each block is burned after the natural return period for the corresponding ecosystem. Similar strategies are also applied in other protected areas (Fig. 2.24).

At Grootbos fires are also used in a selective way. Care is taken to improve and maintain the living conditions for the species of the red data list, and efforts are made to protect the milkwood thickets and the patches of afromontane forest from fire, as mentioned in the conservation objectives of the Management Plan for the reserve (Grootbos Nature Reserve 2002). Of course, one objective is also to protect the lodges and other structures from fire and to prevent the penetration of fire from the neighbouring properties into the nature reserve - that means, prescribed fires are also applied there.

Fire is doubtlessly the most important disturbance factor in the fynbos biome, playing a major role in shaping the ecosystems. However, other disturbance factors should not be neglected. Export-oriented flower harvesting (Fig. 2.25) may play a certain role in some places otherwise not affected by human activities but its real importance remains unclear and more research is necessary, such as that of S. Gernandt at the same time as this study.

### 2.4.1 Human influences

Few terrestrial ecosystems worldwide have remained unaffected by human activities of any type, and the S tip of Africa is no exception.

The pre-european peoples were hardly influenced the natural ecosystems to a significant extent. The impact of the early European settlers following up the descent of Jan Van Riebeeck (1752) was more intense, but it was restricted to the immediate vicinity of Cape Town. However, Dallman (2003: 139) reports extensive use of forests on the Cape Peninsula, particularly for the construction of ships.

With the expansion of the trekboeren (see chapter 1), a colonization process of the vast inland areas of today's South Africa began, and in the Fynbos Biome, more and more land was cultivated or at least used for grazing since the late 17th century, continuing until today.

These impacts on the natural ecosystems are distributed unevenly as indicated by figures compiled by Hoffman (1997: 512). Renosterveld is more severely



Fig. 2.25 (top): Flower picking near Pearly Beach, Agulhas Plain: experimental harvest of *Leucospermum cordifolium* by S. Gernandt (10/2004).

Fig. 2.26 (middle): Totally reshaped landscape of the Agulhas Plain, probably on original renosterveld (11/2004).

Fig. 2.27 (bottom): Afforestation with pine (*Pinus radiata*) in the Jonkershoek Mountains (09/2004).

affected than the fynbos itself (Fig. 2.26). This is especially true for Coastal Renosterveld, 85 per cent of which have been lost due to cultivation and urbanization. This figure rises to 96 per cent if only the SW and the W parts are considered. In contrast, almost three quarters of mountain renosterveld still remain in a near-natural condition. The coastal ecosystems in the fynbos are also more severely affected: 53 per cent still remain, as do 47 per cent of the strandveld. Mountain fynbos has been least affected, as 89 per cent remained in a near-natural condition at the time of those studies. These striking differences among ecosystems may be sufficiently explained by differences in their potential for agriculture. As mentioned above, renosterveld is related to nutrient-rich, shaly substrate. Coastal fynbos often grows on alkaline sands, deposited by the sea during periods of high sea level dating back to the Tertiary. In contrast, the acid, nutrient-poor soils of the mountain fynbos are hardly suitable for cultivation. In some places they carry large afforestations of alien taxa of *Pinus* and *Eucalyptus* (Fig. 2.27).

Cultivation, urbanization and fragmentation due to the construction of infrastructure, such as roads, are the most influential direct impacts of human activities on the natural ecosystems. However, indirect influences may be at least equally important in some cases: one may think of air pollution, but this factor is not supposed to play a major role in the fynbos biome. There is one indirect influence posing a serious threat to the natural ecosystems of the fynbos biome: alien plants.

Introduced plant species play a major role in fynbos, since they are able to affect the natural ecosystems. Several introduced woody species have shown the ability to build up thickets or even forests suppressing

the natural fynbos species due to shading and other competitive effects (Richardson et al. 1997). In contrast to the indigenous trees, the populations of alien trees or big shrubs are all fire-resistant, and many of them are even promoted by fire. Therefore, they have the ability to establish themselves in early post-fire stages, in contrast to the indigenous trees. Shrubs and trees with varying taxonomical position, habit and geographic origin invade coastal fynbos and mountain fynbos.

In the coastal fynbos several taxa of *Acacia*, all of them originating in Australia, pose a major threat to the natural ecosystems. *A. cyclops* (Fig. 2.28), *A. longifolia*, *A. mearnsii* and *A. saligna* are the most common species. Some of them were once introduced to stabilize dunes, protecting cultivated areas and infrastructure from being covered with sand. However, their potential as invaders was not realized at that time. Most of these species are bird-dispersed, meaning that their seeds can be transported over relatively large distances. The conspicuous, bright red arils of *A. cyclops* (better known as rooikrans) indicate this dispersal strategy (Richardson et al. 1997).

Mountain Fynbos is rarely invaded by the genus *Acacia*. But it also has Australian invaders, especially serotinous members of the Proteaceae genus *Hakea*, *H. gibbosa* and *H. suaveolens*, invading natural ecosystems. Another large group of invaders from the northern hemisphere is also serotinous: several species of pines were introduced as timber, like *Pinus halepensis*, *P. pinaster* and *P. pinea* from the Mediterranean Basin, and *P. radiata* from coastal California. Some of these are able to escape from afforestations. *P. pinaster* has the highest potential for invading natural ecosystems. The role of alien plants on Grootbos Nature Reserve will be discussed in chapter 5.



Fig. 2.28: *Acacia cyclops* (rooikrans), one of the most aggressive alien plants of the coastal fynbos, here in the Grootbos Nature Reserve (09/2004).

## 2.5 Summary

Having introduced the essential features of mediterranean shrublands and having discussed the ecology of the fynbos in more detail, the most characteristic and distinctive features of the fynbos can be summarized in comparison with its counterparts:

- adaptation to environmental settings: summer drought is less pronounced in the fynbos than in most of the other mediterranean subbiomes. Sclerophyllly may therefore not be solely interpreted as adaptation to seasonal water stress, but also as helping to cope with the poor nutrient status of the soils.
- vegetation structure: macchia, chaparral and matorral form dense canopies extinguishing nearly all sunlight, so that the understorey is sparse. In many types of fynbos, a sparse

overstorey of proteoid shrubs allows a lot of sunlight to penetrate the deeper layers so that a multi-layered structure is possible.

- fire and reproduction: shrubs with the ability to resprout from suckers play a major role in the chaparral and in the macchia. In contrast, regeneration by seeds (with serotiny or a seed bank) is dominant in fynbos ecosystems.
- species diversity: the alpha-diversity of fynbos performs within the range of mediterranean

shrublands. The regional diversity is extraordinarily high - a feature which can primarily be assigned to speciation history.

- relation to other mediterranean subbiomes: there are pronounced floristical and ecological similarities with SW Australia, both with respect to the flora and to the ecosystem structure and function. Reasons for this may be similar soils and the fact that the continents were unified until the Mesozoic.

## 3 Methods

### 3.1 General aspects

#### 3.1.1 The nature of spatial coincidence

From a methodologist's view, the ecological sciences are a cycle of hypothesis generation and testing, at least in the sense of Critical Rationalism. A common way is to develop a mathematical model, the output of which serves as a hypothesis for further research activities. Of course, the models also have to be based on existing knowledge, so that actually the chicken-and-egg-question arises. Some projects are organized in a way that they first try to evaluate existing hypotheses by field studies (e.g. measurements) and then produce new models - and thus hypotheses - from the acquired data.

As mentioned in chapter 1, one major task of this thesis is to produce a vegetation map for Grootbos Nature Reserve. The second task, however, is to link the distribution of the vegetation units with the prevailing environmental conditions. Within the scope of this thesis it is only possible to generate hypotheses serving as input for further research activities. The hypothetic character of the expected results is based on the character of the studies: relationships between vegetation and hypothetic environmental controls are linked to spatial coincidence - and space alone can

never serve as causal explanation for phenomena in the physical world. If there are two balls on a table, ball A hits ball B and ball B starts to move, this does not necessarily mean that ball A has caused the movement of ball B - there is only spatial and temporal coincidence of two events. This example mentioned by Hume is rather drastic but it should illustrate that it is necessary to verify spatial coincidences with direct measurements, for example based on physiological responses to a certain factor.

The vegetation sampling could be identified as empirical work but it is no process of hypothesis verification, rather a descriptive prerequisite for classification and ordination.

#### 3.1.2 Vegetation and environment - a methodical approach

At the first glance, vegetation looks strange in many cases, without obvious order. For the successful application of any scientific method it is necessary to assume some kind of an order. Two major views are existing about the structure of vegetation (Kent & Coker 1992: 16f):

- The Clementsian View accepts the existence of plant communities. Vegetation is considered as discontinuous with sharp transitions between homogeneous communities.
- The Gleasonian View rejects the existence of plant communities. Vegetation is considered as a continuum reflecting gradients in the environmental controls.

The author strongly believes that the "truth" is located between these two polar views. Favoring the Gleasonian View would mean rejecting the idea that many plants have broad ecological optima, that competition is often more important than the environmental controls and that vegetation can modify its environment by itself, for example by acidification, and develop its internal dynamics. Additionally, it assumes that environmental gradients are continuous, which is realistic in some, but not in all cases. On the other hand, the Clementsian View is an oversimplification of the real world. Transitions are

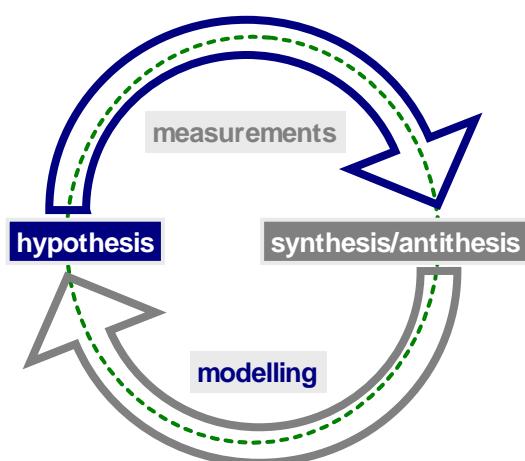


Fig. 3.1: The cycle of hypothesis and syn-/antithesis. Theoretically the cycle would be broken when there is a synthesis, but such a complete synthesis where all possible questions are completely answered is virtually impossible. Designed by the author.

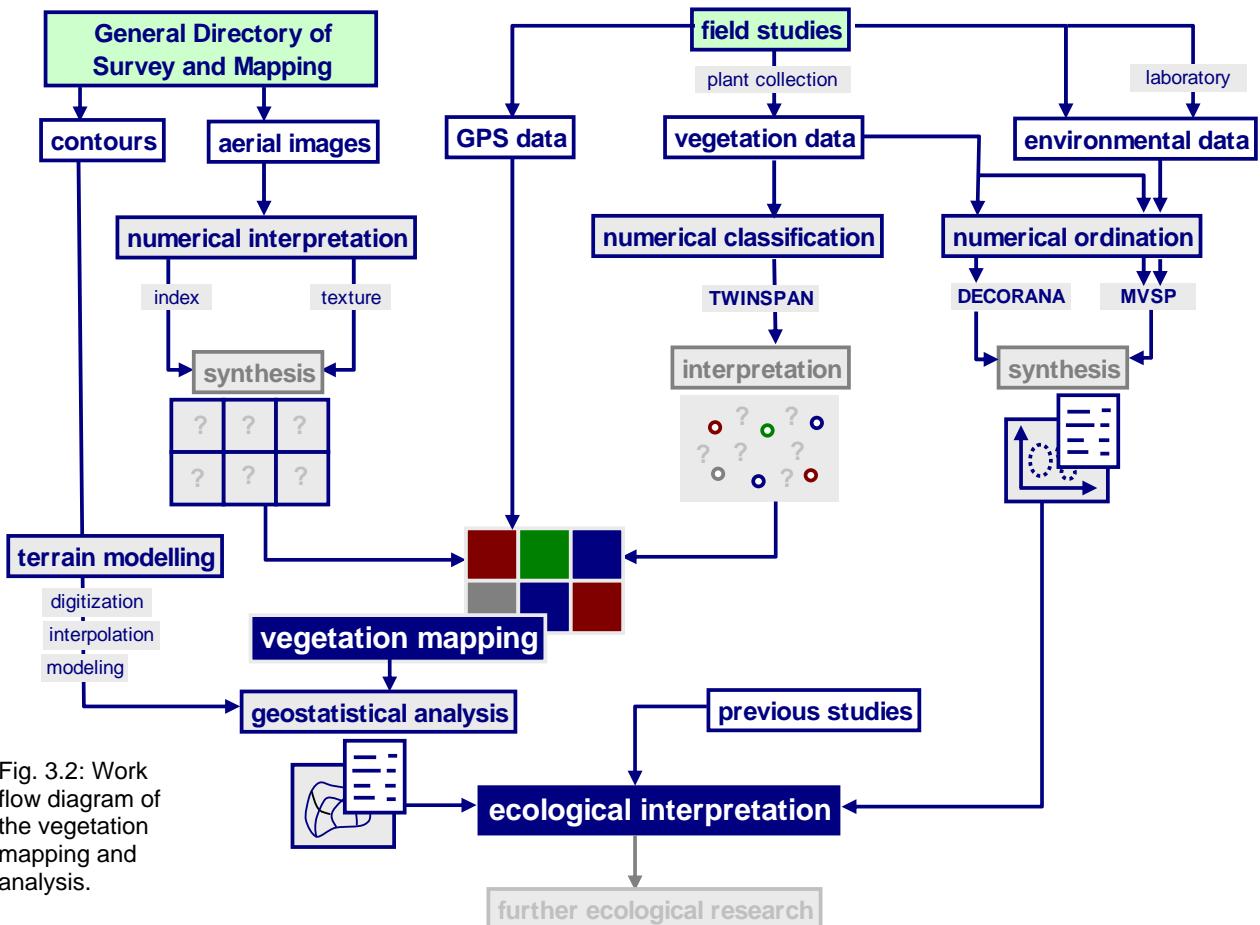


Fig. 3.2: Work flow diagram of the vegetation mapping and analysis.

not always sharp and also within the "homogeneous" domains, variations occur on different spatial scales.

For these reasons the vegetation of Grootbos Nature Reserve will be analyzed according to both views. Plant communities, or at least reasonable vegetation units will be tried to be established for the whole area and to be related to the environmental controls.

Each analysis requires input data, the spatial properties of which can be assigned two two different types:

- two-dimensional (surface) data covering the entire research site: aerial images as rasters and shapefiles of environmental data as polygon vectors can provide data for the whole area but this data is highly generalized due to the limited spatial resolution of the images and the limits of cartography
- one-dimensional (point) data covering certain sites: the floristic inventory and some environmental features are examined in detail for some relevés (the sampling techniques will be discussed below). However, there is no data for the vast area in between the sites.

Analysis of surface data requires different methods than analysis of point data. But the parallel availability

of both types is important so as to approach reality as closely as possible.

Using surface data like aerial images, domains with similar reflection properties can be identified. The presumption that these domains carry similar vegetation is legitimized by the fact that vegetation is the major factor influencing the reflection of visible radiation from the earth's surface (the presumption would not be valid for deserts, for example). However, the spatial resolution of all aerial imagery is far below the threshold allowing the identification of plant individuals and thus, species. This would only be possible for large, single-standing trees but hardly for trees and large shrubs within a canopy and not at all for smaller shrubs, herbs and grasses. For this reason, the domains extracted from aerial or satellite images should be considered as empty boxes to be filled with content, namely - in the ideal case - one vegetation unit for each box.

To identify plant communities - abstract or discrete entities with similar species composition, according to Kent & Coker (1992) - it is first necessary to describe the vegetation of the research area. It is impossible to record the whole area so that a number of relevés (plots, quadrats) of a certain size have to be chosen. The techniques will be discussed in detail below.

In the process of classification, each relevé is assigned to a vegetation unit. The areas between the plots remain black boxes but the data from the plots may be used to assign units to each domain extracted from the aerial images so that the whole research area is covered and a vegetation map is generated.

However, up until now everything has been descriptive, and nothing is known about vegetation-environment-relationships. To be able to use the vegetation map for the extraction of such data, additional information about the environmental controls is necessary. Relating the spatial distribution of these factors to the spatial distribution of vegetation units is called geostatistical analysis and will be discussed in detail below.

It is also possible to investigate vegetation-environment-relationships for point data. This type of analysis is called numerical ordination. The samples from the relevés are examined regarding their floristic correspondence or the species are examined regarding their presence in different relevés. The relevés or species are then aligned along the two or three most significant axes. If environmental data is available from

the plots it is possible to examine which axes correspond to which environmental factor. The different methods and computer programs for numerical ordination will be discussed in more detail below.

Fig. 3.2 gives an overview of the relationships of the major working tasks of the analyses outlined above, as they will be applied in this study.

## 3.2 Numerical vegetation analysis

### 3.2.1 Sampling

Vegetation sampling on Grootbos (Fig. 3.3) has already taken place in 1997. 48 rectangular relevés were analyzed for their floristic composition and their major environmental features. Since as the area of Grootbos Nature Reserve has been extended from 1061 ha to 1700 ha and some parts of the reserve were rather neglected during the previous survey a number of new relevés had to be established. To keep the dataset consistent, the parameters and procedures from the previous samplings were reproduced as exactly as possible.

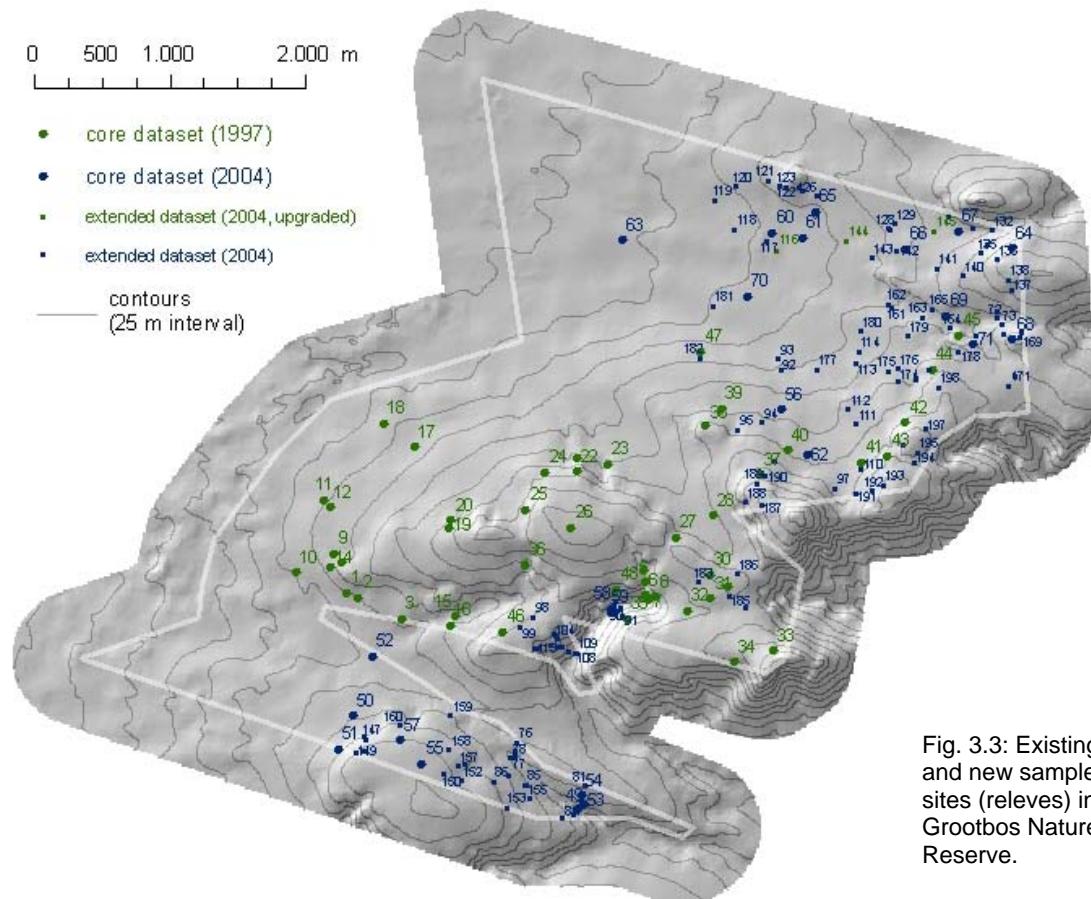


Fig. 3.3: Existing and new sample sites (relevés) in Grootbos Nature Reserve.

variable	unit/remarks	method <sup>1)</sup>	a	b	c	d
elevation	m asl	altimeter / GPS / DEM <sup>1)</sup>	✓	✓	✓	✓
slope	degree	clinometer / DEM <sup>2)</sup>	✓	✓	✓	✓
aspect		compass / DEM <sup>3)</sup>	✓	✓	✓	✓
vegetation age	years time since the last fire (low fire frequency = 100 years, no fires = 1000 years)	map	✓	✓	✓	✓
geology	fertility ▲ 4 Plio-Pliocene dunes and limestone 3 recent sand dunes and sandstone derived colluvium soils 2 ferruginized sands (red) 1 leached sands derived from sandstone	estimation	✓	✗	✗	✗
soil depth	cm depths of more than 100 cm were recorded as 100 cm	steel rod / hardwood rod <sup>4)</sup>	✓	✓	✗	✗
rock cover	per cent	estimation	✓	✓	✗	✗
soil characteristics <sup>5)</sup>						
acidity	pH measured in 0.01 mol l <sup>-1</sup> CaCl <sub>2</sub> solution		✓	✓	✓	✗
texture	nominal Sand, Clay, Loam		✓	✓	✓	✗
resistance	Ω		✓	✓	✓	✗
Na (Sodium)	mg/kg		✓	✓	✓	✗
P (Phosphorus)	mg/kg		✓	✓	✓	✗
K (Potassium)	mg/kg		✓	✓	✓	✗
Ca (Calcium)	mass per cent		✓	✓	✓	✗
Mg (Magnesium)	mass per cent		✓	✓	✓	✗

<sup>1)</sup> DEM data were applied to all analyses<sup>2)</sup> clinometer data was applied by default, DEM data were applied if no clinometer data were available<sup>3)</sup> compass data were applied by default, DEM data were applied if no clinometer data were available<sup>4)</sup> for relevés 01 - 48: steel rod; for relevés 49 - 71: hardwood rod<sup>5)</sup> for relevés 01 - 48: 3 random samples per relevé; for relevés 49 - 71: 1 sample per relevé; all samples were analysed by the Eiensburg College

The relevés were subjectively chosen in order to represent homogeneous patches of vegetation. This can cause problems regarding the analysis because the environmental dataset may not be representative. However, the author chose to prefer the consistency of the dataset. Each relevé covered 50 m<sup>2</sup>, 10 m long

code	growth form (1+2)			leaf form (4+5+6)	
	habit	size	shape	cons.	size (length)
1	2	4	5	6	
0	not relevant	not relevant	not relevant	not relevant	not relevant
1	tree	> 10 m	broad	soft	> 10 cm
2	shrub/shrublet	5 - 10 m	intermediate	hard	> 5 - 10 cm
3	perennial	> 2 - 5 m	narrow/linear	succulent	> 2 - 5 cm
4	geophyte	> 1 - 2 m	dissected	.	> 1 - 2 cm
5	graminoid	> 0.5 - 1 m	reduced	.	<= 1 cm
6	annual	<= 0.5 m	.	.	.
7	climber	.	.	.	.
9	no data	no data	no data	no data	no data

growth form codes		leaf form codes	
TREH	tree, high	1+1	BLH broad leaves hard (1,2)+2+(1,2+3)
TREM	tree, medium	1+2	BLS broad leaves soft (1,2)+1+(1,2+3)
TREL	tree, low	1+3	SHRH shrub, high 2+3
SHRH	shrub, high	2+3	SHRM shrub, medium 2+4
SHRM	shrub, medium	2+4	SHRL shrub, low 2+5
SHRD	shrub, dwarf	2+6	SLS small leaves soft 1+1+4
PERH	perennial, high	3+4	ERI ericoid 2+(1,2)+5;
PERM	perennial, medium	3+5	(2,3)+(1,2)+(4,5)
PERL	perennial, low	3+6	x+x+3
GEOH	geophyte, high	4+4	SUC succulent
GEOM	geophyte, medium	4+5	APH aphyllous 5+x+x
GEOL	geophyte, low	4+6	PIN pinoid 3+(1,2)+(2,3)
GRAH	graminoid, high	5+4	GRAM graminoid, medium 5+5 LNG long 3+(1,2)+
GRAL	graminoid, low	5+6	GRAL graminoid, low 5+6 1
ANNH	annual, high	6+4	DIL dissected large 4+(1,2)+(4,5)
ANNM	annual, medium	6+5	ANNL annual, low 6+6 DIS dissected small 4+(1,2)+(1,2,3)
ANNL	annual, low	6+6	CLIM climber 7+x XXX no data

Tab. 3.1 (top left): Environmental variables recorded during sampling. a = core dataset (sampling 1997), b = core dataset (sampling 2004), c = extended dataset (2004, with soil sampling), d = extended dataset (2004, without soil sampling). Content partly reproduced from Privett et al. (unpublished).

Tab. 3.2a and b (top right): Growth forms and leaf forms assigned to the species of Grootbos Nature Reserve (for a detailed explanation see text).

and 5 m wide. This is between the ranges suggested by Kent & Coker (1992: 42) for heaths and shrublands and thus appropriate for fynbos vegetation. The relevés were divided into 10 cells, 2 x 2.5 mts each. The floristic composition was investigated for each cell, including all identifiable species. This was performed by estimating the cover of each species for each cell and subsequently calculating the average cover for each species over the ten cells. The cover was recorded as a percentage, with a precision of one per cent (but also allowing a cover of 0.5 per cent) for cover values below 20 per cent and a precision of five per cent for more abundant species. Additionally, the environmental parameters listed in Tab. 3.1 were determined. Soil samples were taken at random localities within each relevé, in depths of between five and thirty centimeters depending on soil depth. These depths were chosen since as they correspond to the distribution of the majority of the root systems of

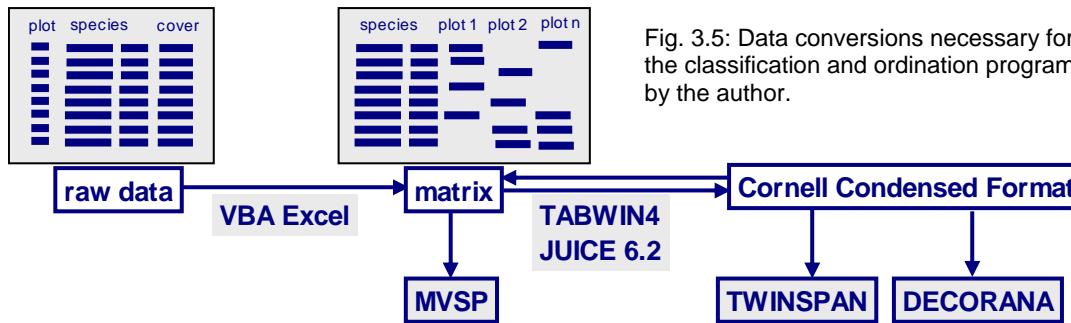


Fig. 3.5: Data conversions necessary for feeding into the classification and ordination programs. Designed by the author.

fynbos ecosystems. For the new relevés established by the author one sample for each relevé was analyzed for the soil characteristics listed in Tab. 3.1 by the laboratory of Elsenburg College. For the relevés analyzed in 1997 three soil samples per relevé were sent to the laboratory. However, the intra-relevé variations in the results were negligible, legitimizing this reduction (Privett, pers. comm.).

23 relevés were added to the existing 48 so that a total of 71 were available for classification and ordination. Each relevé was located with GPS, the coordinates were stored for mapping and relocation. The SW corner of each relevé was marked with a concrete lentil (Fig. 3.4) to enable further monitoring. The other corners were marked with small iron pegs. Where the shallow soil did not support a concrete lentil all four corners were marked with iron pegs.

In addition to the regular relevés 127 sites were analysed to a lesser extent. Without setting up a formal plot only the dominant and easily identifiable species around were recorded. The coordinates were located with a GPS and stored for mapping. No environmental data were investigated directly but the topographical variables were extracted from the digital elevation model. For three sites (116, 144, 145) soil samples were taken.

The numerical vegetation analysis will be referred to as the extended dataset (198 cases) when these additional samplings were included and as the core dataset (71 cases) when they were excluded.

A code for structure (life form) was assigned to each species occurring on the reserve by combining five separate variables describing growth form and leaf form. Growth form was recorded by a combination of life strategy (tree, shrub, perennial, geophyte, graminoid, annual or climber) and above-ground size (six classes). All this information was taken from Goldblatt & Manning (2000). Adaptations were necessary for a number of species occurring as shrub on the reserve but occurring as trees elsewhere. Leaf form was recorded by shape, thickness and size. Shape was separated into broad, narrow elliptic, linear, dissected and reduced. Thickness was recorded as soft, hard and succulent, while five classes were distinguished for the

size. As far as possible the information was extracted from the plant collection available at Grootbos Nature Reserve. Codes were generated from the variables separately for life form (four characters) and for leaf form (three characters), which were then combined. This was done in order to enable classification and ordination using the same methods as for species (Tab. 3.2). The codes were assigned to the sampled species using a VBA Excel script. The complete floristic, structural and environmental data of all relevés is included in App. 2.1.

### 3.2.2 Technical preparation

All analyses were carried out by computer-based numerical methods. There were several reasons for choosing this way. Numerical methods are objective in the sense that they are repeatable with the same result. Additionally, they are quicker than manual methods and less susceptible to error. Furthermore, the best known and probably most sophisticated manual classification method developed by the Zurich-Montpellier-School, the Braun-Blanquet-system, has not really been established in the Cape Region.

Different programs require different input formats. Fig. 3.5 illustrates the conversion mechanisms necessary for feeding the data into classification and ordination programs (described in detail below). The vegetation data were stored as lists (with plot, species and abundance like cover as columns) and as a two-dimensional matrix, in the common formats \*.txt and \*.xls. MVSP requires matrix data with species on the abscisse and plots on the ordinate. Transformation between matrix and list was easily performed by VBA macros. TWINSPAN and DECORANA do not accept the common data formats but they are optimized for a special data type called Cornell Condensed Format. The freely available software TABWIN, in combination with the software JUICE, was applied to perform the transformation from the common formats to Cornell Condensed Format and the reverse.

Before feeding the data into the classification resp. ordination programs, it may be useful to fine-tune them. TURBOVEG (Hennekens & Schaminée 2001)

provides multiple functions for managing vegetation data and adapting it to the specific classification programs. It is distributed commercially but is freely available for academic institutions and students. It was not used for this thesis in the end due to its complicated and inflexible way of species management in the database.

### 3.2.3 Numerical classification

#### General aspects

The purpose of any vegetation classification - whether numerical or manual - is to assign each plot to a community in a way that its floristic composition (or, alternatively, another feature like the spectrum of life forms) is more similar to any plot within the community than to any plot outside the community. Thus, the goal of all numerical classification algorithms is the same, but the ways to attain this goal differ considerably. Possible characteristics of such algorithms are best described by contrasting pairs of terms (Kent & Coker 1992: 278ff):

- hierarchical/non-hierarchical: are the communities generated for different levels of similarity with a dendrogram as a result, or only for one level?
- divisive/agglomerative: does the classification process start with the total dataset and split it up into subdivisions or does it start with one plot, summarizing the plots up to a certain threshold?
- qualitative/quantitative: are all species within a plot treated like as equal or is the abundance of the species taken into account?
- normal/inverse: are the communities generated from the samples or are they generated from species depending on their distribution?

Independently of their exact working mode all algorithms can be related to the widely-used term cluster analysis. A common computer program for the classification of living systems is TWINSPAN, providing divisive, hierarchical and quantitative classifications. It was used for this thesis.

#### TWINSPAN

TWINSPAN was developed by Hill (1979, 1994) and is probably the most widely-used classification algorithm today (Kent & Coker 1992: 290). It is freely available as DOS-executable via the Centre for Ecology and Hydrology of the United Kingdom ([www.ceh.ac.uk](http://www.ceh.ac.uk)). The algorithm is complex so that only its most important and distinctive features are outlined.

It is based on positive and negative indicator species (differential species), being used to divide a community

of a lower hierarchical level into two communities of a higher hierarchical level. An important concept included in the two-way indicator species analysis is that of the pseudospecies. Each species in the dataset is split up into one or more pseudospecies, each pseudospecies representing a certain degree of abundance (the thresholds can be defined by the researcher or the default values can be applied). If, for example, a species has a level of abundance of four, four pseudospecies are generated - one for each level. If a species only has an abundance level of one only one pseudospecies is generated. The purpose of the concept of pseudospecies is to implement abundance into the differential species (Kent & Coker 1992: 291).

The indicator species are investigated by an iterative interplay between relating species to plots and relating plots to species, known as correspondence analysis or reciprocal averaging. At first, a random correspondence value is assigned to each plot. This value is applied to each species in the plot so that each species receives a correspondence value depending on the plots in which it occurs. The values for the species are then applied to the plots, each plot being assigned a correspondence value consisting of the values of the species occurring in the plot. These correspondence values are then normalized. The whole cycle is repeated until the correspondence values remain virtually constant among two or more adjacent cycles. The final correspondence values of the species are then applied to the plots, respectively in reverse. The dataset is split up into two parts based on pseudospecies centered in one of the parts (indicator species).

The process is then repeated separately for each unit, generating a second, more detailed level of communities, which are again split up in a third step. This happens until a community has fewer plots than a minimum defined by the researcher. The result is a dendrogram only consisting of dichotomous splittings. For this thesis, the author applied a debugged version of TWINSPAN. Due to "extremely lax convergence parameters" (Oksanen & Minchin 1997), the original program was unstable. The bug was corrected by the authors and a stable version was released ([www.cc.oulu.fi](http://www.cc.oulu.fi)).

For this thesis the parameters of the program were adapted. For the classification of the core dataset the pseudospecies cut levels were set to 0, 5, 10, 20 and 50, for the extended dataset to 0, 2, 5, 10, 20, 50. The first pseudospecies of the extended dataset was excluded from the classification. Splitting was allowed down to two species (default: 5) for both datasets. No classification was performed for the structural datasets, as the ordination results indicated a huge amount of noise in the fynbos (see chapter 4).

### 3.2.4 Numerical ordination

Numerical ordination shows certain similarities to numerical classification: the species composition of the plots of the dataset or the distribution of the species are analyzed and compared so as to assign a certain order to the dataset by exactly specified rules. The type of order is different: by ordination methods the samples are clustered within one- to multidimensional systems and not within hierarchical, dendritic systems as in many classifications. Each dimension represents an environmental factor influencing species distribution. This factor can be known, but can also be unknown. The former case is called direct ordination, the latter one indirect ordination. Indirect ordination methods generate hypothetical axes being synthetically composed of one or more unknown environmental variables. Basic particularly to indirect ordination is the hypothesis that vegetation depends on environmental variables.

In practice, the results of ordinations are plotted as two- or maximum three-dimensional diagrams. Species with a similar response to the environment are clustered.

In this thesis two of the most common numerical ordination methods were applied to the Grootbos dataset: The Detrended Correspondence Analysis with the computer program DECORANA and the Canonical Correspondence Analysis with the program MVSP.

#### Indirect Ordination (Detrended Correspondence Analysis)

Detrended Correspondence Analysis (an extension of Correspondence Analysis) is a cheap and quick method for indirect ordination as the program DECORANA is freely available as DOS-executable (together with TWINSPAN, [www.ceh.ac.uk](http://www.ceh.ac.uk)) and no additional environmental data are required. The input is more or less the same as for TWINSPAN.

Like TWINSPAN, detrended correspondence analysis is based on reciprocal averaging. The major difference is that after finishing the iteration the dataset is not split into two parts. Instead, the correspondence values are considered as a continuum and the results represent the first axis of the analysis. The second axis is obtained by repeating the whole iteration procedure beginning with the second cycle of the first axis. The calculation of the third axis begins with the third cycle, and so on (Kent & Coker 1992, Hill 1994). One problem with the correspondence analysis is that the second and all higher axes depend on the first axis, a phenomenon called arch effect, which can influence the results significantly. A second major problem is that the ends of each axis are distorted. The Detrended

Correspondence Analysis has implemented algorithms to deal with these problems - improving the situation but introducing still more artefacts.

As correspondence values are assigned to species and to plots both can be viewed as a result. Usually the results are presented as two-dimensional diagrams. Each axis represents an environmental factor or, more frequently, a combination of them. The problem is that due to the missing environmental inputs the axes are actually black boxes so that interpretation and hypothesis-verification is demanding.

The author decided to carry out the detrended correspondence analysis with DECORANA, although it is also supported by the more user-friendly MVSP. However, the original algorithm was not used. As with TWINSPAN, Oksanen & Minchin (1997) discovered some problems (an order-depending programming error and lax convergence criteria). The debugged version is freely available at [cc.oulu.fi](http://cc.oulu.fi) and was used in this thesis. DCAs were performed for the following constellations of the extended dataset:

- complete dataset (floristic composition)
- relevés classified as Fynbos Biome (chapter 4)
- complete dataset (structural composition)

The default parameters suggested by the program were applied.

#### Direct Ordination (Canonical Correspondence Analysis)

The Canonical Correspondence Analysis is more sophisticated than the Detrended Correspondence Analysis. Environmental data are required to supplement the floristic data. The standard computer program for performing the analysis is CANOCO. The algorithm is too complex to be described in this scope. The results are very expressive and Kent & Coker (1992: 235) consider the method as the best among all ordination analyses provided the availability of environmental data.

As in the case of the Detrended Correspondence Analysis two or three axes are plotted, showing the relation between plots or species and an unknown set of environmental conditions. Additionally, several axes (vectors) can be added, each representing one of the environmental variables fed into the ordination. Each of them is characterized by a length representing the significance of the environmental gradient, a direction and an angle to the coordinate system. With this angle, the black boxes of the major axes can be filled with content. Each axis thus represents different proportions of different environmental factors. The interpretation is easier and more confident than for the Detrended Correspondence Analysis.

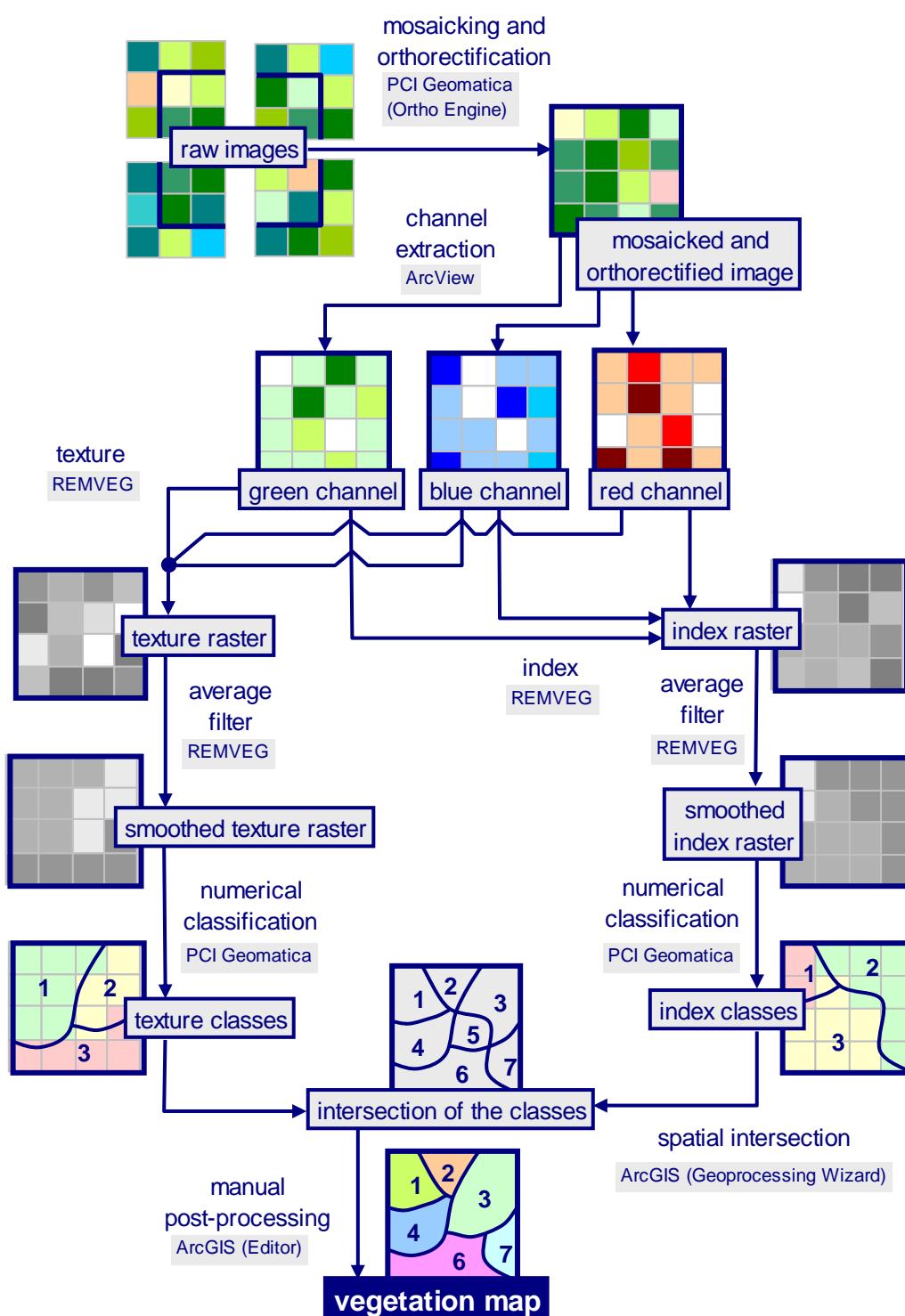
The CCA was only performed for the core dataset due to the availability of environmental data. MVSP, not CANOCO, was used due to its easier availability and the same algorithms. The same constellations as in the DCA were ordinated, applying the default parameters suggested by the program.

Fig. 3.6: Work flow diagram of the aerial imagery interpretation.  
Designed by the author.

### 3.3 Vegetation mapping

#### 3.3.1 Aerial imagery interpretation

Aerial images provide high-resolution remote sensing data from the earth's surface. They represent an unselected mixture of all types of objects, which has to be disentangled to provide the information required by the user, and to help to enhance the understanding of the earth surface's structure. Remote sensing has developed into a separate science, dealing with the



generation and the interpretation of all types of satellite and aerial images of different spatial, temporal, radiometric and spectral resolutions. Concerning vegetation surveys, the spatial and the spectral resolutions are of special interest. Spatial resolution or pixel size determines the scale at which information can be acquired. For surveys covering thousands of square kilometers and aiming at a rough mapping, standard satellite images with 15 to 30 m resolution may be sufficient. For large-scale investigations comprising of a few square kilometers, like in the scope of this thesis, high-resolution imagery with a pixel size of one meter or less is required. In most of these cases, aerial images are applied because high-resolution satellite imagery is still very expensive.

Spectral resolution is important insofar as vegetation has highly selective reflection properties. The highest proportion of incoming radiation is reflected in the near infrared - for this reason color-infrared (false-color) images are most suitable for vegetation surveys. True-color aerial images taken during autumn 2000 with a spatial resolution of 0.75 m and three channels (one each for blue, green and red) have been acquired for the whole reserve. They were also applied for this study. Previously, nine major vegetation units of the reserve were extracted manually and mapped on GIS (see Fig. 1.3). For this study, a numerical interpretation was attempted to be carried out.

Fig. 3.6 outlines the way of numerical interpretation as carried out in this thesis. A combination of surface texture and a vegetation index was applied to generate preliminary units, which had to be post-processed manually. The software packages ArcInfo, ArcView and PCI Geomatica were used for preprocessing, classification and some technical tasks. Texture and index were calculated with REMVEG, a VisualBasic script designed by the author for the purpose of this study.

## Preprocessing

The aerial images were available as color orthophotos. Five orthophotos were necessary to cover the whole Nature Reserve. They were mosaicked to a composite image using the Ortho Engine of PCI Geomatica 9.1, in order to cover the extent of the Nature Reserve with buffer zones of 500 m in each direction.. As the five images were taken at different times they were subjected to different atmospheric and astronomical conditions, resulting in a certain biasing of the information. It was tried to remove this problem by automatically normalizing the images during mosaicking but the results were not satisfactory so that the normalization was finally not applied and the bias had to be taken into account during the manual post-processing. Performing a manual normalization was avoided so as to maintain the reproducibility of the work flow.

To ensure the spatial compatibility of the composite image with the Global Positioning System GPS and with the other spatial datasets used for the subsequent analyses it had to be transformed. Since as the coordinate system of the orthophotos was not known it was reprojected to the UTM System, based on the WGS 84 manually, again by using the PCI Geomatica Ortho Engine. With six Ground Control Points obtained from a road dataset an RMS error not exceeding 5 meters could be achieved. Considering the desired spatial accuracy level of the final map and of the analyses based on the interpretation of the images, this result can be considered as sufficient enough.

Before analyzing the data anthropogenic structures, like buildings and roads, were removed from the data. This was done automatically by setting all pixels with a summarized value of all channels of more than 200 to no data. With this method, some minor vegetated areas were removed as well, but virtually all major roads and many buildings were able to be eliminated to avoid biasing of the results of the subsequent analyses.

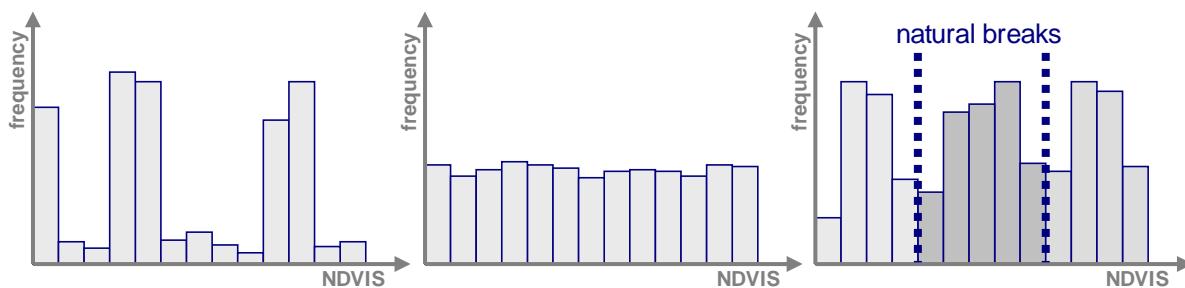


Fig 3.7a-c (left to right): Different types of histograms showing the frequency of different NDVIS classes, reflecting different patterns of homogeneity resp. heterogeneity of the analyzed surface. Designed by the author.

### Index as indicator for the vegetation cover

Aerial images do not only represent vegetation, but also many other objects at the earth's surface and atmospherical and astronomical influences like turbidity or, depending on the sun's angle, shadows as well. The raw value of reflected radiation of a given spectrum, as provided by a canal of an aerial image, does not necessarily tell very much. Since as it is possible to address each canal independently ratio-building is a widely used way to face the problems described above. Objects like vegetation do not reflect radiation independently of frequency. Plants appear green to the human eye because they reflect most of the green radiation while using the majority of incoming blue and red radiation for photosynthesis. Since, invisible to the human eye, near infrared radiation is reflected to an extraordinarily high proportion, the best-known vegetation index - the Normalized Difference Vegetation Index (NDVI) - relates near infrared and visible red.

$$NDVI = \frac{IR - VR}{IR + VR},$$

where IR means the pixel value of the infrared channel and VR means the pixel value of the visible red spectrum. The NDVI is not applicable to the available images from Grootbos because they only have canals for the visible blue, the visible green and the visible red spectral lengths. The differences within the visible spectrum have thus to be applied. The author believes that the following ratio may help to extract information from the images:

$$\frac{VG}{VB + VG + VR},$$

where VG means the pixel value of the visible green channel, VB for the visible blue channel and VR for the visible red channel.

The extraction of the index was performed using REMVEG. To enhance the calculation process the image was downsampled five-fold to a spatial resolution of 3.75 m - in fact, the index was only calculated for each 25th pixel of the orthophoto. Since as the resulting raster was filtered subsequently (see below) this generalization should have no significant negative effect on the results but it did lead to a considerable acceleration of the calculation process.

### Texture as indicator for the vegetation cover

Different vegetation types do not only differ regarding their average pixel values, but also in their texture, meaning the change in the reflection properties over a couple of meters. Grassland ecosystems should have a smoother texture than shrublands, and shrublands a

smoother one than forests. Different texture properties may also be expected for different fynbos ecosystems - for example, lower ericoid fynbos should be smoother than most types of proteoid fynbos.

As input for the texture extraction, the pixel values for the three channels of the orthophoto were summarized, providing a more diverse surface than by using only one channel - for example, small-scaled shadow-effects, quite important for texture identification, were promoted.

Texture can never be measured for one pixel, but only by comparing a certain number of different pixels. Reliable values are not obtained by comparing the considered pixel with one other pixel, but by installing a certain matrix around the central pixel so that the sample size is sufficient for representative results. A circular 31 x 31 matrix was applied in this study, thus including a circle with a diameter of 0.75 m x 31 = 23.25 m. Standard deviation among the pixel values was used as a measure of the surface texture around the considered pixels. As with the index, the raster was downsampled to a spatial resolution of 3.75 m during calculation but all pixels of the input dataset were used for calculating the texture.

One problem with the concept of texture is that it is difficult to model the transitions between different vegetation units. Even if there is a sharp transition in nature, there will be a blurred belt of half the size of the matrix on each side of the transition.

REMVEG was used to carry out the texture extraction as the standard software PCI Geomatica did not provide reasonable results.

(eq. 3.2)

### Classification

Further processing was performed in similar ways for the index dataset and the texture dataset.

The spatial resolution of the available imagery and of the resampled datasets was high enough for the distinction of different structural elements of the fynbos, for example large proteoid shrubs and the ericoid understorey. Though this was an advantage for the application of the texture analysis it bears the problem that the difference in index or texture respectively, within a community may be larger than between two distinctive communities. An extremely fine-grained mosaic providing no useful information would be the result of a classification of these datasets. Once the effective spatial resolution of the images is reduced to a level so that structural elements of the communities are smoothed, the pixel values can be applied to distinguish between different vegetation types. One problem might be that smoothing blurs the transitions between different vegetation communities,

even if the transition is sharp in nature - the same thing as with texture analysis discussed above.

The data were smoothed with a circular average filter in a 9 times 9 matrix (thus including a quadrat with a side length of 33.75 m) without further reduction of the cell size. The filtering was repeated 5 times for each dataset to achieve sufficient smoothing for a reasonable classification. All smoothing was carried out with the software REMVEG.

When creating a histogram illustrating the abundance of pixels with similar index or texture, a pattern like the one shown in Fig. 3.7a would represent the Clementian view. A pattern like in Fig. 3.7b would clearly reject the Clementsian view and favor the Gleasonian view. The author believes that examination of the Grootbos aerial images shows patterns like Fig. 3.7c, reflecting aspects of both concepts.

To classify the data it is most useful to apply natural breaks - that means, depressions in the histogram, indices with a low abundance, reflecting units with low frequency, considered as transitional between meaningful vegetation units.

For the classification of the smoothed dataset the author chose to use a completely automatic way to maintain full reproducibility. The IsoData method supported by the unsupervised classification function of PCI Geomatica was applied to both the texture data and to the index data. The default settings were applied for each dataset except that the maximum number of classes was limited to 7, including a no data class.

The next step was to intersect the two datasets in order to obtain a higher number of classes representing a combined signature of index and texture, as illustrated in Fig. 3.6. The results of this intersection, however, were not used further since they did not prove to provide useful results.

Not all of the output classes necessarily represent meaningful vegetation units and it might also be that one class represents more than one vegetation unit. An automatic classification can never provide an exact, correct and representative vegetation map - the natural conditions are determined at random too much. In addition, in some classes vegetation might not be the dominating factor for surface reflection, but it might be the rock. In fact, the numerical classification should provide an objective basis for further manual fine-tuning. For the purpose of this study the vegetation was mapped manually as well. Subsequently, the results of automatic imagery interpretation and manual mapping were compared.

### 3.3.2 Manual vegetation mapping

A GIS dataset representing the vegetation units as investigated in 1997 was available for a part of the

reserve but not including the recently bought properties Steynsbos, Baviaansfonteyn and Tygerboom. These properties and some selected parts of the remaining reserve were explored by several excursions and assessed according to the subjective impression of the author, supported by the relevés. In addition, a large number of spots were recorded by GPS in order to locate the transitions between vegetation units.

All the point data were transferred to a GIS and mapped onto the composite orthophoto. The information provided by the orthophotos was combined with the point data and the existing GIS dataset to generate a comprehensive map of the plant communities or at least of meaningful vegetation units. The results of the numerical vegetation analysis were tried to be applied as strict as possible, combined with a maximum of detail.

In addition to the vegetation map, maps representing patches invaded by introduced plants and the recent fire history of the reserve were generated. The former task was completed by subjective imagery interpretation combined with existing GIS datasets. For the fire history (vegetation age) map existing datasets provided by Grootbos Nature Reserve and the Agulhas Plain Conservancy were adapted. The most recent fire events not included in the existing datasets were mapped manually by using GPS.

### 3.3.3 Vegetation mapping - synthesis

The spatial dataset resulting from the imagery interpretation was used to create a prediction map based on the manual vegetation map in order to evaluate the correspondence of the two datasets. The same methods as for the geostatistical analysis described below were applied with the index dataset as the independent variable. For reasons discussed in chapter 4 the dataset derived from manual mapping was applied to the final map.

The vegetation map was created using ArcGIS and designed for a scale of 1:12,500 in order to account for the desired level of detail. The following layers were included in the map:

- vegetation units
- patches invaded by alien plants
- recent fire history
- relevés (core dataset and extended dataset)
- infrastructure (roads and buildings)
- topography (5 m contour lines, hilltops, hillshade)

The map is included in App. 4.

### 3.4 Geostatistical analysis

#### 3.4.1 General aspects

Geostatistical analysis is a comprehensive notion, including - among others - interpolation of points to surfaces and explorative data analysis with spatial datasets. The methods may be, but are not necessarily related to the use of Geographical Information Systems (GIS).

The scope of this thesis allowed a geostatistical analysis to be used to perform some kind of ordination with raster datasets. The spatial distribution of vegetation units shall be related to the spatial distribution of environmental variables. This approach, like ordination, is based on the hypothesis that spatial coincidence indicates a causal relationship. A smaller number of variables is available continuously over all the research area rather than for a limited number of relevés. For the given scope the analysis was limited to topographical variables obtained from a digital elevation model (DEM). One reason for this was that many variables affecting the distribution of vegetation units are supposed to be related to topographic variables and should therefore be surrogated by them. Another reason was the lacking availability of spatial datasets representing other variables.

An advantage of the topographic features for such an analysis is that they are not supposed to be influenced by the vegetation (except over very long periods). Variables like fire or soil chemistry can not only influence the related ecosystems, but they may also be influenced by them, so that the direction of hypothetic causal relationships remains unclear. The ordinations described above face this problem.

One important point of all types of ordination - not only of the geostatistical methods - is that the independent variables included in the analysis should not explain each other too much - redundancies may distort the result. This problem can be avoided by testing the variables for correlation before performing the actual analysis.

#### 3.4.2 Terrain modelling

##### Digital Elevation Model (DEM)

5 m contour lines and a certain number of elevation points mapped on older orthophotos (1:10,000) from 1981 were available for the entire reserve. They were obtained as paper copies from the General Directory of Survey and Mapping in Mowbray. All contour lines and altitude points were digitized manually and interpolated to a DEM. Kriging was chosen as the interpolation method using the default settings for Ordinary Kriging of the ArcGIS Geostatistical Analyst, except for the semivariogram environment where an elliptic environment was

chosen. The cell size of all terrain modelling was at with 15 m since as the contour spacing did not serve for a higher information density. A buffer zone of 500 m around the Nature Reserve was included. All of the following topographic variables - summarized with the term Digital Elevation Model or DTM - were directly or indirectly derived from the DEM.

##### Digital Terrain Model (DTM) - basic variables

The most basic characteristics of a certain terrain are altitude and – as derivates of the latter – slope and aspect. Most geospatial software provides functions to ease compute rasters representing these parameters. The DEM was used to generate rasters representing slope and aspect. All operations were performed by using the ArcGIS Spatial Analyst, applying the default parameters. The aspect dataset was recalculated in order to reflect the exposition of a certain pixel towards N or S. Values higher than 180 (hence, between S and N directed towards E) were subtracted from 360, so that - for example - the same value (90) was assigned to E as to W and to SE the same value (135) as to SW (Fig. 4.10). Fig. 3.8a and b illustrate the slope and the adapted aspect dataset respectively. The DEM is represented in Fig. 1.6.

The purpose of the terrain model is not only the geostatistical analysis, but also graphic presentation (see Fig. 1.5). The function hillshade was applied to enhance the performance of certain maps included in this thesis, although it does not serve as a variable for an analysis.

Despite the fact that elevation, slope and aspect may be successfully applied in order to discriminate different vegetation units they are not causally related to vegetation. More advanced datasets representing parameters being hypothetically more closely linked to ecological variables directly affecting the vegetation were therefore generated additionally: wind exposition, solar irradiation and flow accumulation.

##### Wind as a driving force for veld fires

The major force triggering the spread of veld fires in the fynbos (and also elsewhere) is wind. Fire-bearing winds predominantly approach the reserve from a SE direction due to the prevailing climatic settings during summer, but they can also originate from other directions. A certain point highly exposed to those winds has a higher probability of being hit by a fire originating from any other spot than a point less exposed. On the other hand, a fire originating at a certain spot has a higher chance of spreading if the point is exposed to those winds.

For these reasons, the understanding of the spatial patterns of the wind regime may be a substantial point

for understanding and predicting fire patterns on the reserve.

The wind patterns on the reserve were investigated by using the visibility analysis provided by the Spatial Analyst of ArcGIS, applying the default settings. Two assumptions had to be set:

- all of the wind would originate at a point at a distance of 200 km from the Garden Lodge. Due to the acute angle the theoretical streamlines of the wind closely approach parallelity (similar to solar radiation).
- the probability of the wind to originate from a certain direction was assumed to follow a symmetric Gaussian distribution, with the maximum for SE:

$$p = e^{-\sqrt{\varphi}}$$

where  $p$  is the probability,  $e$  is the Euler constant and  $\varphi$  stands for the angle in radian ( $SE = 0$ ).

Nine wind directions were analyzed: SE, S, SW, W, NW, N, NE and E. For each of them, the viewshed function was applied to eight levels of elevations as virtual viewpoints (5, 10, 15, 20, 25, 35, 50 and 80 km), located at a horizontal distance of exactly 200 kms from the Garden Lodge. The resulting rasters therefore consisted of nine classes representing different levels of exposition to wind from a given direction. The probability of the wind approaching from that direction was calculated with the equation for the Gaussian distribution. The nine resulting rasters were added but each raster was weighted according to the probability calculated for the corresponding wind direction. The resulting map is supposed to give a realistic picture of the exposition to fire-bearing winds - SE winds should dominate due to their higher weight but also winds from other directions are not completely neglected. Fig. 3.8c illustrates the wind exposition raster.

### Solar irradiation as a measure for the moisture regime

As mentioned in chapter 2, the availability of moisture is supposed to be one of the most important factors determining the vegetation of the Fynbos Biome. However, it has not been taken into account at all until now. Precipitation may vary to some degree due to local and regional topo-climatic effects but there are no sufficient records to support a reliable analysis. The records of evapotranspiration and runoff are poor as well. The only easy way to surrogate the moisture regime on a local scale is solar irradiation as the major driving force of evapotranspiration. It may be the major factor influencing the moisture regime of the reserve due to low variation in other variables.

Solar irradiation is tightly connected to the aspect, but due to topography-induced shading effects, the aspect is no sufficient representative. Some geospatial software provides tools to generate rasters with solar irradiation based on a digital elevation model. For the given purpose it was chosen to use the Solar Analyst for ArcView. The default settings were applied to calculate the radiation sums for the entire year. The twelve rasters were added without applying any weighting. Fig. 3.8d represents the solar irradiation raster.

### Flow accumulation as a measure for soil depth and accumulation of alkaline sands

Soil depth is supposed to be a major variable discriminating different vegetation units. It is relatively easy to measure on a one-dimensional basis, but not over all of a given surface. Since soil depth on the local and regional scale may mainly be determined by erosion and accumulation of sand by wind and water, and these processes are tightly coupled to topography, suitable parameters can be extracted from the digital terrain model. Since as gravitation applies to sand in the same manner as to water, flow accumulation algorithms successfully applied in hydrology are expected to work for soil too. A number of GIS-programs serve for such algorithms. One of the most common is the Hydrology Tool for ArcGIS, which was applied for the given purpose. The raw value for flow accumulation was not fed into the analysis. The relationship

$$acc_{adapted} = {}^{10} \log(acc_{original} + 1),$$

was applied in order to remove the bias towards low values characterizing the dataset. The adapted flow accumulation dataset is shown in Fig. 3.8e.

### 3.4.3 Relating vegetation and topography

The analysis was performed for three combinations of environmental predictors:

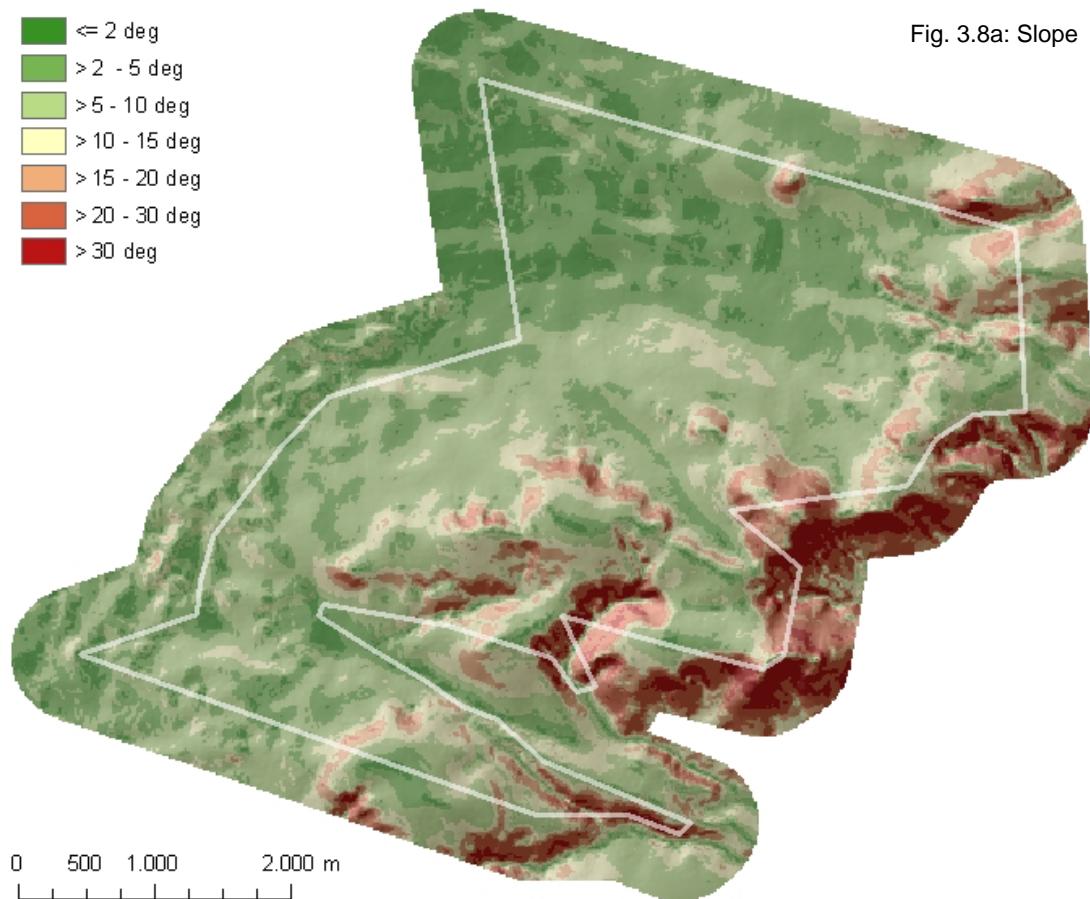
- basic: elevation, slope and aspect
- advanced: solar irradiation, flow accumulation and wind exposition
- complete: elevation, slope, aspect, flow accumulation, solar irradiation and wind exposition

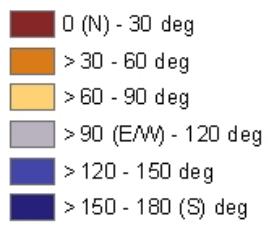
These modes were applied to varying levels of vegetation units (see chapter 4).

Knowledge was tried to be obtained about the extent to which the distribution of the mapped vegetation units can be explained by the distribution of topographic variables. Prediction maps were generated

as well, representing the vegetation units as they would be distributed if fully mirroring the variables included in the analysis. The most suitable tool to do this is not provided by the common GIS programs but by the statistical software SPSS. All spatial data was exported

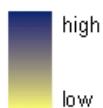
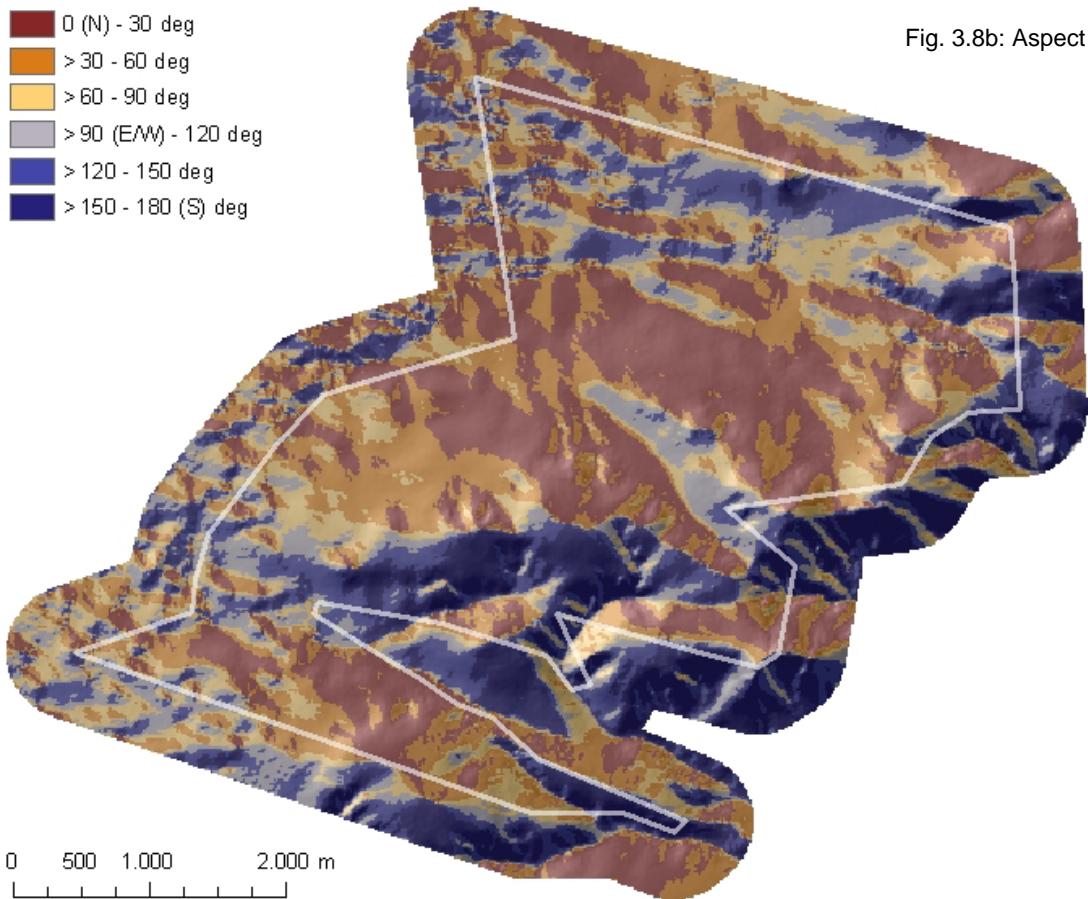
from the raster format using the program tosis, provided by the Working Group for Ecology, University of Innsbruck, to allow the import to SPSS, where the discriminant analysis was applied.





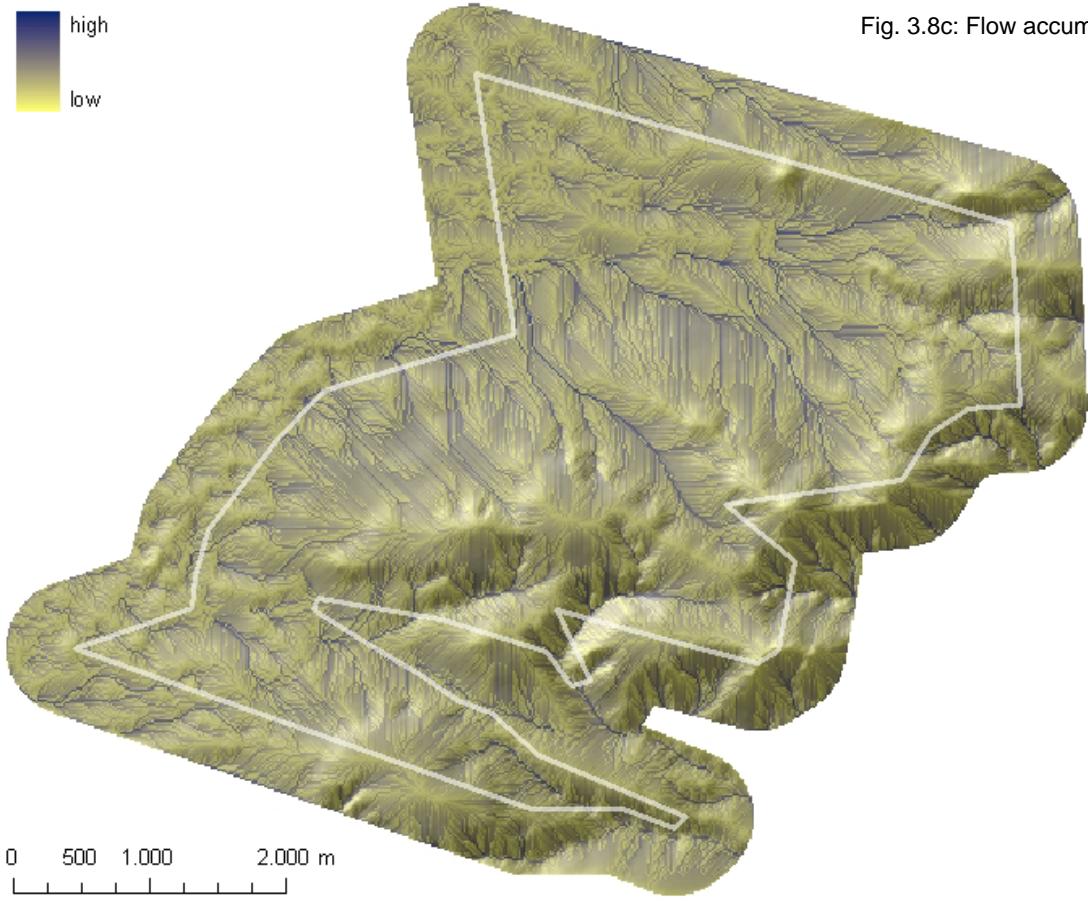
0 500 1.000 2.000 m

Fig. 3.8b: Aspect



0 500 1.000 2.000 m

Fig. 3.8c: Flow accumulation



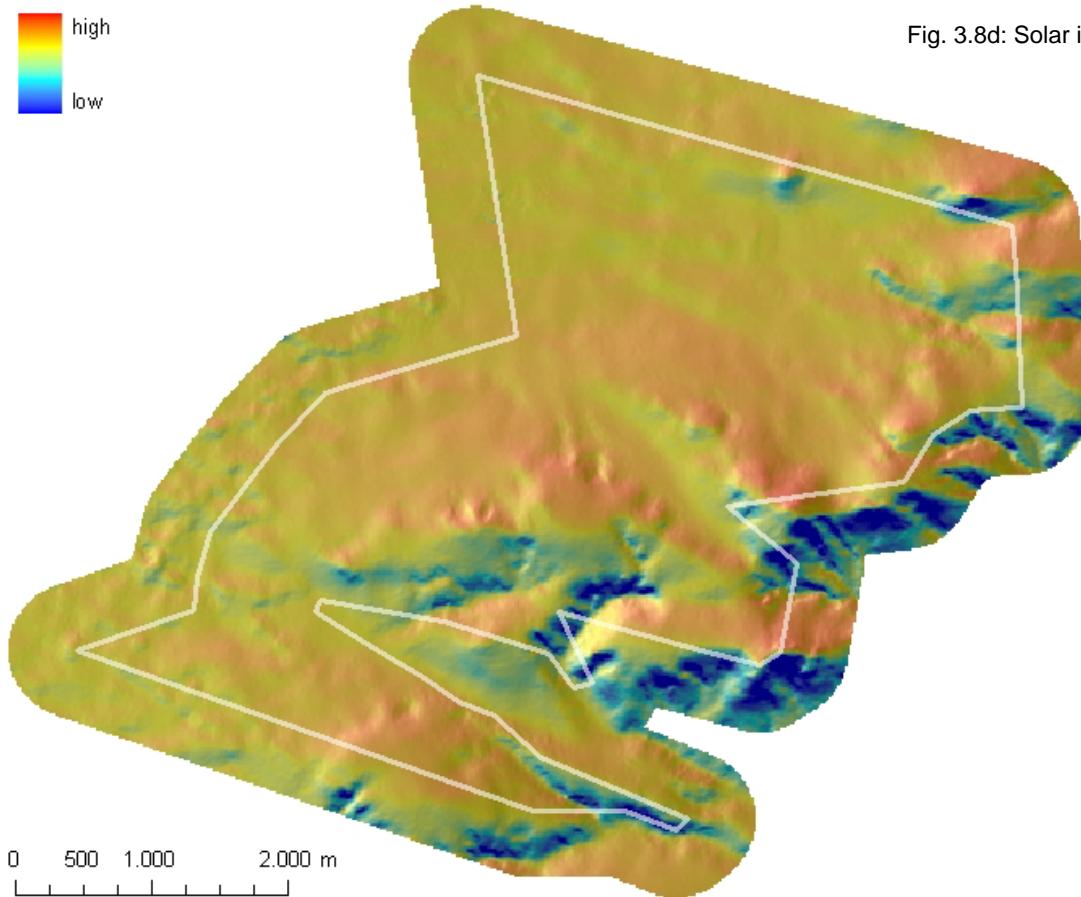


Fig. 3.8d: Solar irradiation

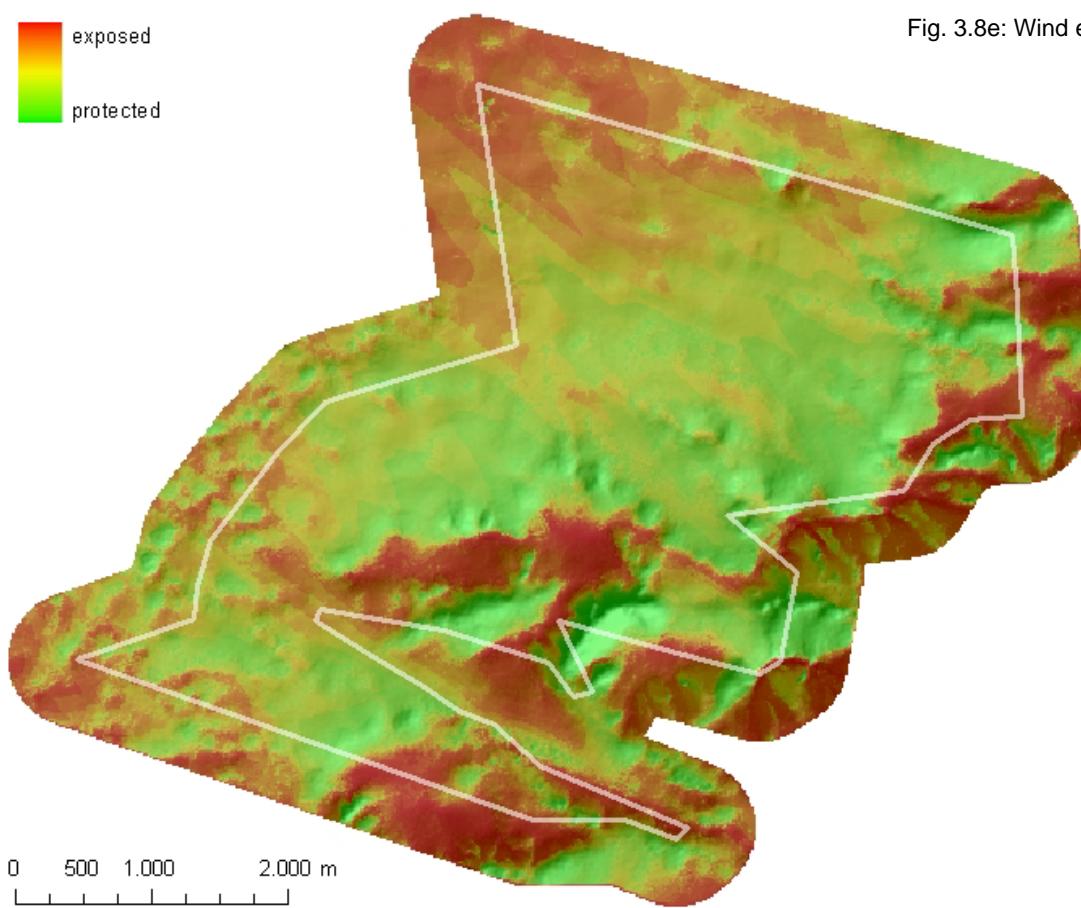


Fig. 3.8e: Wind exposition

## 4 Results

### 4.1 Numerical vegetation analysis

#### 4.1.1 Species ordination (fynbos only): CCA

##### Complete environmental dataset

Elevation appeared as the most powerful predictor (biplot score for the first two axes 0.66), followed by pH (0.65) and soil depth (0.60). Ca, resistance, rock cover and Na showed values of 0.50 or higher. The eigenvalues of the axes decreased continuously from the first to the fourth axis (0.57, 0.47, 0.41, 0.34). Texture had its highest score on the third and the fourth axis (0.43 and 0.30, respectively), aspect also attained a high value on the fourth axis (0.26).

There is certainly some degree of redundancy in the variables. The negative correlation between elevation and pH was as high as -0.78. Rock cover showed correlations of 0.54 with slope and 0.51 with K. Soil depth correlated negatively to rock cover (-0.71) and K (-0.61). pH appeared to be connected to high contents of Na (0.67) and Ca (0.77), while resistance was associated with low contents of all nutrients, especially Na (0.62), K (0.58), Ca (0.52) and Mg (0.72). In addition, there were a lot of positive correlations among the elements: Na with P 0.64, with Ca 0.80 and with Mg 0.70; P with Ca 0.69 and K with Mg 0.75. Correlation values below 0.5 are disregarded in this description.

The CCA indicated a fairly clear distinction between alkaline and acid preferentials, the latter emerging along a gradient of decreasing pH, Ca and Na and increasing altitude, weakly correlated with increasing rock cover and decreasing soil depth (Fig. 4.1a). 10 out of 15 Proteaceae present on the reserve were located in the acid cluster, as well as the Ericaceae *Erica glabella* and *E. sessiliflora*. The latter was slightly separated from the main cluster along a gradient of increasing slope and resistance. *Protea repens* showed a distinctive character since as it appeared to be associated with extraordinarily high values of resistance. *Leucadendron coniferum* and *Leucospermum patersonii* were also associated with rather high resistance, but nevertheless, in general they appeared to prefer intermediate conditions. *Thamnochortus erectus* showed associations with somewhat deeper soils and higher pH. *Erica coccinea* var. (yellow) and *E. irregularis* were associated with low altitude, high pH and high contents of Ca and Na, the latter species showing a preference for deeper

soils. *Protea obtusifolia* and *Thamnochortus fraternus* constituted a distinctive cluster among the common species, weakly associated with low soil depth, high rock cover, high pH and high content of Ca, K and Na. They were strongly associated with steep slopes and Mg-rich soils. The red data species were scattered all over the diagram. However, all of them were associated with rather extreme conditions regarding one or more environmental variables. None of these species were located in the vicinity of the center. One relatively compact cluster was centered in the vicinity of *Erica coccinea* var. (yellow), another, less compact, among the acid sand proteoids. The scores of the first four axes for all recorded species and the environmental variables are listed in App. 2.4.1.

##### Chemical variables (Fynbos only)

pH and resistance attained the strongest predictive force with biplot scores of 0.68 and 0.62 respectively. Ca (0.54) and Na (0.51) also showed scores above 0.5. The eigenvalues decreased continuously from the first to the fourth axis (0.51, 0.40, 0.32 and 0.28). P attained its highest score on the fourth axis (0.43). Correlations between the environmental variables correspond to those for the CCA regarding the complete environmental dataset. The patterns were quite similar to those mentioned above, indicating that variables representing soil chemistry explain the majority of species distribution (Fig. 4.1b). The acid cluster was associated with low pH and to a less extent with low Ca, Na and P. *Protea acaulos* was split from the cluster, being associated with high content of K. *Erica glabella* as well as *E. sessiliflora* were included in the acid cluster, not being associated with high resistance any more. In contrast, *P. repens* kept its distinctive status regarding high resistance. *Leucospermum patersonii* showed some approach to the acid cluster, while *Leucadendron coniferum* and *Thamnochortus erectus* remained in the neutral domain. *Erica coccinea* var. (yellow) showed more affinity with *Protea obtusifolia* and *Thamnochortus fraternus*, associated with high Ca, K, Mg and N, but rather weakly associated with high pH, in contrast to *E. irregularis* with clear preferences to alkaline conditions. For the red data species similar patterns as above were observed, but with less clustering in the alkaline domain. All scores are listed in App. 2.4.2.

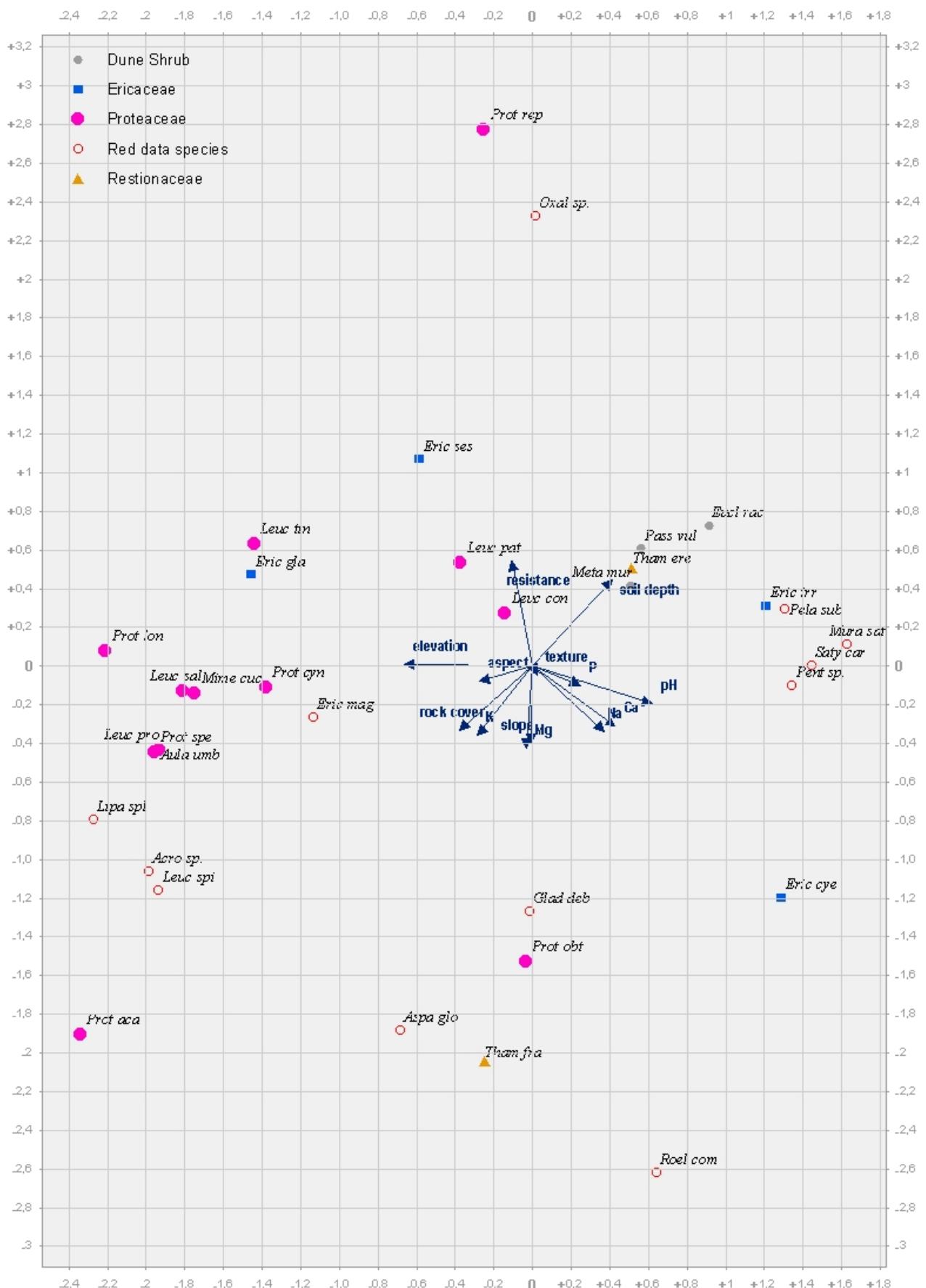


Fig. 4.1a: Results of the CCA including the complete dataset of environmental variables for the fynbos relevés, regarding selected species: Plot of the first two axes (x=first axis, y=second axis).

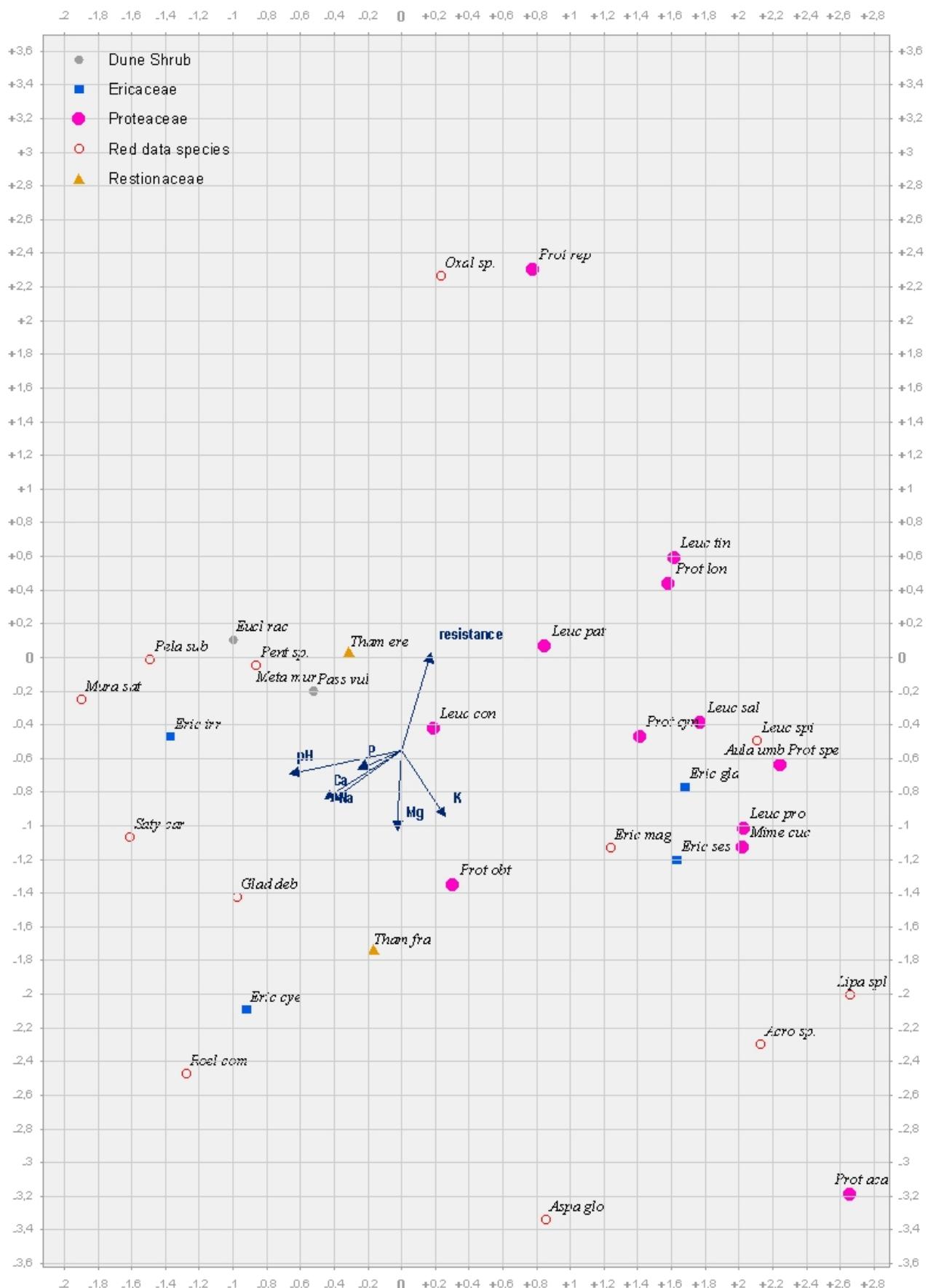


Fig. 4.1b: Results of the CCA only including environmental variables representing soil chemistry for the fynbos relevés, regarding selected species: Plot of the first two axes (x=first axis, y=second axis).

### 4.1.2 Two-way indicator species analysis

#### Core dataset

The classification of the core dataset indicated a clear separation between fynbos and forest at the first level of classification (eigenvalue 0.93). The wetland relevés 32, 58 and 59 were assigned to the forest branch (fig. 4.2).

The fynbos subsequently split up in two moderately significant clusters (eigenvalue 0.43), one of them indicated by species associated with acid, shallow soils: *Leucadendron salignum*, *Mimetes cucullatus* (see figs. 4.1a and b) and *Trichocephalus stipularis*. The second cluster was not indicated by any species. The classification protocol indicated sufficient floristic difference to consider the two branches as separate units: an Acid Sand Fynbos Complex and an Alkaline Sand Fynbos Complex. Below this level of separation the significance of clustering was insufficient to support the recognition of further classes at a lower level of generalization. This was especially true for the Acid Sand Fynbos Complex, only represented by a small number of relevés despite a relatively high eigenvalue at the third level (0.48). For the Alkaline Sand Fynbos Complex, two clusters separating at the fourth level indicated by the *Thamnochortus fraternus* (eigenvalue 0.41) on the one hand and *Protea repens* and *Cliffortia ilicifolia* (eigenvalue 0.48) on the other hand were observed in more detail. However, not enough species had their major range of distribution within the clustered relevés to support the recognition of communities.

The forest/wetland branch divided into forest and wetland (eigenvalue 0.85). Since as the wetlands only contained two relevés (32, 59), further subdivisions were disregarded and the cluster recognized as Wetland Complex. The expected separation between Milkwood Scrub Forest and Afromontane Forest was performed at the third level, with an eigenvalue of 0.60. No further subdivisions were taken into consideration for the Milkwood Scrub Forest, since an eigenvalue of 0.24 at the fourth level of division indicated a homogeneous floristic composition of the clustered relevés. At the same level, relevé 58 divided from the Afromontane Forest, supported by an eigenvalue of 0.53. The relevé was later included into the wetland cluster, supported by the classification of the extended dataset.

#### Extended dataset

The classification of the extended dataset provided slightly different patterns of division already at the lower levels of division. A separation of forest/thicket from wetland/fynbos with an eigenvalue of 0.84 was performed at the first level.

Wetland and fynbos were subsequently discriminated with an eigenvalue of 0.68, indicated by the wetland species *Mariscus thunbergii*. Relevé 58, which was misclassified to forest/thicket at the first level of division, was subjectively assigned to the wetland cluster. No further division of the wetlands was taken into account. The fynbos cluster behaved as expected and divided into an Acid Sand Complex and an Alkaline Sand Complex as for the core dataset, with *Leucadendron salignum*, *Mimetes cucullatus* and *Erica glabella* as indicators for the acid cluster (eigenvalue: 0.49). The higher levels of division with eigenvalues hardly approaching 0.5 were examined but did not support the recognition of further classes.

The forest/thicket branch divided into a Milkwood Scrub Forest/thicket cluster and an Afromontane Forest cluster (eigenvalue 0.62) on the third level. Subsequently, Milkwood Scrub Forest divided from the Thicket Complex with an eigenvalue of 0.59. Relevé 106 was assigned to the Milkwood cluster as a borderline case but it was subjectively reassigned to the thicket. No further subdivisions were recognized.

#### Manual post-processing

Despite a few contradictory statements the classification results for the core dataset and the extended dataset largely indicated clear patterns in the vegetation of Grootbos Nature Reserve and provided valuable assistance for the recognition of vegetation units on different levels of generalization. Three biomes are therefore present on the reserve: Forest, Wetland and Fynbos. While no further subdivision was supported for the wetland, the Forest Biome may be separated into the complexes of Afromontane Forest, Milkwood Scrub Forest and Thicket. The Fynbos Biome shows a clear division between an Acid Sand Complex and an Alkaline Sand Complex. For the Thicket and the Wetlands, but especially for the fynbos complexes, finer patterns of resolution are indicated by the observation of those ecosystems. However, subdivisions of the existing clusters are not or are only poorly supported by the analysis results. One reason for this problem is the frequent phenomenon in fynbos ecosystems that one or a few characteristic species are dominant, the rest being widespread all over either of the two complexes and thus only representing noise for a finer classification (Privett, pers. comm., Simmons, unpublished). The ecological background of this issue will be discussed in detail in chapter 5 but now its implications for the recognition of finer vegetation units, referred to as formations, are of interest: those entities had to be chosen subjectively, based on the presence or absence of one or a few dominant species. The following rules were applied:

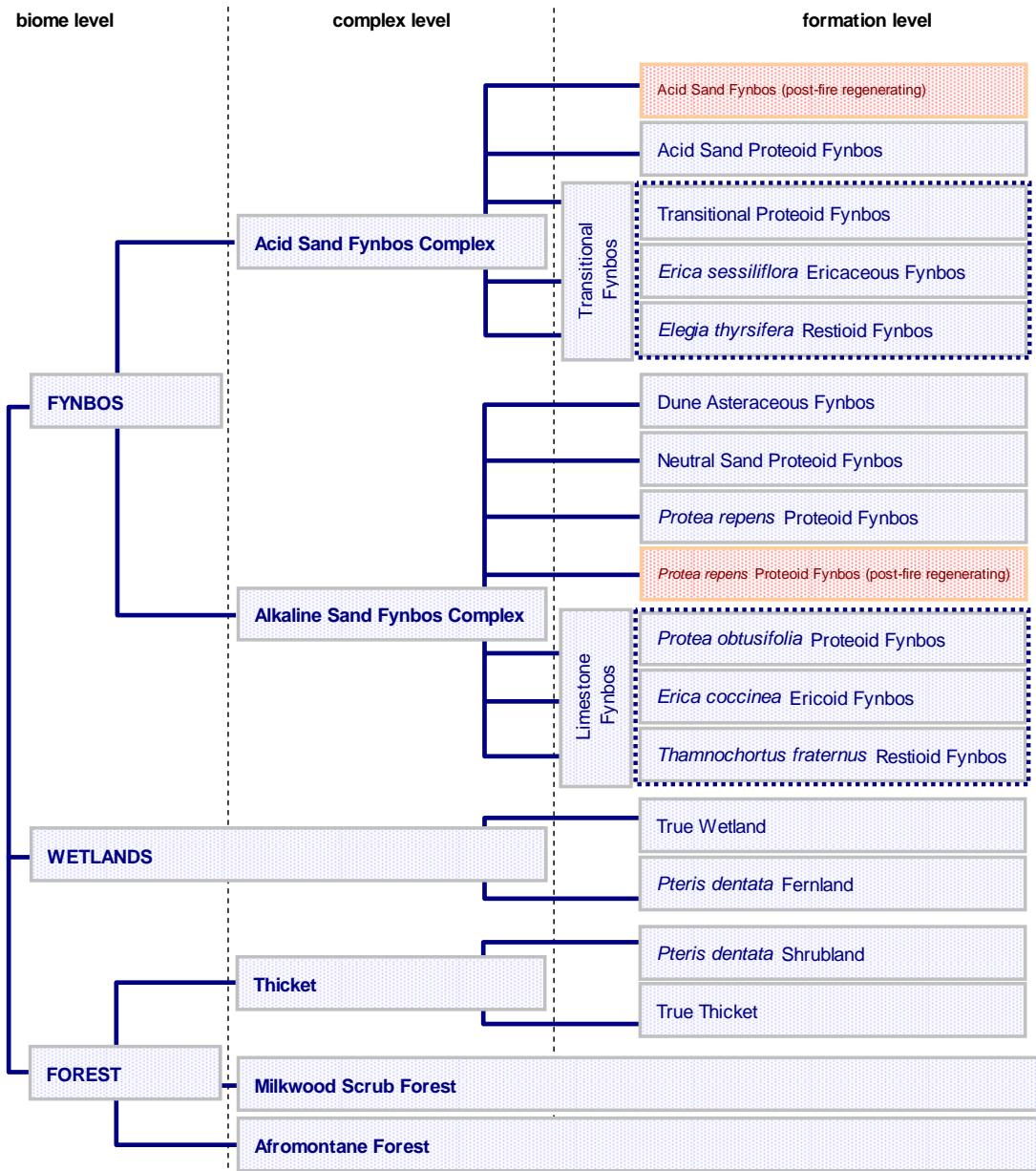


Fig. 4.2: Dendrogram representing the different levels of vegetation units on Grootbos Nature Reserve. Designed by the author.

- all the clustering was based on the classification protocol of the TWINSPAN-classification of the extended dataset
- species with high cover values were preferred
- dominant, easily recognizable species (especially proteoids, but also large ericoids and restioids) were preferred to smaller species
- all relevés within the considered complex containing the chosen species were clustered into one formation, excluding those relevés with a cover of that or those species below a certain pseudospecies level (the detailed criteria are summarized in Tab. S.1)

- if two or more of the chosen species were present on a relevé the species with the higher pseudospecies level resp. the higher cover was used, or the ordination results were taken into account

This kind of manual post-processing resulted in a number of clusters for each of the fynbos complexes and for the wetlands. The formations were named after the dominant species or, if none were present, characteristic habitat features, as well as after the dominant structural elements. The criteria for the recognition of all the formations are given in detail in Tab. S.1. Five formations were recognized for the Acid Sand Fynbos Complex:

- Acid Sand Fynbos (post-fire regenerating)
- *Erica sessiliflora* Ericaceous Fynbos
- *Elegia thrysifera* Restioid Fynbos
- Transitional Proteoid Fynbos, based on *Leucadendron coniferum* and *Leucospermum patersonii*
- Acid Sand Proteoid Fynbos, based on the absence of the above species

The first three formations may be clustered as Transitional Fynbos since they contain elements which are also common in the Alkaline Sand Fynbos Complex. The post-fire regenerating Acid Sand Fynbos should be considered as a successional stage rather than as formation. Hence, it will be discussed in connection with the post-fire succession (chapter 5).

Six formations were established for the Alkaline Sand Fynbos Complex, excluding the immediate post-fire stage. The first three formations may be clustered as Limestone Fynbos:

- *Protea obtusifolia* Proteoid Fynbos
- *Erica coccinea* Ericoid Fynbos
- *Thamnochortus fraternus* Proteoid Fynbos
- *Protea repens* Proteoid Fynbos
- Neutral Sand Proteoid Fynbos: based on *Leucadendron coniferum* and *Leucospermum patersonii*
- Dune Asteraceous Fynbos: based on the absence of all the above species
- *Protea repens* Proteoid Fynbos (post-fire regenerating)

The post-fire regenerating formation will be considered as successional stage and therefore be discussed in chapter 5. Two formations were recognized for the Wetland Complex:

- *Pteris dentata* Fernland
- True Wetland, based on the absence of *P. dentata*,

and also for the Thicket Complex:

- *Pteris dentata* Shrubland
- True Thicket, based on the absence of *P. dentata*

All of these formations will be described in detail below. The classification tables are included in App. 2.2.

#### 4.1.3 Indirect relevé ordination: DCA

The CCA case scores are plotted in the diagrams in Fig. 4.3 and will be discussed for all three analyses instead of the environmentally constrained site scores, because the author opines that the former provide more useful information.

#### Complete dataset - floristic composition

Fynbos, Thicket/Wetland and the two forest complexes were discriminated along the first axis (eigenvalue: 0.91), while the differentiation among the fynbos relevés is predominantly represented by the second (eigenvalue: 0.65) and to a less extent by the first axis. The dominance of the first axis becomes obvious in Fig. 4.3a. The complete statistics of all DCAs are included in app. 2.3.

The fynbos is concentrated in a readily compact cluster with an internal structure largely corresponding to the classification. The Acid Sand Proteoid Fynbos relevés are located at one end of the cluster, with the transitional relevés classified as *Elegia thrysifera* Restioid Fynbos, *Erica sessiliflora* Ericaceous Fynbos and Transitional Proteoid Fynbos leading to the Neutral Sand Proteoid Fynbos and the *Protea repens* Proteoid Fynbos, the latter two being mixed together. The Limestone Fynbos and the Dune Asteraceous Fynbos are intermixed as well, but together constituting a well-defined cluster. For relevé 15 (disturbed fynbos) a very distinctive character is indicated by the DCA.

The Milkwood Scrub Forest and the Afromontane Forest constitute well-defined clusters.

Intermediate between Fynbos and Forest, Thicket and Wetland relevés are intermixed without any obvious internal pattern. Relevé 72 (classified as Acid Sand Proteoid Fynbos) is of special interest as its transitional character between Fynbos and Wetland becomes obvious.

#### Fynbos dataset - floristic composition

The strong dominance of the first axis observed for the complete dataset disappeared when only the fynbos relevés were ordinated (Fig. 4.3b). The first and the second axis showed almost the same significance, with eigenvalues of 0.68 and 0.62 respectively. In general, the patterns are similar to those described above but with the following exceptions: Relevés of the *Erica sessiliflora* Ericaceous Fynbos form a separate cluster. Regenerating Acid Sand Fynbos shows a transitional character between the Acid Sand Fynbos Complex on the one hand and the majority of Neutral Sand Proteoid Fynbos and *Protea repens* Proteoid Fynbos on the other hand. The latter two formations are clearly separated. Relevés assigned to the *Protea obtusifolia* Proteoid Fynbos are partly intermixed with the Neutral Sand Proteoid Fynbos. The *Thamnochortus fraternus* Restioid Fynbos constitutes a separate cluster. The same is true for the relevés 67, 129 and 171, all of them being classified as post-fire regenerating *Protea repens* Proteoid Fynbos.

### Complete dataset - life form composition

The dominance of the first axis is less pronounced than for the DCA with floristic composition (Fig. 4.3c). The eigenvalue of the first axis is 0.76, and of the second axis 0.50. Fynbos, Thicket/Wetland and Forest were clearly discriminated along the first axis. Wetland and Thicket were clearly discriminated along the second axis, as well as Milkwood Scrub Forest and

Afromontane Forest. The relevés 4 and 5 (classified as Afromontane Forest) occupied a position intermediate between the two forest types. A considerable number of Neutral Sand Proteoid Fynbos relevés were intermixed with the thicket relevés. The pattern within the compact fynbos cluster is rather poor with the exception of the relevés 112 and 159 (*Erica coccinea* Ericoid Fynbos), which form a separate cluster.



Fig. 4.3a: Results of the DCA including the complete data-set: Plot of the first two axes (x=first axis, y=second axis).

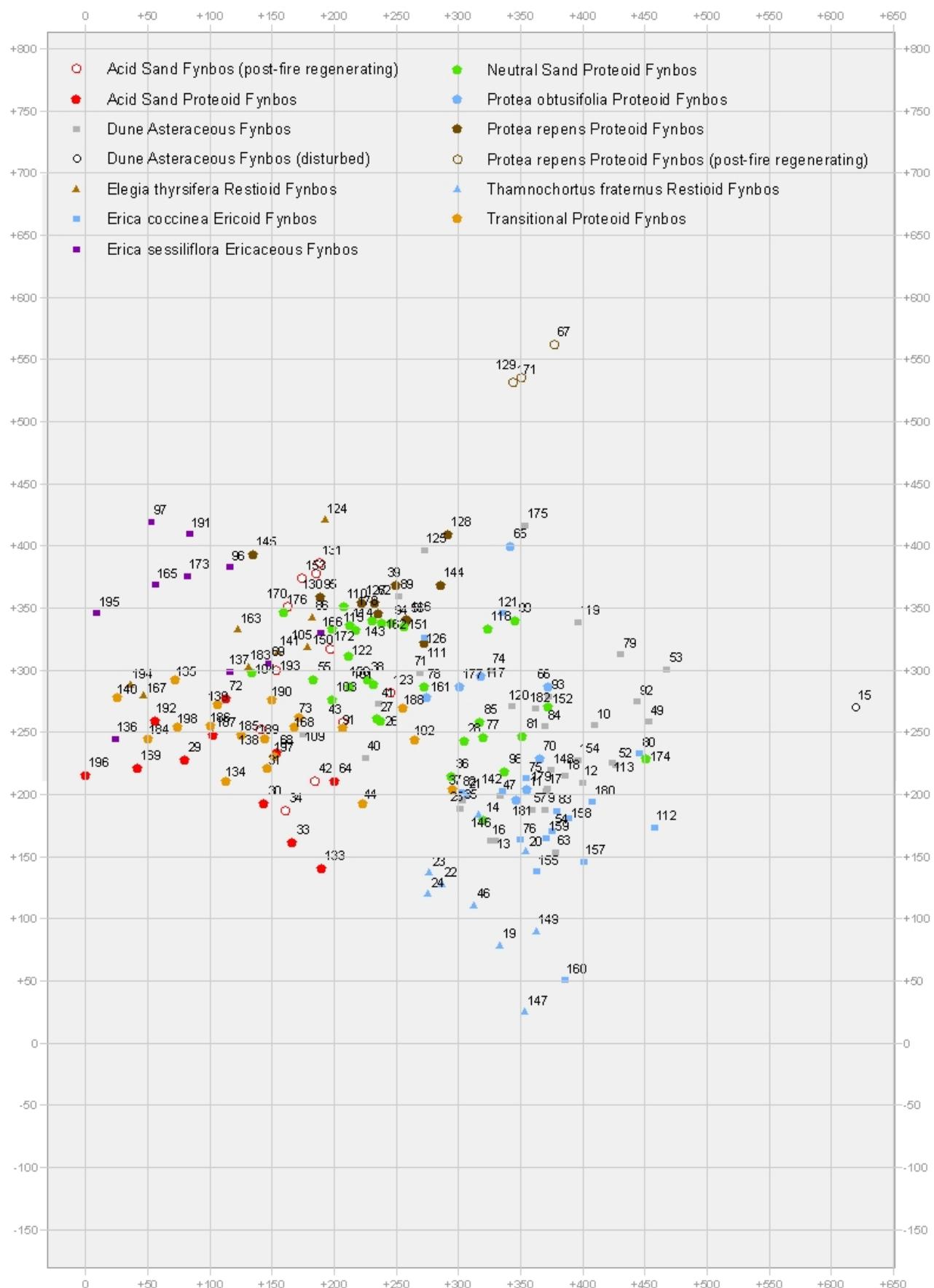


Fig. 4.3b: Results of the DCA including only the relevés classified as fynbos: Plot of the first two axes (x=first axis, y=second axis).



Fig. 4.3c: Results of the DCA including the complete dataset, according to life form composition: Plot of the first two axes (x=first axis, y=second axis).

#### 4.1.4 Direct relevé ordination: CCA

##### Complete dataset - floristic composition

Vegetation age appeared as an extraordinarily strong predictor with a biplot score of above 0.99 for the first two axes. K (0.85), P (0.82) and Mg (0.78) attained values above 0.7. Irradiation (0.66), resistance (0.61), Na (0.56), wind exposition, slope (0.54 each) and elevation (0.53) showed scores above 0.5. pH stayed

below that threshold but rose to 0.62 if the third and the fourth axis were included, due to the high pH score on the fourth axis (0.83). A number of other variables also significantly increased their scores when those axes were included. This phenomenon is connected to the fact that the eigenvalue of the second axis (0.63) was not significantly higher than the eigenvalues of the third and the fourth axis (0.58 and 0.51 respectively). In contrast, the first axis clearly

dominated (0.95) due to the strong predictive force of vegetation age. All the case scores and biplot scores are included in App. 2.4.1.

The results may be biased by a certain amount of redundancy: slope appeared to be associated with K (0.55) and Mg (0.56). The correlation of irradiation with aspect was 0.73, with K -0.57 and with Mg -0.51. Vegetation age showed notable correlations with resistance (-0.59), Na (0.57), P (0.80), K (0.62) and Mg (0.66). pH correlated negatively to elevation (-0.72) and positively to Ca (0.71). Resistance was negatively correlated to the levels of all measured elements: Na (-0.65), P (-0.62), K (-0.62), Ca (-0.53) and Mg (-0.68). All correlations between elements were positive: Na with P (0.61), K (0.68), Ca (0.65) and Mg (0.81); P additionally with K (0.72), Ca (0.55) and Mg (0.69); and K with Mg (0.91).

The plot (Fig. 4.4a) indicated a clear ecological separation between the major biomes. Fynbos was discriminated from the forest by the presence of frequent fire events. High resistance was also associated with fynbos, while higher levels of all soil nutrients appeared to promote forest or vice versa.

Milkwood Scrub Forest and Afromontane Forest constituted separate clusters. The former was more compact and the latter was somewhat more dispersed along an axis representing a combination of slope, pH and soil depth. The Milkwood Scrub Forest was associated with low altitudes, low rock cover and deep, Ca-rich soils. In contrast, the soils supporting Afromontane Forest are shallow and rocky. K and Mg are abundant at high levels but solar irradiation is limited compared with the other clusters. This forest type was also associated with higher values for elevation and slope as well as for wind exposition.

The fynbos relevés were discriminated along a gradient of pH, elevation, soil depth and rock cover, and also wind exposition. Due to the high significance of fire incidence the relevés representing this major biome were aligned in a predominantly one-dimensional pattern.

### Fynbos dataset - floristic composition

Fig. 4.4b shows the results of a CCA excluding all non-fynbos relevés, fire and the advanced topographical variables from the ecological dataset. The biplot scores and correlation values were the same as for the species ordination including the whole set of environmental variables. App. 2.4.2 lists the case scores of this ordination.

The relevés were scattered more equally and a couple of variables were approximately the same powerful in explaining the patterns, indicating that the mix of fynbos units is a complex system driven by the

interaction of several environmental factors, with continuous rather than with discrete boundaries. Nevertheless, the clusters derived from the classification were recognizable.

The Acid Sand Fynbos Complex and the Alkaline Sand Fynbos Complex were discriminated along gradients of pH and elevation. No useful patterns could be observed within the latter cluster. Within the Alkaline Sand Fynbos Complex a distinctive character was indicated for the *Protea repens* Proteoid Fynbos, which appears to be associated with extraordinarily high resistance values. The Neutral Sand Proteoid Fynbos, located close to the center of the diagram, formed a well defined cluster adjacent to the Dune Asteraceous Fynbos and the Limestone Fynbos. These, however, were intermixed without an apparent separation. One cluster showed an association with low elevation, high pH and deep soils, the other with high Mg, steep slopes and low resistance. Four relevés (49, 53, 54 and 57, and also 15, representing disturbed fynbos) appeared to be associated with high pH, Na and Ca.

A relatively clear line could be drawn to discriminate between relevés with and without proteoids, which would run perpendicular to the gradients of pH and the levels of several soil nutrients. Nutrient-rich alkaline soils do not really support members of the family of Proteaceae.

### Complete dataset - life form composition

Vegetation age (biplot score 0.99) appeared as the strongest variable for explaining the vegetation patterns. The levels of a number of elements also served as good predictors: The biplot score for P and K was 0.83 each, for Mg 0.74 and for Na 0.57. Also irradiation (0.70) and resistance (0.62) showed values exceeding 0.5. The biplot scores for elevation (0.24), soil depth (0.19) and pH (0.12) were extraordinarily low compared to the results described above. Among the axes the first was clearly dominating (eigenvalue 0.83) with values of 0.44 for the second, 0.33 for the third and 0.18 for the fourth axis. The correlation between the environmental variables is the same as for the floristic ordination. App. 2.4.3 lists all the case and biplot scores.

The results of the site ordination regarding life forms are represented in fig 4.4c. Afromontane Forest and Milkwood Scrub Forest were concentrated in separate clusters with the *Pteris dentata* Wetland showing some affinity to the Afromontane Cluster. Fynbos is concentrated in one big cluster without any obvious distinctions between different subtypes. As already indicated above, a classification of the fynbos based on structural criteria is not supported by the chosen life form concept.

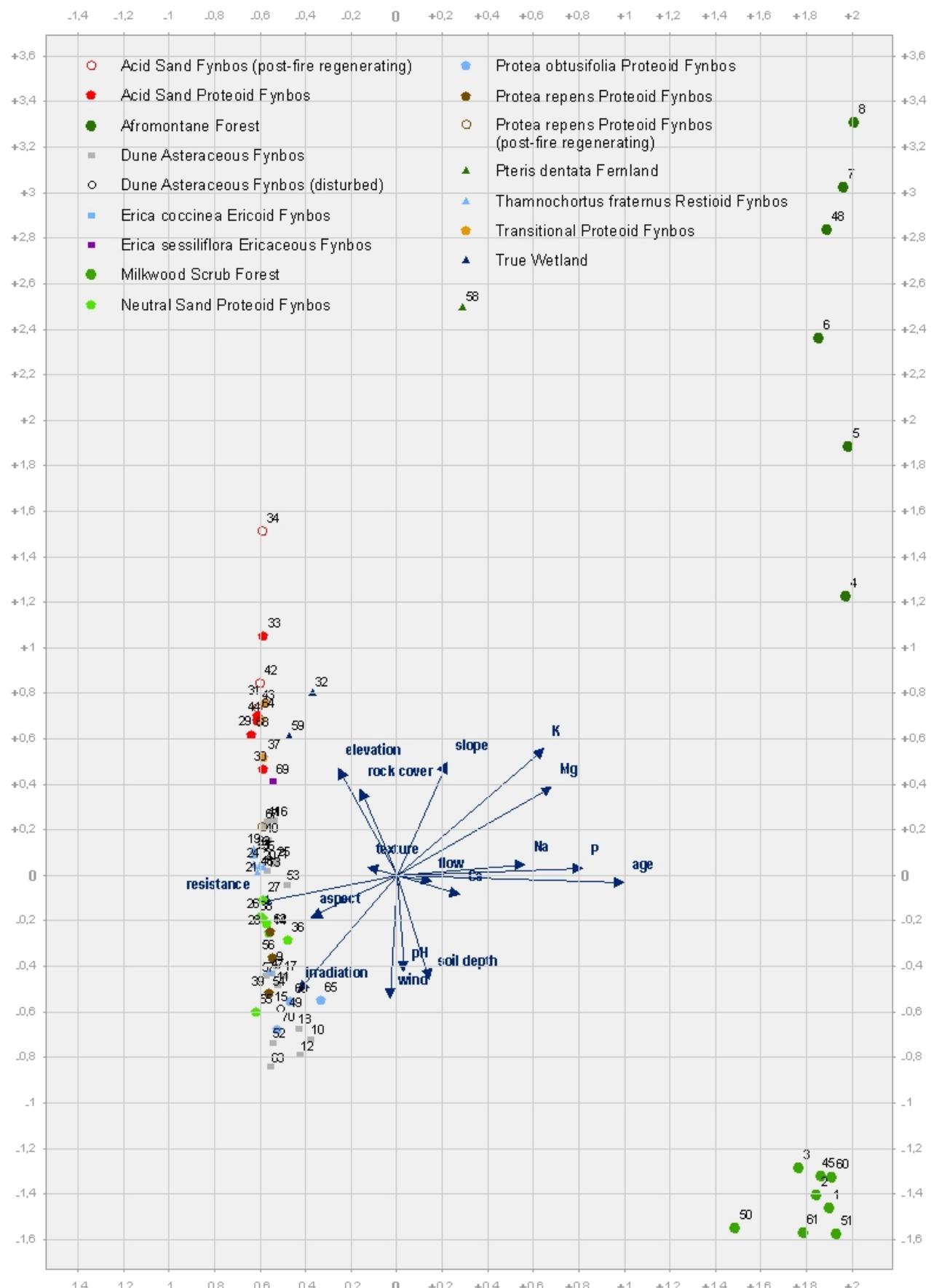


Fig. 4.4a: Results of the CCA including the complete core dataset, according to floristic composition: Plot of the first two axes (x=first axis, y=second axis).



Fig. 4.4b: Results of the CCA including the relevés classified as fynbos of the core dataset, according to floristic composition: Plot of the first two axes (x=first axis, y=second axis).

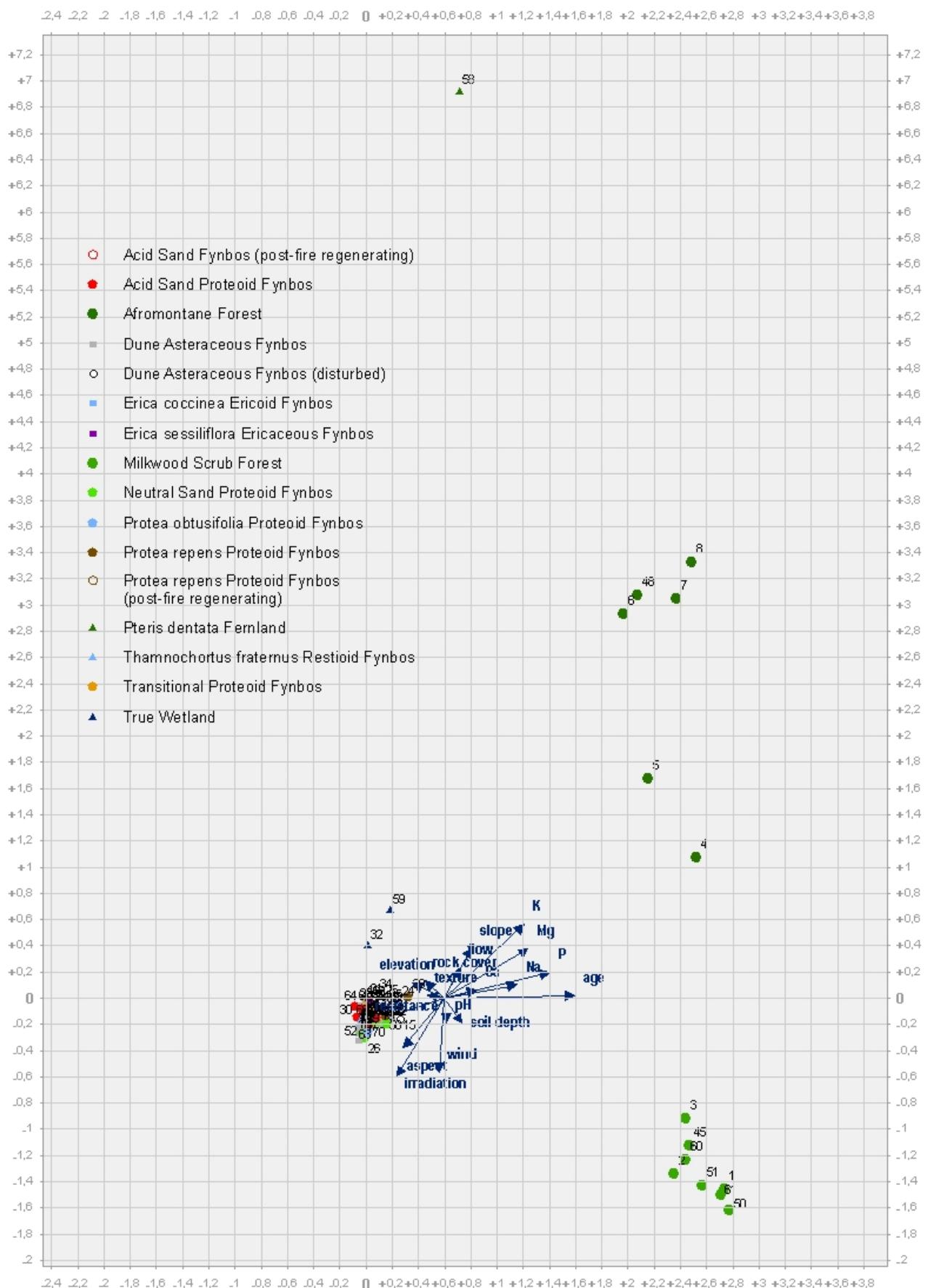


Fig. 4.4c: Results of the CCA including the complete core dataset, according to life form composition: Plot of the first two axes (x=first axis, y=second axis).

## 4.2 Vegetation mapping

### Numerical imagery interpretation

Fig 4.5a and b show the histograms for the filtered index and texture dataset, respectively. The hypothesis of natural breaks between relatively homogeneous clusters has to be rejected. Both datasets show single-peaked, left-biased distributions without any clear clustering. The latter is more noisy, which may be explained by the higher number of possible values - the index graph is smoothed automatically due to the low range of values (about one tenth of texture data). The essential knowledge gained from the graphs is that the Gleasonian view appears to be applicable to the vegetation of Grootbos Private Nature Reserve.

The IsoData classification resulted in six index and texture classes each (excluding the no data classes). The classification results for the two datasets are represented in Fig. 4.6a and Fig. b. Considering the index dataset the high values for forested areas, especially for the Milkwood Scrub Forest, are obvious. Among the lower classes different types of fynbos are supposed to be characterized by different class values. The fynbos situated NE of the Milkwood Scrub Forest seems to be more productive than most of the other areas covered by this vegetation unit. Very high values were also attained for the cultivated land close to the N edge of the reserve. The texture dataset generally provides similar patterns as the index dataset. Forested areas are characterized by the highest class values. Surfaces with low vegetation cover and thus strong influence of the substrate on the reflection properties also show very high class values. The same is true for sparsely vegetated areas with anthropogenic structures like buildings. As with the index dataset, different fynbos types are supposed to reflect different surface texture. A striking difference between the two datasets is that the spatial structure of index classes hardly reflects the road system of the Reserve, while the texture classes clearly reflect it despite the fact that the

roads were removed from the input data. The reason may be the edges of the roads which have different reflection properties than the adjacent vegetation.

### Manual mapping

Fig. 4.7 summarizes some quantitative results obtained from the manual vegetation mapping. Fig. 4.8 illustrates the spatial patterns of the units as they were applied to the geostatistical analysis. They largely correspond to the results of the numerical vegetation analysis. However, some changes were made. Patches regenerating from recent fire events were mapped separately if it was not possible to predict the vegetation unit establishing at maturity. The formations of the Limestone Fynbos were mapped separately, but they were summarized in the statistics due to a large amount of overlapping. Both *Pteris dentata* units were assigned to the Forest Biome due to their close association to the patches of Afromontane Forest. Some of the formations were further subdivided. Since these sub-units are only based on the subjective impression of the author and do not necessarily support a recognition as separate entities, they were generally disregarded in the statistics of Fig. 4.7 and the subsequent geostatistical analysis. Two exceptions are the *Gunnera perpensa* Wetland and the dry formation of the Neutral Sand Proteoid Fynbos, since those were supposed to be clearly associated with certain topographic variables. The sub-formations will be discussed in detail below, in connection with the description of the vegetation units.

The vast majority of the reserve is covered in Fynbos (1620 ha or 95.3 per cent). The Forest Biome accounts for 78 ha or 4.6 per cent (the Milkwood Scrub Forest for 43 ha or 2.5 per cent), while only 1.4 ha (0.1 per cent) are covered in Wetland. Dune Asteraceous Fynbos covers more than half of the reserve (914 ha or 53.8 per cent), and the whole Alkaline Sand Fynbos Complex occupies 1385 ha or 81.5 per cent.

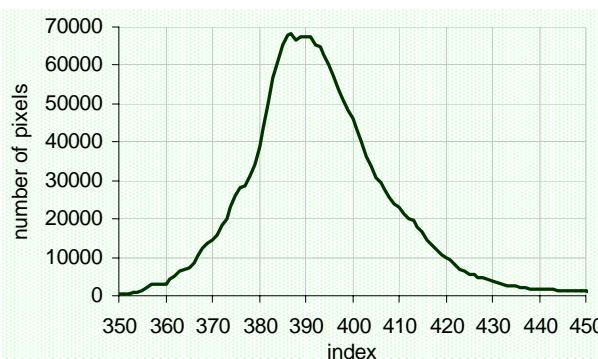
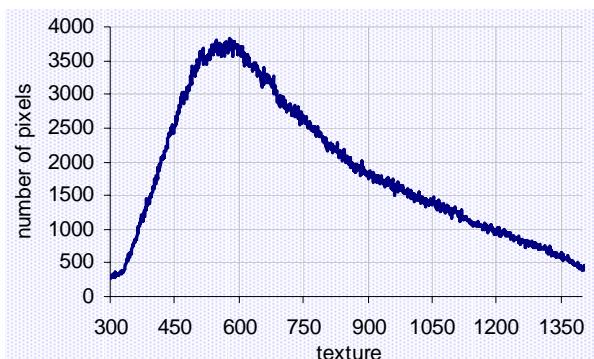


Fig. 4.5a (left) and b (right): Histograms (pixel values plotted versus number of pixels) for the filtered texture and index datasets, limited to the range of values with the highest abundance in the considered dataset. For a detailed discussion compare text above. Designed by the author.

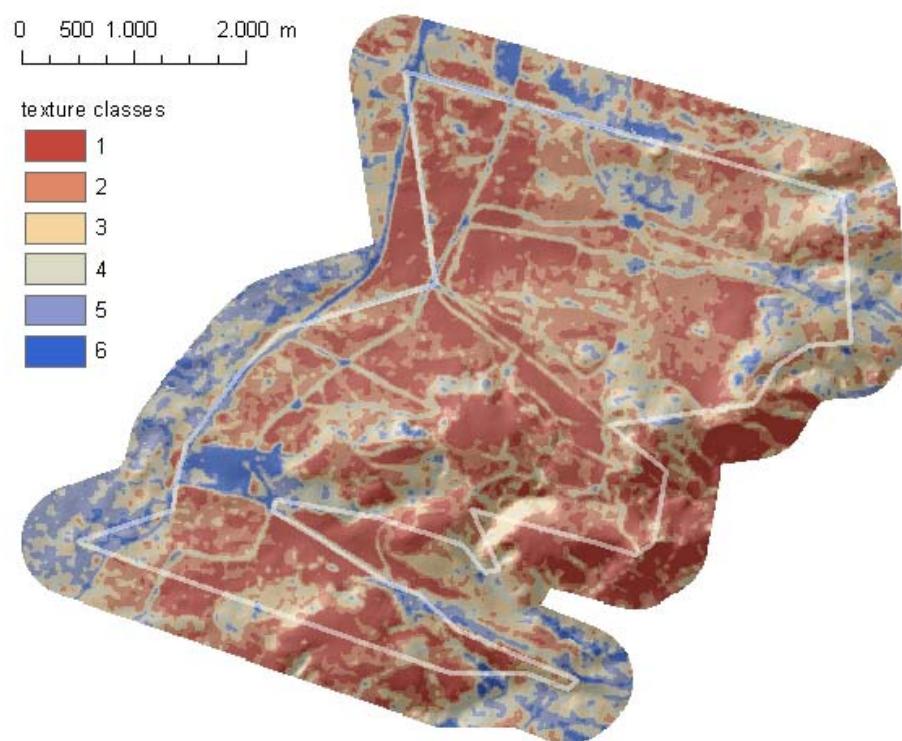
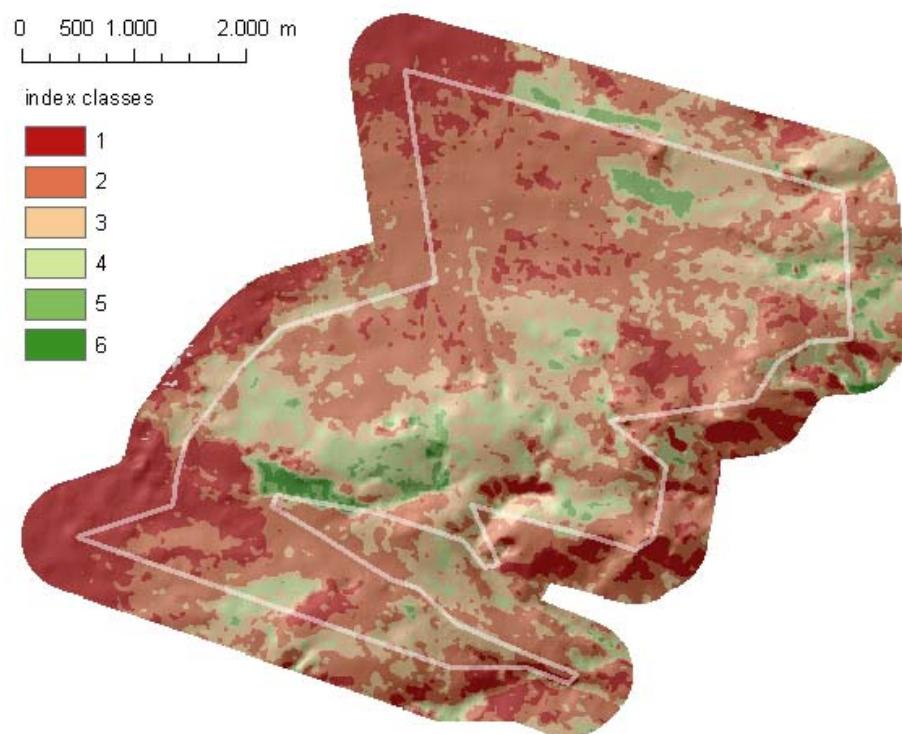
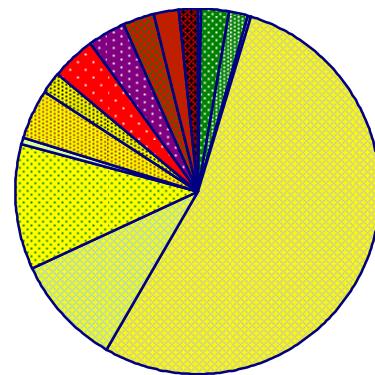


Fig. 4.6a (upper) and b (lower): Index and texture classes of the land surface of Grootbos Nature Reserve, obtained from orthophotos

class	a	b	c	d
<b>Forest Biome</b>	<b>78,03</b>	<b>4,6</b>	<b>8</b>	<b>9,75</b>
Afromontane Forest	4,07	0,2	5	0,81
Milkwood Scrub Forest	43,11	2,5	4	10,78
<b>Thicket Complex</b>	<b>30,85</b>	<b>1,8</b>	<b>11</b>	<b>2,80</b>
True Thicket	27,47	1,6	8	3,43
<i>Pteris dentata</i> Fernland	0,54	0,0	1	0,54
<i>Pteris dentata</i> Shrubland	2,84	0,2	2	1,42
<b>Wetland Biome</b>	<b>1,37</b>	<b>0,1</b>	<b>4</b>	<b>0,34</b>
<b>Fynbos Biome</b>	<b>1620,25</b>	<b>95,3</b>	<b>3</b>	<b>540,08</b>
<b>Alkaline Sand Fynbos Complex</b>	<b>1385,30</b>	<b>81,5</b>	<b>3</b>	<b>461,77</b>
Dune Asteraceous Fynbos	913,84	53,8	3	304,61
Limestone Fynbos	162,03	9,5	27	6,00
Neutral Sand Proteoid Fynbos	191,49	11,3	2	95,75
Neutral Sand Proteoid Fynbos (dry)	9,54	0,6	9	1,06
<i>Protea repens</i> Proteoid Fynbos	76,46	4,5	3	25,49
Alkaline Sand Fynbos (post-fire regenerating)	31,94	1,9	2	15,97
<b>Acid Sand Fynbos Complex</b>	<b>234,95</b>	<b>13,8</b>	<b>5</b>	<b>46,99</b>
Acid Sand Proteoid Fynbos	65,69	3,9	7	9,38
<i>Erica sessiliflora</i> Ericaceous Fynbos	55,15	3,2	2	27,58
Transitional Proteoid Fynbos	45,94	2,7	7	6,56
<i>Elegia thrysifera</i> Restioid Fynbos	37,88	2,2	2	18,94
Acid Sand Fynbos (post-fire regenerating)	30,29	1,8	7	4,33
<b>total</b>	<b>1699,65</b>			



- Afromontane Forest
- Milkwood Scrub Forest
- True Thicket
- *Pteris dentata* Fernland
- *Pteris dentata* Shrubland
- Wetland Biome
- Dune Asteraceous Fynbos
- Limestone Fynbos
- Neutral Sand Proteoid Fynbos
- Neutral Sand Proteoid Fynbos (dry)
- *Protea repens* Proteoid Fynbos
- Alkaline Sand Fynbos (post-fire regenerating)
- Acid Sand Proteoid Fynbos
- *Erica sessiliflora* Ericaceous Fynbos
- Transitional Proteoid Fynbos
- *Elegia thrysifera* Restioid Fynbos
- Acid Sand Fynbos (post-fire regenerating)

Fig. 4.7: Surface statistics based on the vegetation mapping - a = total surface on the reserve in ha, b = percent of total reserve surface, c = number of patches, d = average patch size in ha.

Even the second largest formation of this complex, the Neutral Sand Proteoid Fynbos (191 ha or 11.3 per cent), approaches the same amount of cover as the whole Acid Sand Fynbos Complex (235 ha or 13.8 per cent).

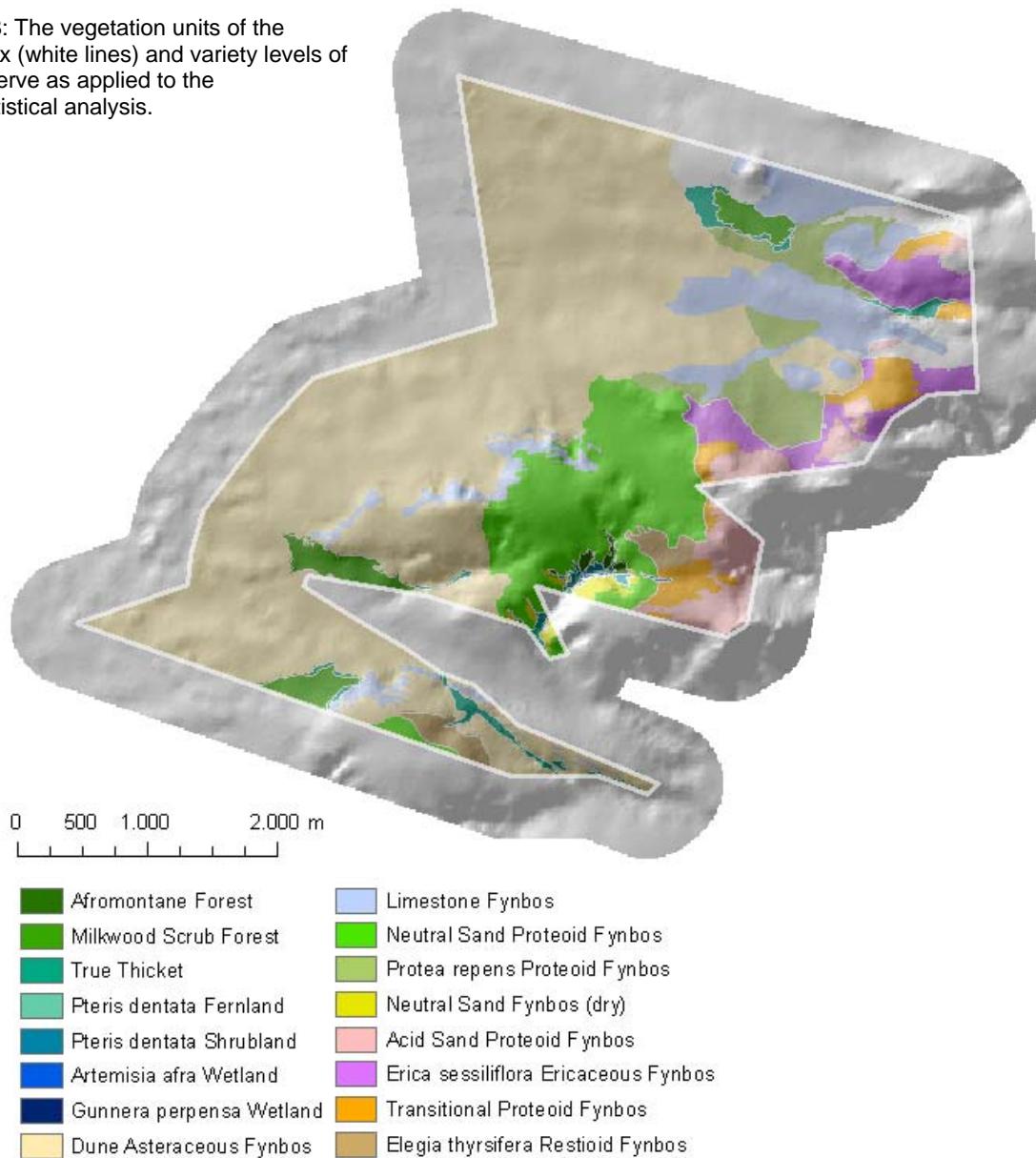
Fig 4.7 also provides information about the fragmentation of the vegetation units. The interpretation of this information has to be approached with caution because the fragmentation may be caused by different factors, including the shape of the reserve. Dune Asteraceous Fynbos and Neutral Sand Proteoid Fynbos cover continued, hardly fragmented areas with patch sizes of 305 and 96 ha respectively. *Protea repens* Proteoid Fynbos and *Erica sessiliflora* Ericaceous Fynbos also exceed average patch sizes of 25 ha. In contrast, the distribution of Limestone Fynbos is rather patchy, with 27 patches ranging from tens of ha of *Protea obtusifolia* Proteoid Fynbos to tiny limestone outcrops covered with *Thamnochortus fraternus* Restioid Fynbos. The average patch size (6 ha) is not representative in this case, nor is it for the dry Neutral Sand Proteoid Fynbos. In the Forest Biome the patch size of the highly fragmented Afromontane Forests remains below 1 ha (0.81), while the patches of

Milkwood Scrub Forest occupy slightly more than 10 ha on average.

It is highly problematic to provide quantitative measures for the accuracy of the vegetation map due to the fact that it is based on the subjective impression of the author supported by a sparse network of relevés. The map should be considered as a rough approach to the real conditions. Where it was possible to use the images for a delimitation of different units, the error does not exceed a few meters, but it may account several tens of meters in some places where the imagery did not provide useful support. The units of the map are not necessarily identical to the units of overlying relevés - a phenomenon that is connected to the subjective approach of the vegetation mapping. Furthermore, it has to be taken into account that the orthophotos supporting the mapping were four years old at the time of the survey, which may cause a lot of bias in a rapidly changing biome like the fynbos.

The problems mentioned above are also especially valid for the mapping of the distribution of the introduced plant species. They are partly based on subjective estimations of the author. Recent imagery would be necessary to achieve more accurate results.

Fig. 4.8: The vegetation units of the complex (white lines) and variety levels of the reserve as applied to the geostatistical analysis.



### Correspondence to the imagery interpretation

A qualitative comparison of the units derived from the imagery interpretation and from manual vegetation mapping indicates a good correspondence for the Milkwood Scrub Forest and rather poor correspondence for all of the other units. Predictions were attempted for the distribution of the vegetation units with the index as the independent variable and the index derived from the manual vegetation mapping as the dependent variable. The methods were the same as for the geostatistical analysis.

For the biome level, 68.4 per cent were predicted correctly. The accuracy decreased drastically with the degree of generalization: 17.1 per cent for the complex level and 8.9 per cent for the formation level indicated

a poor predictive value of the imagery on the complex and formation levels.

For the biome level (Fig. 4.9, App. 3.1.1), between 60 and 70 per cent of all three biomes were predicted correctly. However, 22.3 per cent of the Forest Biome and 22.9 per cent of Fynbos were predicted as Wetland, resulting in an overrepresentation of the Wetland Biome in the prediction map. 16.5 per cent of Forest were predicted as Fynbos and only 8.2 per cent of Fynbos were predicted as Forest. Among the initially ungrouped pixels beyond the borders of the reserve, 76.7 per cent were predicted as Fynbos and 5.9 per cent as Forest. 17.5 per cent prediction as Wetland increased the overrepresentation of this unit.

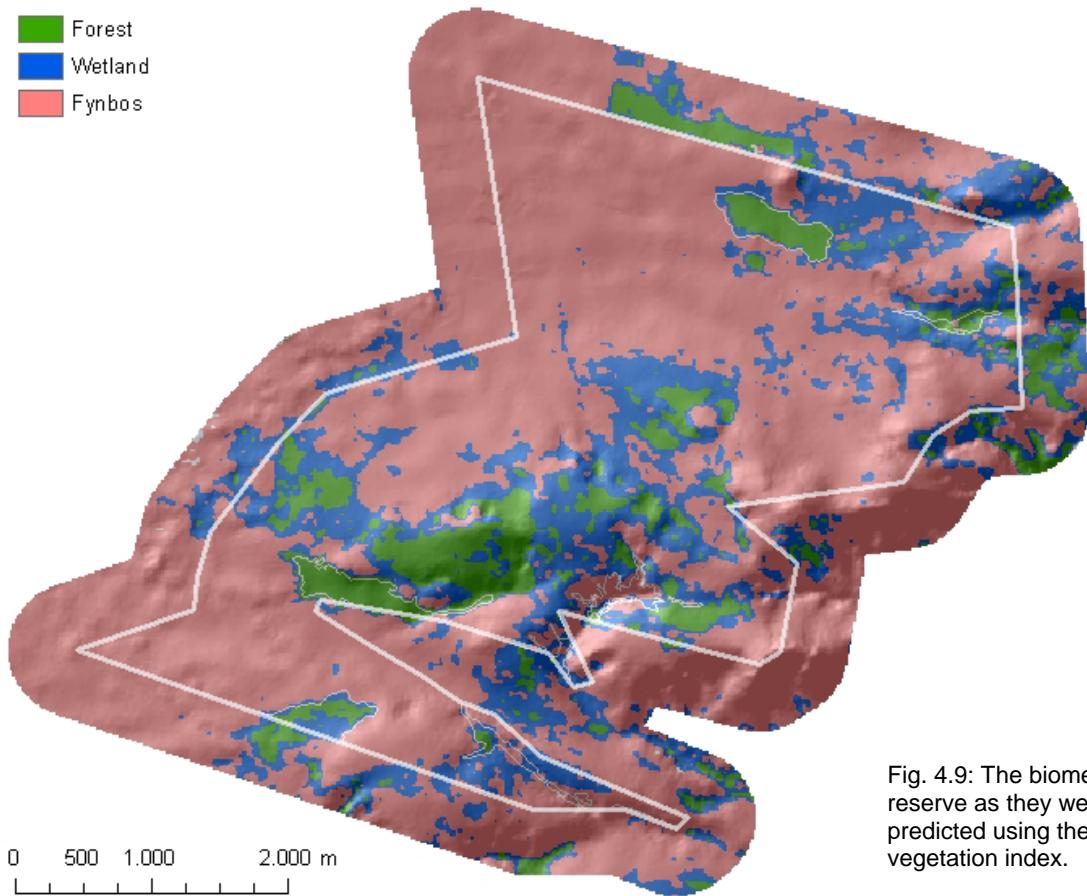


Fig. 4.9: The biomes of the reserve as they were predicted using the vegetation index.

On the complex level (App. 3.1.2), the Afromontane Forest (68.8 per cent) and the Milkwood Scrub Forest (70.8 per cent) are the only units with prediction scores exceeding 50 per cent. However, the result for the Afromontane Forest provides an incorrect picture, since a lot of fynbos pixels were predicted as Afromontane Forest, as were 44.7 per cent of initially unclassified pixels, leading to an overrepresentation of Afromontane Forest in the prediction map. The same is true for the Wetland, 44.8 per cent of which were predicted correctly. The fynbos complexes were predicted with accuracies of 12.9 per cent (Alkaline Sand Fynbos Complex) and 29.1 per cent (Acid Sand Fynbos Complex).

For the formation level (App. 3.1.3), the prediction patterns were similar to the complex level. The overrepresentation of the Afromontane Forest was even more pronounced (32.5 per cent of ungrouped pixels and values above 10 per cent for several units) probably because its index approached that of large areas of the Dune Asteraceous Fynbos due to shading effects. The formations of the Fynbos Biome were predicted poorly with accuracies not exceeding 10 per cent.

Detailed statistics are added in App. 3.1. Due to the generally poor prediction, especially for the fynbos, which can clearly be assigned to problems with

imagery interpretation, the results of the manual vegetation mapping were applied for the vegetation map (App. 4) and the geostatistical analysis.

### 4.3 Geostatistical analysis

The percentage of pixels predicted correctly ranged from 17.7 per cent to 77.5 per cent, depending on the combination of predictors and the level of generalization of the vegetation units (Tab. 4.1). In general, the highest values were attained by predicting lower levels of generalization with a combination of a higher number of variables. A combination of the advanced predictors (flow accumulation, solar irradiation and wind exposition) resulted in the poorest predictions on the formation level but the most accurate for the biome level. Combinations of the basic topography on one hand and the elevation combined with the advanced topography on the other hand provided approximately equal powerful predictions. On average, the complete dataset proved to supply the most accurate results, which will therefore be discussed in more detail. The combination of elevation with the advanced topography provided almost equal results. The basic topography (elevation, slope and aspect) showed an intermediate predictive value.

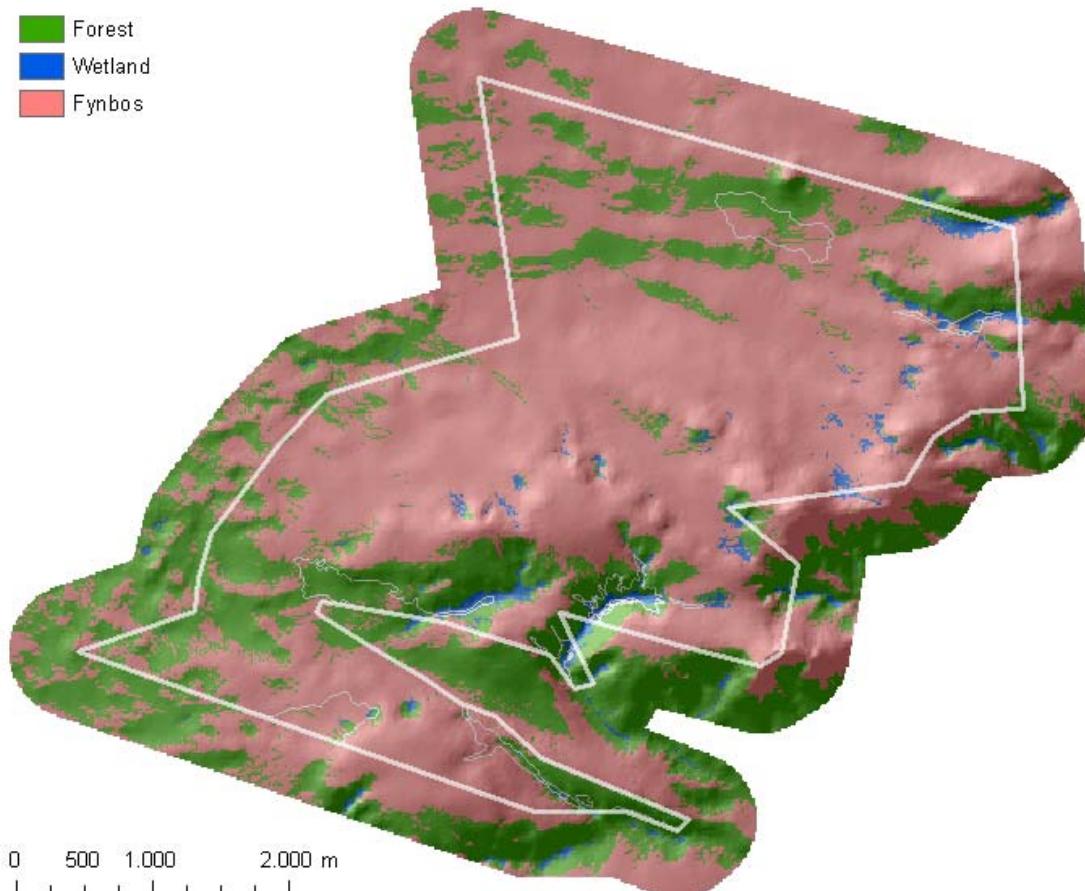
	predictors				
	adv	bas	alt	all	average
<b>variety level</b>	17,7	40,0	47,9	47,9	38,4
<b>variety level*</b>	20,2	43,0	51,8	51,7	41,7
<b>complex level</b>	55,6	50,0	57,7	58,6	55,5
<b>biome level</b>	77,5	59,1	74,7	75,1	71,6
<b>average</b>	42,8	48,0	58,0	58,3	51,8

\* Limestone Fynbos excluded

Tab. 4.1: Correct predictions in per cent for different levels of vegetation classes and different combinations of topographic variables (adv = advanced variables, bas = basic variables, alt = elevation and advanced variables, all = all variables).

These results indicated a certain amount of redundancy between the independent variables, only partly supported by the correlation matrices. Solar irradiation and aspect showed correlations between 0.56 and 0.58. Irradiation correlated with slope by scores of 0.41 to 0.45. All other scores remain below 0.4. More detailed statistics are included in App. 3.2.

### Biome level



75.1 per cent of the distribution of the biomes (Forest, Wetland and Fynbos) are explained by topographical variables. The prediction map is illustrated in Fig. 4.10a, the statistics are listed in App. 3.2.1.

The Wetland Biome was predicted with an accuracy of 72.4 per cent. Only 1.7 per cent of all wetland pixels were assigned to the Forest Biome, but 25.9 per cent to the Fynbos Biome. In reverse, 10.7 per cent of the Forest Biome, and only 2.1 per cent of Fynbos were recognized as Wetland. Therefore, a certain proportion of the Wetland Biome would theoretically support fynbos according to its topography, and a certain proportion of the Forest Biome would support wetland, but in both cases the reverse would hardly be realized.

76.4 per cent of Fynbos and 47.9 per cent of Forest were predicted correctly. 41.4 per cent of the Forest Biome were predicted as Fynbos, while 21.4 per cent of Fynbos were assigned to the Forest Biome. Among the originally ungrouped cases beyond the borders of Grootbos, 44.0 per cent were assigned to the Forest Biome, a proportion significantly higher than what would be expected according to the general distribution patterns (Fig. 4.7). 1.5 per cent of the ungrouped cases were recognized as Wetland, and 54.5

Fig. 4.10a: Prediction map for the biome level.

per cent as Fynbos.

### Complex level

The geostatistical analysis for the complex level (the prediction map is illustrated in Fig. 4.10b, the statistics are included in App. 3.2.2) indicated that 58.6 per cent of the distribution of the vegetation complexes on the reserve are explained by a combination of topographical variables.

77.5 per cent of the Afromontane Forest were predicted correctly. The Milkwood Scrub Forest was predicted with a score of 53.5 per cent, 37.0 per cent were assigned to the Alkaline Sand Fynbos. Thicket was poorly recognized with 12.0 per cent correct predictions, but 22.8 per cent were predicted as Milkwood Scrub Forest, 17.5 as Afromontane Forest, 28.2 as Alkaline Sand Fynbos and 18.4 as Wetland. With 70.7 per cent accuracy the Wetland appeared to be fairly well explained by topographic predictors. However, 24.1 per cent were assigned to the Acid Sand Fynbos.

Among the fynbos complexes, the correct predictions for the Acid Sand Fynbos were as high as 75.8 per cent, with only 5.4 per cent predicted as Alkaline Sand Fynbos. Only 56.9 per cent of the latter, however, were correctly predicted. 18.0 per cent were recognized

as Milkwood Scrub Forest. 16.2 per cent of Alkaline Sand Fynbos were predicted as Acid Sand Fynbos, considerably more than the reverse.

Among the originally ungrouped pixels, the predictions as Afromontane Forest (13.3 per cent) and Milkwood Scrub Forest (27.6 per cent) were extraordinarily high compared to their abundance on the reserve, but the abundance of Alkaline Sand Fynbos (34.4 per cent) was significantly lower (Fig. 4.7).

### Formation level (Limestone Fynbos excluded)

When the Limestone Fynbos formations (*Erica coccinea* Ericoid Fynbos, *Protea obtusifolia* Proteoid Fynbos and *Thamnochortus fraternus* Restioid Fynbos) were excluded from the dataset the distribution of units on the formation level appeared to be explained by topographic variables with an accuracy of 51.7 per cent. Fig. 4.10c represents the prediction map, the complete statistics are included in App. 3.2.3.

Afromontane Forest and Milkwood Forest were discriminated almost perfectly. 47.4 per cent of Afromontane Forest were predicted correctly. 23.1 per cent were assigned to the *Pteris dentata* Shrubland. Milkwood Scrub Forest was predicted with an accuracy of 54.9 per cent, 26.7 per cent were mispredicted as Dune Asteraceous Fynbos, 11.4 as True Thicket. The

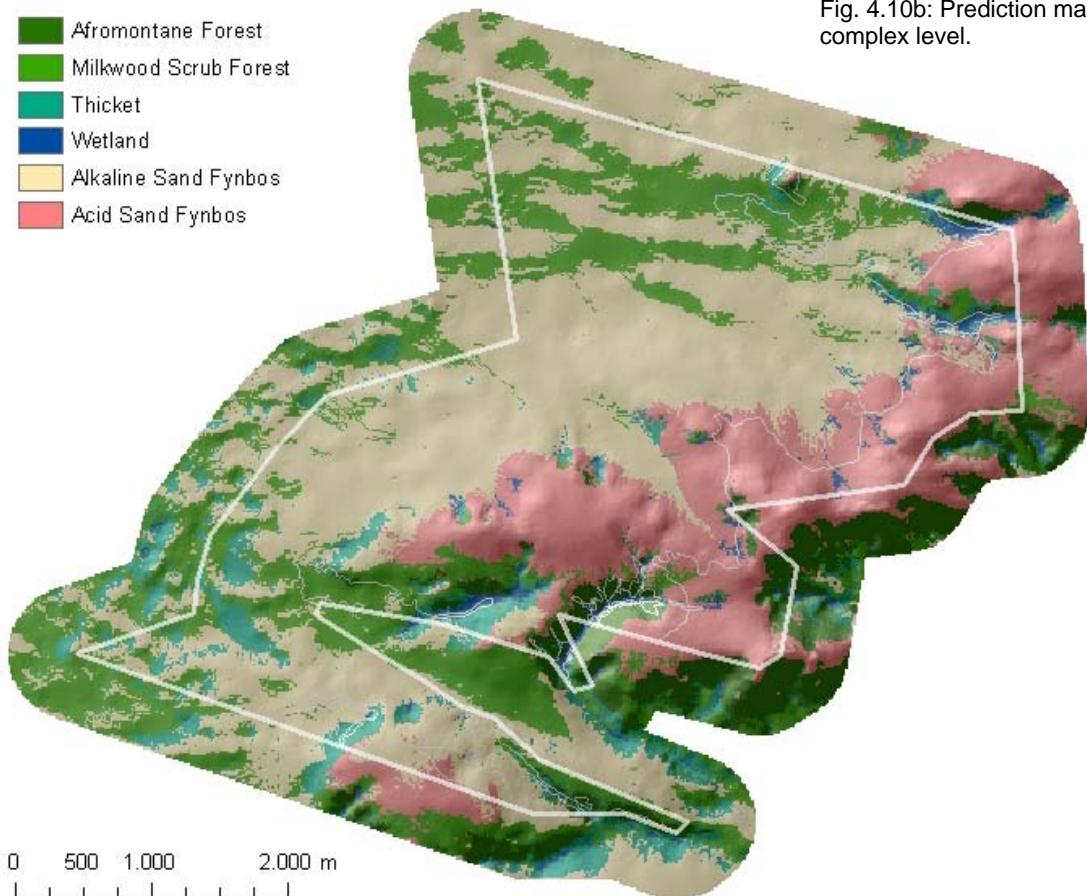


Fig. 4.10b: Prediction map for the complex level.

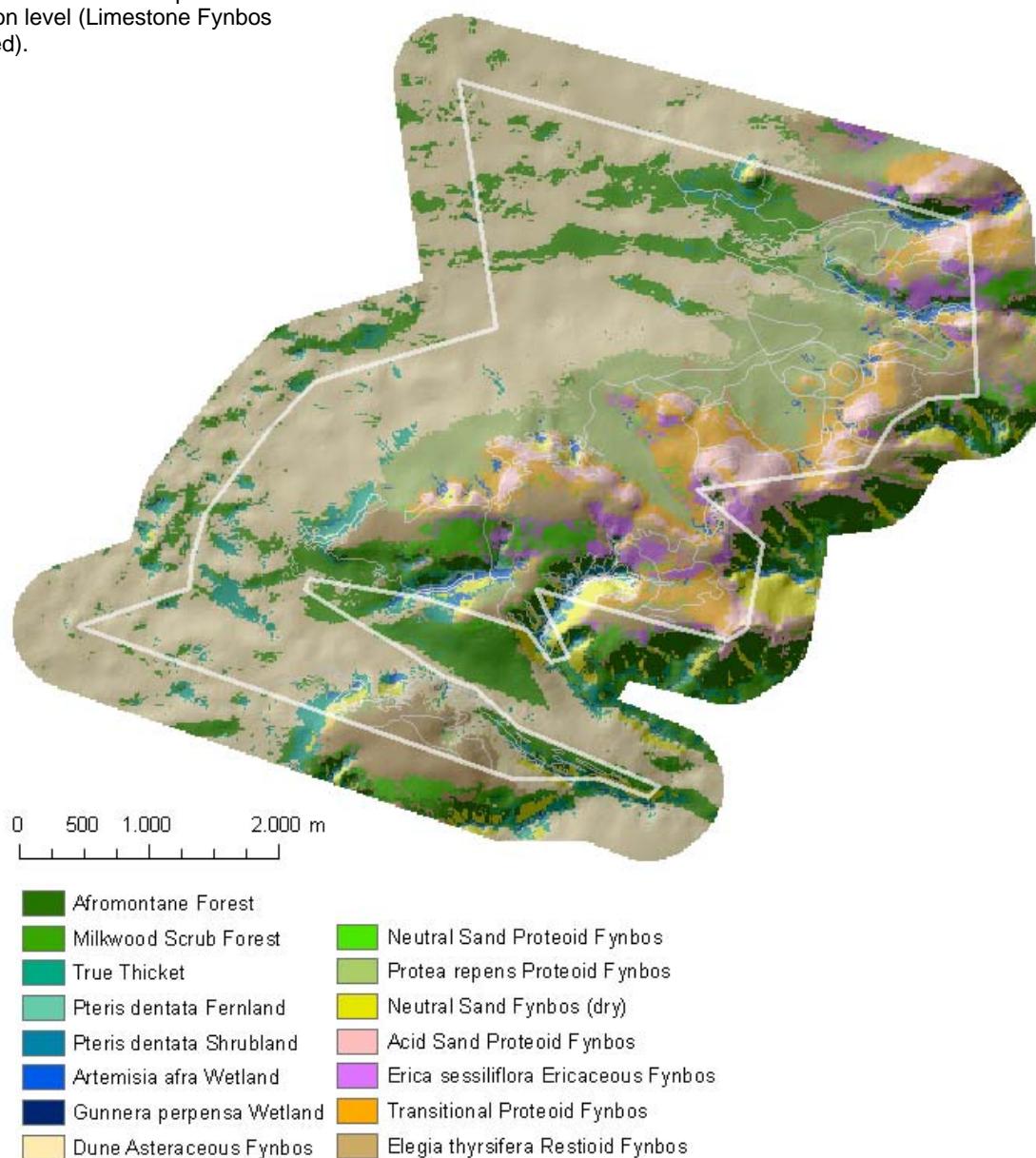
distribution of the latter is poorly explained by the available topographical variables with only 10.4 per cent correct predictions. The rest of the predictions is predominantly dispersed to Milkwood Scrub Forest (21.3 per cent), *Artemisia afra* Wetland (11.9) and Dune Asteraceous Fynbos (28.3). 46.2 per cent of *Pteris dentata* Fernland were recognized, 30.8 and 15.4 per cent were identified as suitable for *Gunnera perpensa* Wetland and *Pteris dentata* Shrubland respectively. 53.8 per cent of the latter were identified correctly, but 20.5 per cent as dry Neutral Sand Fynbos. 12.1 per cent were predicted as *Pteris dentata* Fernland.

51.2 per cent of *Artemisia afra* Wetland were predicted correctly. It is interesting that 27.9 per cent were misinterpreted as *Protea repens* Proteoid Fynbos. From the *Gunnera perpensa* Wetland, 53.3 per cent were recognized correctly but 20.0 per cent were predicted

as *Artemisia afra* Wetland and 26.7 as *Pteris dentata* Fernland.

Dune Asteraceous Fynbos was predicted with an accuracy of 63.1 per cent. Mispredictions were concentrated to the Milkwood Scrub Forest (12.0 per cent) and the *Protea repens* Proteoid Fynbos (11.1 per cent). Only 11.6 per cent of Neutral Sand Proteoid Fynbos were predicted correctly. 17.6 per cent were classified as *Protea repens* Proteoid Fynbos. Interestingly, the majority of the pixels was assigned to formations of the Acid Sand Fynbos Complex: 18.9 per cent to the *Elegia thyrsifera* Restioid Fynbos, 21.7 to the Transitional Proteoid Fynbos and 12.9 to the *Erica sessiliflora* Ericaceous Fynbos. In contrast, 70.8 per cent of the *Protea repens* Proteoid Fynbos were identified correctly without major misinterpretations. The same is true for the dry Neutral Sand Fynbos with a score of

Fig. 4.10c: Prediction map for the formation level (Limestone Fynbos excluded).



64.1 per cent.

In the Acid Sand Fynbos Complex, 41.0 per cent of the Acid Sand Proteoid Fynbos were predicted correctly but 25.2 per cent were assigned to the Transitional Proteoid Fynbos. 15.5 per cent of the *Erica sessiliflora* Ericaceous Fynbos were recognized, the major mispredictions being Transitional Proteoid Fynbos (29.3 per cent) and *Elegia thrysifera* Restioid Fynbos (22.6). The prediction for the Transitional Proteoid Fynbos showed an accuracy of 44.8 per cent with misinterpretations distributed all over the Acid Sand Fynbos Complex, predominantly Acid Sand Proteoid Fynbos 21.3 and *Elegia thrysifera* Restioid Fynbos 15.9 per cent. 61.2 per cent of the *Elegia thrysifera* Restioid Fynbos were predicted correctly, 17.7 per cent were mispredicted as *Erica sessiliflora*

Ericaceous Fynbos.

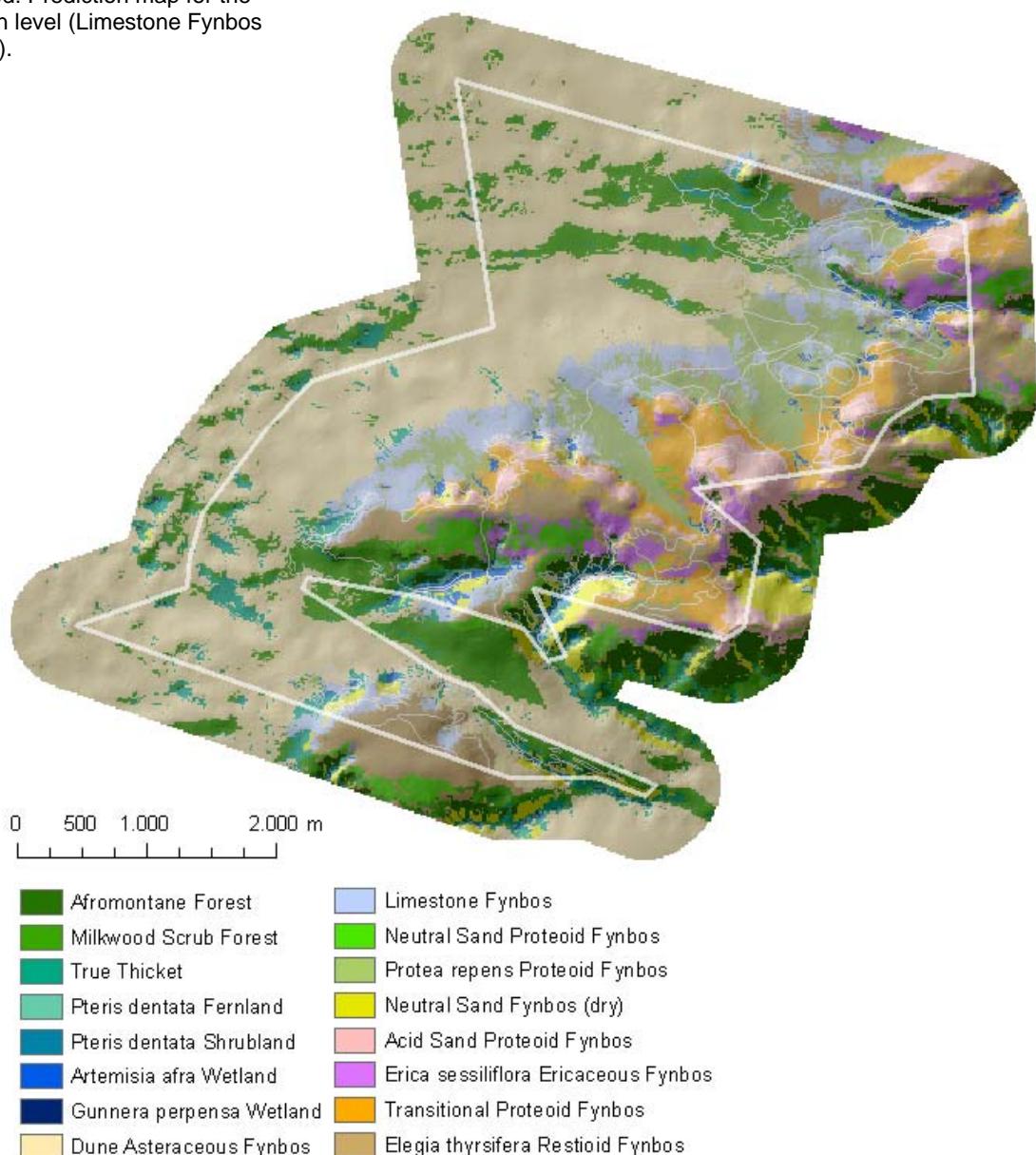
Among the initially ungrouped pixels, 6.6 per cent were assigned to the Afromontane Forest and 12.5 to the Milkwood Forest - both scores being significantly higher than the abundance of these forest ecosystems on the reserve (Fig. 4.7).

### Formation level

With all units included in the analysis, 47.9 per cent of the distribution of the formations of Grootbos Nature Reserve were explained by a combination of the available topographic variables. The prediction map is represented in Fig. 4.10d, the statistics are compiled in App. 3.2.4.

Afromontane Forest and Milkwood Scrub Forest showed quite similar patterns as for excluded

Fig. 4.10d: Prediction map for the formation level (Limestone Fynbos included).



Limestone Fynbos, with variations lower than 5 per cent. The recognition of Thicket is worse, with only 9.7 per cent correct predictions (the major mispredictions are similarly distributed as with excluded limestone formations). The scores of correct predictions for the *Pteris dentata* formations were largely similar to the analysis with excluded limestone formations, as well as those for the formations of the Wetland Complex.

The score for the Dune Asteraceus Fynbos remained approximately constant (62.0 per cent correct predictions). 27.1 per cent of the Limestone Fynbos were correctly classified, with major misclassifications as *Protea repens* Proteoid Fynbos (26.6 per cent) and Dune Asteraceous Fynbos (12.8). Neutral Sand Proteoid Fynbos largely shows similar patterns as for the analysis with excluded limestone formations. The same is true for the dry Neutral Sand Fynbos. 59.9 per cent of the distribution of *Protea repens* Proteoid Fynbos have been predicted correctly, which is significantly lower than for excluded Limestone Fynbos. This phenomenon is readily explained by 16.4 per cent mispredictions as Limestone Fynbos. The dry Neutral Sand Fynbos showed little change but mispredictions as *Pteris dentata* Shrubland rose slightly to 10.3 per cent. No major changes compared to the analysis with excluded limestone formations were observed for the formations of the Acid Sand Fynbos Complex since as misinterpretations as Limestone Fynbos were limited. The predictions of Acid Sand Proteoid Fynbos as *Elegia thyrsifera* Restioid Fynbos rose slightly to 10.1 per cent as did the prediction of the latter as Transitional Proteoid Fynbos (12.0 per cent).

As for the analysis on the formation level with excluded Limestone Fynbos, a disproportionately high share of the originally ungrouped pixels was predicted as Afromontane Forest and Milkwood Scrub Forest (7.5 per cent and 12.2 per cent respectively, Fig. 4.7).

#### 4.4 The vegetation of Grootbos Nature Reserve

##### 4.4.1 Afromontane Forest

The aerial images represent the vast majority of Grootbos Nature Reserve in a clear and proper way. Only a few small pieces of land are situated in extreme shade. These steep, S-facing ravines (Fig. 4.11), not supporting fynbos, are mainly covered in Afromontane Forest, constituting a sharp contrast to the surrounding fynbos and wetland ecosystems. Five patches of Afromontane Forest of different sizes and shapes are present on Grootbos Nature Reserve, altogether covering 4.1 ha (corresponding to 0.2 per cent of the surface).

The CCA suggested an association of the Afromontane Forest with shallow soils with neutral to slightly acid reaction (pH between 6.0 and 7.4), containing high levels of K and Mg. The relief is characterized by steep, wind-protected slopes. A comparatively small amount of solar irradiation can penetrate to the forest.

Afromontane Forests form tall canopies with heights of more than ten meters (Fig. 4.12). The canopy is frequently dominated by *Rapanea melanophloeos*. The well developed subcanopy is three to six meters high, built up by species like *Chionanthus foetidissimus*, *Diospyros whyteana*, *Kiggelaria africana*, *Olinia ventosa* and *Sideroxylon inerme*. Most of these elements have the potential to grow to canopy height. The ground layer is usually sparse with *Asplenium adiantum-nigrum*, *Droguetia iners* and *Ehrharta erecta* as the most common species. Climbers are present, *Asparagus aethiopicus*, *A. scandens* and *Cynanchum obtusifolium* are fairly abundant (Fig. 4.13, 4.14). The forest is usually easily penetrable for human beings.

The leaves of many common trees are lauriphylloous, rather than sclerophyllous. Following the concept of zonobiomes introduced by Walter (e.g. Walter & Breckle 2002), the forests appear to fit in as an extrazonal patch of the temperate rainforests (Zonobiome V). Temperate forest ecosystems titled as Afromontane Forests are dispersed all over the mountains of the Southern Cape but their range stretches into the Eastern Cape, to KwaZulu-Natal and also far into tropical Africa, where this type of forest occurs at higher altitudes (Midgley et al. 1997). The same authors have reviewed research on the population dynamics of Afromontane Forests near Knysna and on the Cape Peninsula: In contrast to other forest types like Tropical Rainforests, very small-scaled patterns are prevailing. Most trees die standing, leaving gaps of limited size. As the tree species of Afromontane Forests are shade-tolerant they can grow up continuously and attain canopy height when such a small gap opens. The consequence is a continuous range of stem diameters, with constant size-class-distributions over time. Randomness appears to decide which species gain dominance in a certain site. Turnover is very low, with mean stand half-lives of well over 100 years.

The Afromontane Forests of the Agulhas Plain are ecologically similar but floristically distinct from those of the mountains farther N and of the Afromontane Forests like those considered by Campbell (1985). They show affinities to the dune forests of the Tongaland-Pondoland Forests. These forests, and also the Afromontane Forests along the S Coast (Knysna, Tsitsikamma), have a significantly higher species diversity than the forests on the reserve. They host

lineages not present on Grootbos Reserve, such as Podocarpaceae and Cyathaeaceae. One reason for the declining diversity towards SW may be that more and more species loose their competitive force as the climatic conditions become harsher.

Indeed, the species diversity is low at the 50 m<sup>2</sup> level, averaging at 13.2 identifiable species for all six relevés (4, 5, 6, 7, 8, 48). 24 species occur on all sites together, none are included in the red data list (with the exception of *Droguetia iners*, which is classified as not threatened). The most striking biogeographical feature of the Afromontane Forests of Grootbos Nature Reserve is their extraordinarily low alpha-diversity, especially when compared with the adjacent fynbos. From a floristic point of view the forest is a completely different system, having virtually no species at all in common with fynbos and hosting no species endemic to the Cape Floristic Region. Many families of higher plants are represented with one or a maximum of two species, indicating a convergent evolution leading to morphologically and functionally similar species, for example *Chionanthus foreolatus* (Oleaceae), *Rapanea melanophloeos* (Myrsinaceae) and *Sideroxylon inerme* (Sapotaceae). Most of the families represented in the Forest are cosmopolitan (Poaceae) or have a tropical (Sapotaceae) to subtropical focus of distribution. The poor representation of true temperate elements in contrast to the moist-temperate character of the forest may be readily explained by distributional restrictions - the large temperate forest biomes are far away and no families concentrated in moist-temperate ecosystems, like Fagaceae, Betulaceae or Nothofagaceae are native to Southern Africa.

The absence of elements typical of the Cape Flora underlines the distinct nature of Afromontane Forest environments. This phenomenon is closely related to the fact that Afromontane Forests are fire-free ecosystems - the species are not flammable but their regeneration is connected to extended fire-free periods. A detailed discussion regarding fire and its connection to the forest-fynbos boundary will follow in chapter 5.

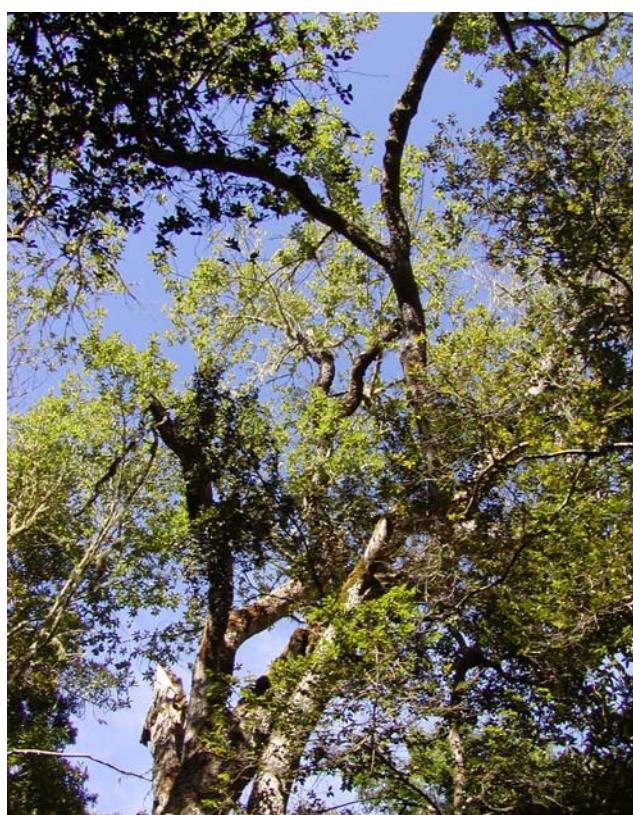


Fig. 4.11 (top): Afromontane Forest patches occupying S-facing ravines, surrounded by Neutral Sand Proteoid Fynbos and *Pteris dentata* Shrubland (10/2004).

Fig. 4.12 (middle): The canopy of a tall Afromontane Forest (11/2004).

Fig. 4.13 (bottom): Leaf collection from the Afromontane Forest - from left to right and from top to bottom: *Kiggelaria africana*, *Rapanea melanophloeos*, *Asplenium adiantum-nigrum*, *Asparagus scandens* and *Diospyros whyteana*.

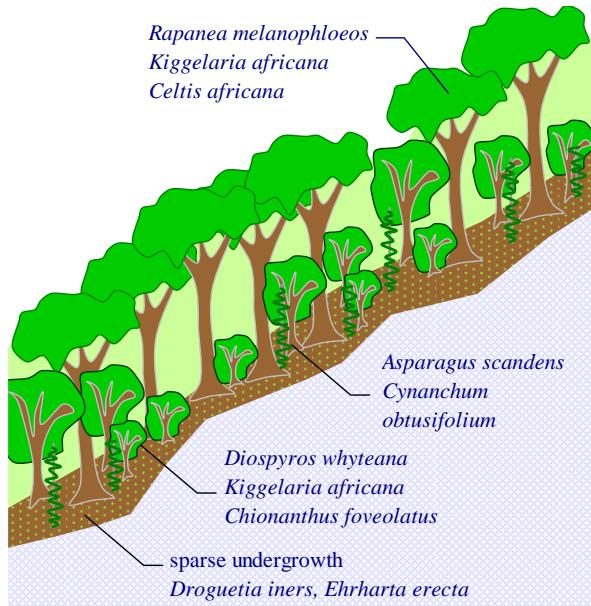


Fig. 4.14: Schematic profile across an Afromontane Forest on the reserve. Only the dominant elements are represented. Designed by the author.

#### 4.4.2 Milkwood Scrub Forest

Milkwood Scrub Forests (Fig. 4.15) belong to the most conspicuous elements of Grootbos Nature Reserve, constituting a sharp contrast to the fynbos covering the vast majority of the surface. Three large patches are present: Tygerboom and Grootbos (Fig. 4.16) in the S part, and Steynsbos in the N part. One smaller pocket is located adjacent to the Steynsbos Dam. Altogether, 43.1 ha or 2.5 per cent of Grootbos Nature Reserve are covered in these ecosystems. It is an indicator of the distinctiveness of these forests that their names were chosen to be the names of some of the farms constituting the Nature Reserve today. Another, at least as equal important indicator for their attractivity and their distinctive character is that both lodges - Garden Lodge and Forest Lodge - were placed in the immediate vicinity of large patches of these Scrub Forests. White Milkwood (*Sideroxylon inerme*), is

widespread in coastal forests and thickets along the S and E Coastlines of South Africa, but this type of forest is restricted to the Stanford-Gansbaai-area, with the only protected patches on Grootbos Nature Reserve.

The CCA suggested an association of the Milkwood Scrub Forest with deep, sandy, colluvial soils at low elevations with high contents of Ca and P. The pH ranges from 6.3 to 7.9, with a peak around 7.5. In contrast to the Afromontane Forest, a negative spatial coincidence with the fire-bearing SE winds was not indicated. The high levels of mineral components appear to be a distinctive feature of this type of ecosystem. Ca in particular is considerably richer in the forest than anywhere else on the reserve. In addition, the soils are very fertile due to plant-induced organic enrichment (Thwaites & Cowling 1988), which makes them suitable for agriculture and thus susceptible to anthropogenic disturbance. The vertical structure of Milkwood Scrub Forests is relatively simple (Fig. 4.17). A single tree layer rises to a height of hardly more than six meters, usually dominated by *Sideroxylon inerme*. The gnarled trunks of old individuals give the forest its unique ambience. *Euclea racemosa* can form canopies in some places as well. Further elements of the tree layer are *Chionanthus foveolatus*, *Gymnosporia buxifolia* and the winter-deciduous *Celtis africana*, but they do not really achieve dominance. The soil is covered by a 5 - 30 cm high herb layer, which is very sparse in deeply shaded places but can constitute a dense ground cover where more light penetrates the tree canopy. *Droguetia iners* dominates in most places and is accompanied by the grass *Ehrharta erecta*. There is hardly a substantial shrub layer within the canopy. The only true shrub species within the full shade of the forest is *Myrsine africana* which can grow higher than 1 m. In damp sites the arum lily *Zantedeschia aethiopica* can also reach a considerable height. In some places young plants of *Chionanthus foveolatus* may contribute to a low intermediate layer with a slightly higher density. All in all, the shady environment appears to limit the growth of shrubs. Like in other moist forest ecosystems, the

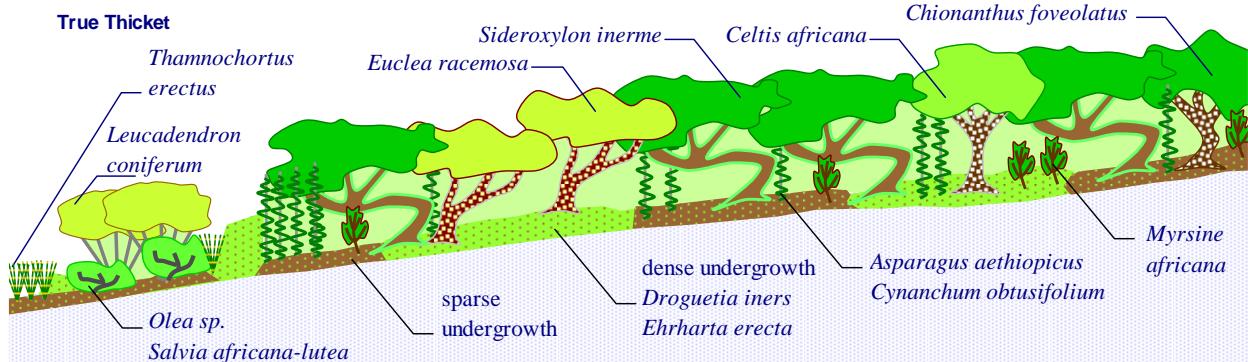


Fig. 4.15: Schematic profile across a Milkwood Scrub Forest and the adjacent thicket. Designed by the author.



Fig. 4.16 (top): The Grootbos Forest, surrounded by Dune Asteraceous Fynbos (10/2004).



Fig. 4.17 (middle): The interior of a Milkwood Scrub Forest, with *Droguetia iners* in the undergrowth (10/2004).



Fig. 4.18 (bottom): Plant collection from the Milkwood Scrub Forest - from left to right and from top to bottom: *Sideroxylon inerme*, *Euclea racemosa*, *Celtis africana*, *Asparagus aethiopicus*, *Myrsine africana*, *Chionanthus foveolatus*, *Zantedeschia aethiopica*, *D. iners*, *Cynanchum obtusifolium*, twig and spines of *A. aethiopicus*, *Ehrharta erecta*.

having a thicket-like character, being penetrable only with difficulty and pain. However, the majority of the forest leaves plenty of free space under the tree canopy and is quite easily penetrable for a human being. In general, it is much easier to move within the forest than to enter or to leave it.

*Sideroxylon inerme* is a very slow-growing species, with an estimated three centimeters growth per year (S. Privett, pers. comm). In contrast, it can live for a very long time. The oldest individuals in Grootbos Forest are estimated to be about 800 years old. Like the other dominant tree species the White Milkwood is almost fire-proof when mature but needs a fire-free environment during its youth.

The majority of species making up the Milkwood Scrub Forest are broad-leaved evergreen, with a sclerophyllous to lauriphylloous character, excluding *Celtis africana* as the only deciduous tree (Fig. 4.18). It is problematic to compare the ecosystem with forests of the remaining mediterranean subbiomes. Like the Afromontane Forest, it may be rather similar to an extrazonal Zonobiome V, according to Walter (e.g. Walter & Breckle 2002). The high abundance of epidendric cryptogames and the tendency to lauriphylly are indicators against pronounced summerly drought stress. Another indicator for the moist character is the small amount of litter and humus covering a deep mineral soil promoted by rapid deterioration processes, like as happens under warm and ever-moist conditions. However, the Milkwood Scrub Forest is often considered as a late successional stage of dune thicket and thus as Subtropical Thicket as described by Midgley et al. (1997), since as some species are centered in the latter vegetation unit.

The floristic composition of the Milkwood Scrub Forest is nevertheless comparable to that of the Afromontane Forest regarding diversity and biogeographical patterns. The number of tree species and families, however, is lower. The species diversity is low at the 50 m<sup>2</sup> level, averaging at 11.0 identifiable species. 24 species were recorded on all eight relevés (1, 2, 3, 45, 50, 51, 60, 61) together. Concerning red data species, the same as for the Afromontane Forest is true.

abundance of lianas and epiphytes (both cryptogames and phanerogames) is considerable. *Asparagus aethiopicus* is omnipresent in the Milkwood Scrub Forests of Grootbos Nature Reserve and *Cynanchum obtusifolium* is also widespread. Epidendric mosses and lichens are very common in the forest, covering the stems especially of the White Milkwood. In contrast, there are hardly any visible cryptogames on the soil surface. The soil surface is covered by a minor layer of undeteriorated dead plant material, which is hardly connected with the soil. The humus layer is a few centimetres thick, covering a deep, densified, ever-moist mineral soil.

Dead vertical branches of the spiny *Asparagus aethiopicus* are particularly responsible for parts of the forest

#### 4.4.3 Thicket

The fynbos-forest-boundary is rarely sharp, but is often made up of a thicket of varying height and density. This vegetation unit does not necessarily correspond to the Subtropical Thicket like that described by Midgley et al. (1997), although it may share certain characteristics with it.

Thickets - covering 30.9 ha or 1.8 per cent of Grootbos Nature Reserve - are characterized by a mixture of forest and fynbos elements. No relevés of the core dataset were available for thickets, but the vegetation unit does appear to occur in sites where fire frequency or intensity have been reduced over a certain period, but not sufficient to support forest:

- the buffer zones between the fire-prone fynbos and the fire-free Milkwood Scrub Forest (Fig. 4.18).
- protected ravines as a successional stage from fynbos to forest
- S-facing slopes of the forest valley

The thicket on the S-facing slope of the forest valley (adjacent to the Afromontane Forest, Fig. 4.11, 4.19) is dominated by the fern *Pteris dentata*, which attains a very high cover in these places. These ecosystems are therefore considered as separate formations (*Pteris dentata* Shrubland). Forest edge thickets and valley thickets (Fig. 4.20), in contrast, are floristically similar so that a separation into two formations is not supported despite the supposed ecological difference.

The broad-leaved subtropical shrub species (Cowling et al. 1997a, Fig. 4.21), mainly *Euclea racemosa*, *Olea capensis*, *Olea exasperata* and various species of *Rhus*, often gain dominance together with *Salvia africana-lutea*, but they can not be used as diagnostic since they also occur as thicket elements in the fynbos. Among the true fynbos elements, large individuals of *Leucadendron coniferum* and *Thamnochortus erectus* are most common. Certain forest elements - most commonly *Sideroxylon inerme* may join the thicket but thicket species may also occur as trees in the Milkwood Scrub Forest, like *Euclea racemosa*. *Olea capensis* ssp. *macrocarpa*, occurring as shrub or small tree in the Valley Thickets of Grootbos Nature Reserve, attains dominance as a 30 m high tree in the canopy of the Knysna Forest.

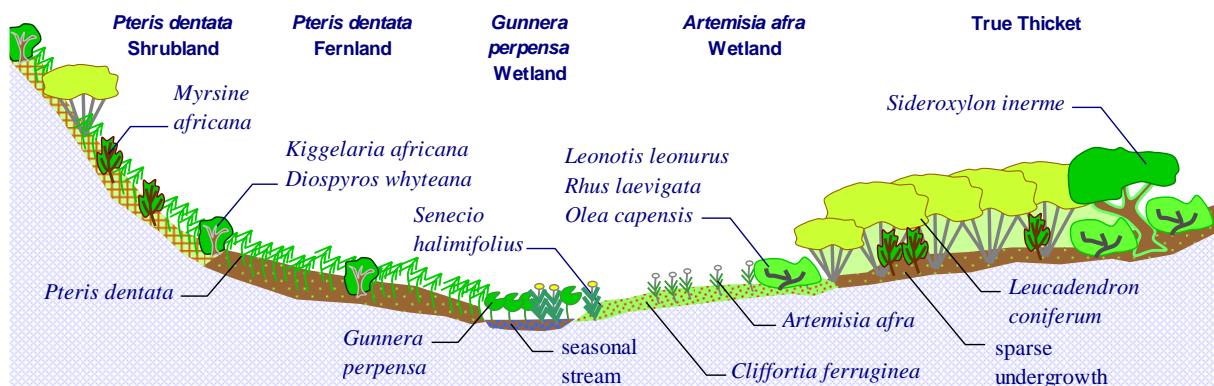
The composition and cover attained by the aforementioned species in different thickets may shift over a broad range. Some places in the forest valley are covered in five meter high closed canopies of *Leucadendron coniferum*, with an undergrowth of forest elements. The edges of Milkwood Scrub Forest patches are frequently dominated by *Salvia africana-lutea*, *Thamnochortus erectus* and several forest elements. Transitions between thicket and fynbos, and also thicket and wetland are common.



Fig. 4.19 (top): *Pteris dentata* Shrubland (10/2004).

Fig. 4.20 (middle): Valley thicket in the Tygerboom Kloof, foreground: damp slope with *Ischyrolepis leptoclados* (10/2004).

Fig. 4.21 (bottom): Thicket plant collection - from left to right and from top to bottom: *Olea exasperata*, *Chrysanthemoides monilifera* (predominantly in Dune Asteraceous Fynbos), *Cassine peragua*, *Rhus laevigata*, *Olea capensis*.



#### 4.4.4 Wetlands

The catchment areas supplying Grootbos Nature Reserve are not large enough to support permanent streams under the prevailing precipitation regime. In winter some springs can develop and small rivers may persist until the end of October. Due to these settings and the connected lack of a shallow aquifer the distribution of true wetlands is extremely limited on Grootbos Nature Reserve and is confined to a few suitable habitats (1.4 ha or 0.1 per cent of the reserve). Nevertheless the diversity of different wetland habitats is considerable and it is difficult to point out one type of wetland characteristic of the reserve. As the different types are located adjacently along several environmental gradients, they will be treated as one entity (Fig. 4.22).

Wetlands are related to soils with a high content of organic matter, indicated by the dark color. The ordinations placed the wetland relevés between forest and fynbos without clear relationships to any of the measured variables. The pH ranges from 6.1 to 7.9 but the relevé with the highest value is situated below a slope that may have an alkaline character.

The wetlands of Grootbos Nature Reserve appear to be potentially three-layered: The overstorey - up to four meters high - is usually sparse and often even missing. It is composed of forest and thicket shrubs like *Kiggelaria africana*, *Psoralea arborea*, *Rhus laevigata*,



Fig. 4.22: (top): Schematic profile across the wetlands and thickets of the forest valley. Designed by the author.

Fig. 4.23 (middle left): *Pteris dentata* Fernland in the forest valley (10/2004).

Fig. 4.24 (middle right): *Gunnera perpensa* Wetland in the forest valley (10/2004).

Fig. 4.25 (bottom): Wetland plant collection - from left to right and from top to bottom: *Artemisia afra*, *Hippia frutescens*, *P. dentata*, *Helichrysum cymosum*, *Stoebe plumosa*, *Psoralea arborea*, *G. perpensa*, *Cliffortia ferruginea* and *Senecio halimifolius*.

*Sabia africana-lutea* or even small individuals of the tree *Rapanea melanophloea*. This layer only occurs at the transition to thickets.

The medium layer, which is one to a maximum of two meters high, can be formed by sparse to dense stands of *Artemisia afra* or by dense thickets of the fern *Pteris dentata* (S-facing slopes adjacent to patches of Afromontane Forest, recognized as the formation *Pteris dentata* Fernland, relevé 58, Fig. 4.23). *Leonotis leonurus* is not uncommon. Directly in the temporary stream monospecific canopies of *Gunnera perpensa* (Fig. 4.24) are very common, as are dense stands of *Senecio halimifolius*. This vegetation has been considered as a separate formation (*Gunnera perpensa* Wetland) in mapping and geostatistical analysis, but recognition as phytosociological formation is not supported by the existing relevés. The large Cyperaceae *Mariscus thunbergii* is a conspicuous element of all wet sites.

The ground layer is extremely variable, depending on the moisture regime and - especially - on the amount of photosynthetic active irradiation which can penetrate the overstorey. In the fernland it is almost completely missing (only young shrubs and the shade-loving *Zantedeschia aethiopica* are present). On valley bottoms with sparse or missing overstoreys, a nearly monospecific mat of *Cliffortia ferruginea*, a few to several centimeters thick, can develop. *Helichrysum cymosum* and *Hippia frutescens* may also be present.

The leaf forms (Fig. 4.25) show considerable variation among the different elements constituting wetlands on the reserve. As a general rule one could point out that the upper and lower layers are dominated by sclero- to lauriphylloous leaves, while the major elements contributing to the medium layer have large, mesophyllous, often pinnatifid leaves (especially *Artemisia afra* and *Pteris dentata*). The reason for these patterns appears somewhat unclear. The overstorey elements are not restricted to wetlands - they have their centre of distribution in ecosystems more prone to water stress. In addition, they experience higher wind speeds than the lower layers, triggering transpiration.

The sclerophyll (*Cliffortia ferruginea*) of the ground layer may be connected to temporal water stress, since as the habitats hosting dense mats of this species are slightly N-sloped. The scarcity of soil nutrients may also contribute - and even be the major causal explanation - to the prevailing leaf forms. Also in other nutrient-poor ecosystems all over the world (including fynbos, but also moist-temperate heathlands and boreal mires), the abundance of sclerophyllous elements is high, not necessarily linked to the moisture regime. As nutrients are limited, the carbon content and thus the sclerophyllous character of the leaves may increase as long as photosynthesis remains unaffected.

The lack of Ericaceae in the wetlands seems somewhat strange: they are widespread throughout wetlands in other parts of the world (e.g. Breckle 2002), there is a huge pool in the adjacent fynbos and they are common in wet formations of the fynbos.

One characteristic feature of the wetlands is their low alpha-diversity with an average of 9.3 species for the three 50 m<sup>2</sup> relevés of the core dataset (32, 58, 59, altogether 20 species), containing no red data species. There are no families with conspicuous abundance. Most families represented in the wetlands are cosmopolitan, like Asteraceae, Rosaceae and Cyperaceae. Many species are widespread as well, such as *Artemisia afra* or *Pteris dentata*.

#### 4.4.5 Alkaline Sand Fynbos Complex

As discussed in chapter 2, the Fynbos Biome is characterized by acid, nutrient-poor substrates derived from the widespread formation of Table Mountain Sandstone. Fynbos units associated with these soils will be discussed in detail in the following section. However, the substrate of the lower slopes of the reserve is lacking the shallow, acidic character of the higher parts. Vast areas are covered in deep, alkaline sands derived from the coastline, constituting dunes covered by a low type of fynbos lacking proteoids. Upslope, the pH of the dune sands decreases due to the increasing influence of acidic sands derived from Table Mountain Sandstone. These Neutral Sands are frequently covered in dense, high proteoid fynbos sometimes entirely built up by *Leucadendron coniferum*. As the unit is poorly established in both the ordinations and classifications it was discriminated from the dune fynbos by the presence of the latter species or of *Leucospermum patersonii*.

Towards the mountain slopes limestone outcrops are quite common, often providing sloping habitats with shallow soils. Due to their alkaline character they support a completely different vegetation than do the acidic sands. Some species, like *Erica coccinea* var. *yellow*, *Protea obtusifolia* and *Thamnochortus fraternus* are concentrated to these outcrops, constituting three different formations, which are, however, frequently intermixed. Most species are shared with the rest of the Alkaline Sand Fynbos.

Some of the lower slopes intermittent between dune fynbos, limestone fynbos and Neutral Sand Proteoid Fynbos are covered in dense proteoid fynbos dominated by *Protea repens*.

The Alkaline Sand Fynbos covers 1385 ha or 81.5 per cent of the reserve. 200 species were recorded on 42 relevés, averaging at 24.9 species per relevé. Among the 9 red data species (excluding those classified as not threatened), 7 are endemic to this complex.

### Dune Asteraceous Fynbos

The entire W half of Grootbos Nature Reserve is covered in an extensive matrix of low ericoid/restioid fynbos, higher ericoid fynbos and thicket dominated by broad-leaved shrubs (Fig. 4.26 - 4.29). More than half of the area covered by the reserve supports this formation (914 ha or 53.8 per cent). Since a resolution of the mosaic in a couple of different units would require a lot more sampling effort the formation should be treated as one entity. As indicated by the CCA, it occurs over a wide range of habitats. The majority of the relevés is connected to low elevation, high pH (between 7.9 and 8.1 for most of the sites), deep soils (usually more than 100 cm) and low rock cover. Among the core dataset, the relevés 9 - 13, 16 - 18, 25, 35, 40, 41, 47, 49, 52, 53, 63 and 71 represent the formation. Relevé 15 was set up on a disturbed patch.

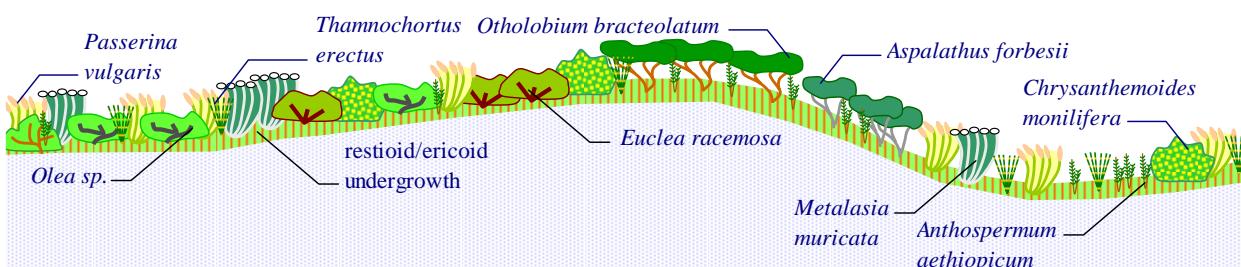
Ericoid shrubs are the structural dominants of the vegetation. *Metalasia muricata* and *Passerina vulgaris* are most common. They can grow up to more than two meters, as can the broad-leaved Asteraceae *Chrysanthemoides monilifera*. A considerable number of species are associated with dune fynbos. Among the genus *Erica*, *E. irregularis* is the most common, but a number of non-ericaceous ericoids is widespread, such as *Anthospermum aethiopicum* or certain species of *Phyllica*. Among the restioids, *Thamnochortus erectus* is most conspicuous but the lower *Ischyrolepis eleocharis* has a very high cover in some sites. A characteristic feature of the Dune Fynbos is the lack of proteoids. If they occur

Fig. 4.26 (top): Dune Asteraceous Fynbos with a young individual of *Otholobium bracteolatum* (foreground), *Metalasia muricata* (background and the thicket species *Olea capensis* ssp. *capensis*) (11/2004).

Fig. 4.27 (upper middle): Four year old Dune Asteraceus Fynbos dominated by *Eriocephalus racemosus* and *Ischyrolepis eleocharis* (10/2004).

Fig. 4.29 (lower middle): Dune Asteraceous Fynbos plant collection (thicket species excluded) - from left to right and from top to bottom: *Ischyrolepis eleocharis*, *Erica irregularis*, *O. bracteolatum*, *Anthospermum aethiopicum*, *Metalasia brevifolia*, *Oedera capensis*, *M. muricata*.

Fig. 4.29 (bottom): Schematic profile across the Dune Asteraceous Fynbos. Designed by the author.



(especially *Leucadendron coniferum* and *Protea obtusifolia*) they indicate a transition to other formations. However, in the Dune Asteraceous Fynbos the ericoid layer of about one meter is sometimes topped by a tree-like overstorey of varying density and a height up to 2.5 m, frequently built up by Fabaceae, mainly *Otholobium bracteolatum* or *Aspalathus forbesii*.

Lower individuals of the subtropical shrub species are very common all over the Dune Asteraceous Fynbos, attaining considerable ground cover in most of the relevés. *Euclea racemosa*, *Olea capensis* ssp. *capensis*, *Olea exasperata* and *Rhus laevigata* are most common. Where fire has been excluded for an extended period, such as along roads or adjacent to cultivated areas or housing places, they can grow higher and gain dominance, frequently together with large individuals of *Metalasia muricata*. Thickets at forest edges or in valleys have already be described above.

The Dune Asteraceous Fynbos on Grootbos Nature Reserve, especially on the recently bought properties like Steynsbos, has been used for grazing or agriculture until very recently. The aerial imagery even shows structures clearly indicating the growing of crops. Grazing was tightly combined with frequent burning, which affected the natural vegetation in a considerable way. High cover of grasses or of *Pelargonium betulinum* may be indicators of frequent fires in the recent past.

A considerable part of the dune asteraceous fynbos - again predominantly on Steynsbos - is affected by infestations with the introduced *Acacia cyclops*, also known as Rooikrans. Various clearing efforts have been taking place since the 1980s. At a considerable amount of sites, *A. cyclops* has shown the ability to recover within a couple of years. Other Australian acacias, *A. mearnsii* and *A. saligna*, have also invaded the dune fynbos but to far less spatial extent.

### Neutral Sand Proteoid Fynbos

Most species typical of the Dune Asteraceous Fynbos are also present in other formations of the Alkaline Sand Fynbos Matrix. However, as one moves upwards towards the hills and mountains of the reserve, they lose their structural dominance and open space to one of the most distinctive elements of the fynbos biome: the proteoid shrubs of the family Proteaceae. One of the most widespread types of proteoid fynbos present on Grootbos Nature Reserve is the Neutral Sand Proteoid Fynbos (Fig. 4.30 - 4.33), covering 200 ha (11.9 per cent of the reserve) and being represented by 8 relevés of the core dataset (14, 26 - 28, 36, 38, 55 and 67).

According to the CCA, Neutral Sand Proteoid Fynbos is associated with intermediate conditions concerning all environmental variables. The pH, however, ranges from 4.8 to 7.8. The soils are usually shallower than those supporting Dune Asteraceous Fynbos, but the depths range from 0 to more than 100 cm. According to Privett (pers. comm.), wind-blown alkaline sands lying over the acidic Table Mountain Sandstone provide habitats which are in between the Dune Asteraceous Fynbos and the Acid Sand Fynbos Complex.

In the automatic imagery interpretation parts of the Neutral Sand Proteoid Fynbos were predicted as forest. This is not surprising, as relatively old, almost monospecific stands of *Leucadendron coniferum* resemble low forests with canopy heights of up to five meters, but with an extremely high density of thin stems, making them almost impenetrable. But the Neutral Sand Proteoid Fynbos includes much more than these forest-like canopies. It is a mosaic of patches of different ages and is connected to different environmental settings, mirrored by changing abundances of proteoid, ericoid and restioid elements and by a changing vertical canopy structure. In young or disturbed stands, easily penetrable (and thus mainly chosen as relevés), the proteoids *Leucadendron coniferum* and *Leucospermum patersonii* are approximately equally abundant. A clearly visible ericoid layer is present. As in the Dune Fynbos, *Thamnochortus erectus* is the most

Fig. 4.30: Schematic profile across the Neutral Sand Proteoid Fynbos. Designed by the author.

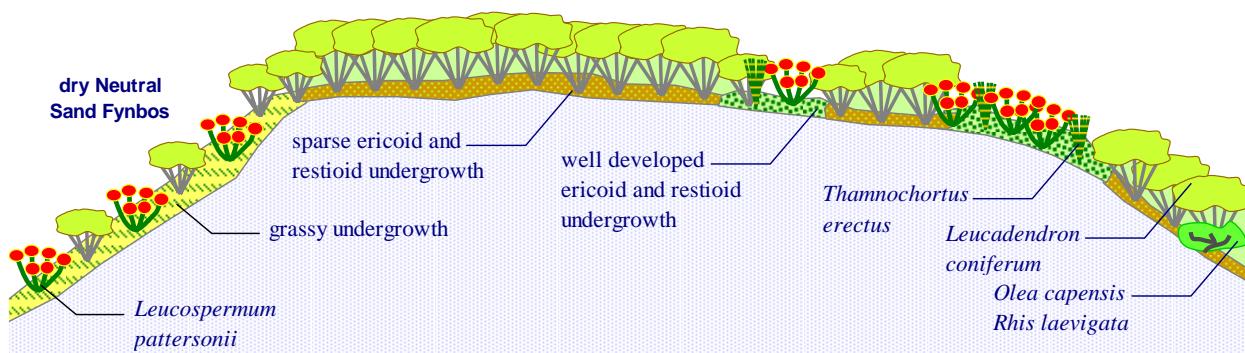




Fig. 4.31 (top): Neutral Sand Proteoid Fynbos leaf collection - from left to right and from top to bottom: *Thamnochortus erectus*, *Phyllica dodii*, *Leucadendron coniferum*, *Leucospermum patersonii*, *Erica lineata*

Fig. 4.32 (middle): Large canopy of *L. coniferum*, Acid Sand Fynbos in the foreground (11/2004).

Fig. 4.33 (bottom): The forest valley with dense canopies of *L. coniferum* at the top and dry Neutral Sand Fynbos on the opposite slope (10/2004).

Neutral Sand Proteoid Fynbos of the reserve, these mature stands were widespread at the time of the survey. The high frequency of the fern *Asplenium adiantum-nigrum* indicates that these canopies provide forest-like habitats with a moisture regime not necessarily coupled to the free atmosphere.

Thicket shrubs are not that abundant except in the transition to the Dune Fynbos and along road and forest edges (absence of fire), and also S-facing slopes of the forest valley, where certain transitions to Thicket take place (the *Leucadendron coniferum* thicket mentioned above may be one of these).

N- and E-exposed slopes of the forest valley are covered in a different vegetation unit (9.5 ha or 0.6 per cent of the reserve). Due to the high frequency of *Leucadendron coniferum* and *Leucospermum patersonii* and the scarcity of species indicating a different unit, it has been assigned to the Neutral Sand Proteoid Fynbos. In the map and in the geostatistical analysis, however, it has been considered as dry Neutral Sand Proteoid Fynbos. The only relevé (35, not clearly assigned to any unit, neither in the classification nor in the ordination) has a pH of 5.9, but the wetland at the base of the slope has a pH of 7.9. Individuals of *Leucadendron salignum* (indicator of acid conditions) and *Protea obtusifolia* (indicator of limestone) are present at very low abundances. The structure is characterized by scattered individuals of *Leucadendron coniferum* and *Leucospermum patersonii* as well as by a high abundance of grasses (*Cymbopogon emarginatus*, *Pseudopentameris macrantha*). More sampling is necessary to explore the character of these slopes.



conspicuous restioid element, while low restioids occur at the ground layer, together with species of the sedge *Ficinia*.

As the Neutral Sand Proteoid Fynbos becomes older, the longer-lived *Leucadendron coniferum* increases its height and density and suppresses the other elements. If fire remains excluded for a couple of decades elements of the Milkwood Forest are able to invade. *Leucospermum patersonii*, the reproduction of which is strongly fire-dependent, can not persist. Since the previous fire dates back to 1990 over most of the

#### ***Protea repens* Proteoid Fynbos**

The lower slopes of Swartkransberg heading northwards towards the broad Steynsbos Valley, as well as large parts of the Steynsbos Valley itself are covered in a distinctive formation, occupying a surface of 76.5 ha, corresponding to 4.5 per cent of the reserve. It shares the majority of its species with the Dune Asteraceous Fynbos and the Neutral Sand Proteoid Fynbos, but it is clearly dominated by *Protea repens*, which is almost missing in the other formations of the Alkaline Sand Fynbos. The *P. repens* Proteoid Fynbos is represented by 3 relevés of the core dataset: 39, 56, and 62, as well as by the Fig. 4.34 - 4.37.

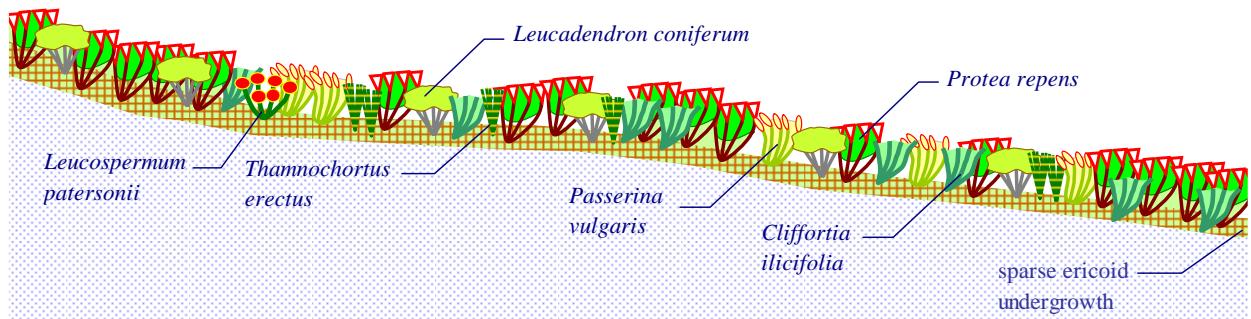


Fig. 4.34: Schematic profile across the *Protea repens* Proteoid Fynbos. Designed by the author.

Fig. 4.35 (upper middle): Plant collection from the *P. repens* Proteoid Fynbos - from left to right and from top to bottom: *Willdenowia teres*, *P. repens*, *Cliffortia ilicifolia*, *Aspalathus salteri*, *Dipogon lignosus*, *Phylica disticha*, *Diosma subulata* var. *subulata*.

Fig. 4.36 (lower middle): The Steynsbos Valley is largely covered in *P. repens* Proteoid Fynbos, disrupted by patches of Dune Asteraceus Fynbos and Limestone Fynbos (view from Swartkransberg, 11/2004).

Fig. 4.37 (bottom): *P. repens* Proteoid Fynbos, Swartkransberg in the background (11/2004).

The CCA indicated an association of the formation with extraordinarily high values for electrical resistance of the deep (more than 100 cm), slightly acid soils. The pH ranges from 6.4 to 6.7 and at the transition to the Acid Sand Fynbos it is 5.6.

In general, the formation can be described as dense, medium-height to high proteoid fynbos. Dense stands of proteoid shrubs are intermixed with more open patches dominated by ericoids and restioids on a scale of few meters (a sub-relevé-size scale). The dense patches are clearly dominated by *Protea repens*, growing to canopy heights of about 2.5 meters. *Leucadendron coniferum* is intermixed frequently but with changing abundance. A sparse to medium-dense undergrowth reaches heights of some tens of centimeters. The ericoid *Phylica disticha*, some species of *Clutia* and various species of Cyperaceae are most common, but several other ericoid, restioid and other graminoid elements may also appear. However, they do not really form a dense understorey.

The more open patches are made up of a variety of species providing the vast majority of higher plant diversity of the formation. The ericoids *Cliffortia ilicifolia* and *Passerina vulgaris* are very frequent, growing up to more than 1.5 meters, as do the restioid *Thamnochortus erectus*. The ericoid *Diosma subulata* ssp. *subulata* may reach considerable abundance in some places, as can the lower ericoid *Aspalathus salteri*. Several broad-leaved thicket species, especially *Euclea racemosa* and *Rhus*

*laevigata*, can join the formation, too. The undergrowth is somewhat sparse but in many places the soil is covered with a dense layer of dead stems and branches making the penetration somewhat difficult for humans. The species of the undergrowth are generally the same as in the dense patches. An element occurring in the formation, but with low abundance, is *Leucospermum patersonii*, indicating the transitional character of the *Protea repens* Proteoid Fynbos.

The rather sparse undergrowth is meant to be a consequence of lacking photosynthetic irradiation penetrating the dense proteoid stands and the layer of dead plant material, but it may also be because of a lack of space.

### ***Protea obtusifolia* Proteoid Fynbos**

Exposed limestone ridges occur all over the lower portion of the reserve. They support three types of fynbos: A proteoid, characterized by *Protea obtusifolia*, an ericoid, characterized by *Erica coccinea* var. yellow, and a restioid, dominated by *Thamnochortus fraternus* (Fig. 4.38 and 4.39). As they are frequently intermixed and show a variety of transitions they were considered for the purpose of geostatistical analysis as an entity called Limestone Fynbos, occupying 162 ha or 23.2 per cent of the reserve.

The *P. obtusifolia* Proteoid Fynbos is represented by 3 relevés of the core dataset: 65, 66 and 70. The CCA indicated an association with deep, alkaline soils and with low rock cover. The pH ranges from 6.9 to 8.1. The formation is characterized by about two meters high, sparse to medium dense stands of *Protea obtusifolia* often intermixed with *Leucadendron coniferum* and sometimes with *Leucospermum patersonii*. However, the bulk of the species also occurs throughout the Alkaline Sand Fynbos.

Some relevés with high cover of *P. obtusifolia* (22, 23,

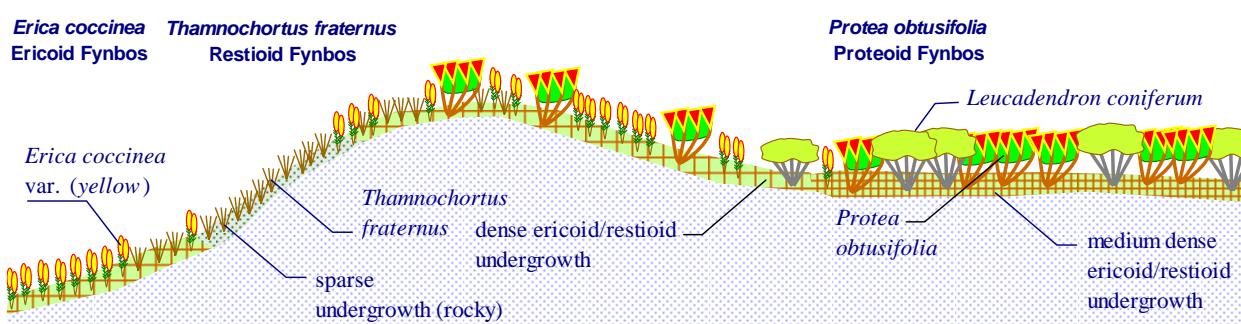
Fig. 4.38 (top): Collection of the limestone fynbos Proteoid Fynbos - from left to right and from top to bottom: *Cullumia squarrosa*, *Indigofera brachystachya*, *Erica coccinea* var. (yellow), *Thamnochortus fraternus* and *Protea obtusifolia*.

Fig. 4.39 (bottom): Schematic profile across the different formations of Limestone Fynbos. Designed by the author.

24) also show a high cover of *T. fraternus*. As suggested by the ordination, the relevés were assigned to the *T. fraternus* Restioid Fynbos. The formation is also frequently intermixed with *E. coccinea* Ericoid Fynbos (Fig. 4.40), Neutral Sand Proteoid Fynbos or even formations of the Acid Sand Fynbos Matrix (relevé 69) on a very fine scale of a few tens of meters and sometimes even less, corresponding to the distribution of alkaline substrate.

### ***Erica coccinea* Ericoid Fynbos**

The only relevé of the core dataset clearly representing this formation (54) is associated with 30 cm deep, alkaline (pH 8.0) soil containing high levels of Na and Ca. The formation is not uniform but it occurs predominantly on moderately steep to steep outcrops. It is characterized by a high cover of *E. coccinea*, giving the slopes a bright yellow appearance during spring. The dominant species is most frequently joined by *Indigofera brachystachya* and *Cullumia squarrosa*. Transitions to *P. obtusifolia* Proteoid Fynbos and *T. fraternus* Restioid Fynbos are common, as well as to the



Dune Asteraceous Fynbos. Some relevés with low abundances of *E. coccinea* var. (yellow) were classified as Dune Asteraceous Fynbos, but according to the CCA, they would better correspond with the *E. coccinea* Ericoid Fynbos.

On damper sites on the slopes of Tygerboom Kloof, a two meter high overstorey of *Aspalathus forbesii* has developed (relevé 53). The high abundance of thicket species (*Cassine peragua*, *Olea capensis* ssp. *capensis*, *Olea exasperata*) indicates a limited influence of fire. Altogether, the extent is too limited to consider it as a separate formation. Even more limited is another formation classified as Limestone Ericoid Fynbos represented in relevé 49: a steep S-facing slope near to the valley bottom covered in medium dense stands of *Ischyrolepis leptoclados* of more than one meter in height with poor representation of *E. coccinea* var. (yellow).

The steep limestone slope directly S of the Steynsbos Dam (relevé 71), which was hit by a fire in 2001,

supports fynbos dominated by the more than one meter high hemiparasite *Thesium strictum* and by the grass *Pseudopentameris macrantha*. Altogether, the floristic composition is similar to that of relevés with the same topographic settings but classified as post-fire regenerating Acid Sand Fynbos - with the difference that *Mimetes cucullatus* is replaced by small quantities of *E. coccinea* occurring at the upper edge of the slope.

#### ***Thamnochortus fraternus* Restioid Fynbos**

On steep limestone slopes supporting shallow, rocky, Mg-rich soils with low resistance and a pH between 7.6 and 8.0, a restioid formation of limestone fynbos can gain dominance (Fig. 4.41). It covers the majority of the limestone hills ranging from the Garden Lodge towards Swartkransberg and can also be encountered on the slopes E of the Forest Lodge. Seven relevés of the core dataset (19, 20, 21, 22, 23, 24 and 46) were classified as *T. fraternus* Restioid Fynbos. It is structurally dominated by less than one meter high stands of the limestone endemic *T. fraternus*. The usually sparse ground cover is made up of shrubs like *Indigofera brachystachya* or *Cullumia squarrosa*, and also *Erica coccinea* var. (yellow), the latter indicating a transition to the *E. coccinea* Ericoid Fynbos (relevé 20). *Protea obtusifolia* (relevés 22, 23 and 24) and small individuals of *Leucadendron coniferum* may appear as well.

#### **4.4.6 Acid Sand Fynbos Complex**

The Acid Sand Fynbos Complex is indicated by the presence of one or more Proteaceae species associated with shallow, acidic soils derived from Table Mountain Sandstone, represented by *Mimetes cucullatus* and *Leucadendron salignum* in the extended TWINSPLAN classification. The higher hills of the Reserve are entirely covered in this complex, although altitude may only be an indirect explanatory variable for a deficient budget of sand accumulation due to high relief energy and high wind speed. 235 ha (13.8 per cent of the reserve) support Acid Sand Fynbos.

The complex is anything but uniform. Different formations alternate in a fine-grained pattern as a response to the local set of environmental variables. The indicator species of the Acid Sand Complex may be joined by several species being centered in or even indicators of other complexes. Such ecosystems have some transitional character (Fig. 4.46), mainly to the Alkaline Sand Fynbos Complex, but sometimes also to the Wetlands, as the *Erica sessiliflora* Ericaceous Fynbos. In contrast, there are also true acid sand ecosystems (Acid Sand Proteoid Fynbos), mainly on the highest peaks, lacking that kind of transitional character. Acid Sand Proteoid Fynbos has the highest species diversity among the complexes of Grootbos Nature Reserve,



Fig. 4.40 (top): Transition between *Protea obtusifolia* Proteoid Fynbos and *Erica coccinea* Ericoid Fynbos in the Steynsbos Valley (11/2004).

Fig. 4.41 (bottom): *Thamnochortus fraternus* Restioid Fynbos with *Crassula expansa* in the foreground (11/2004).

averaging at 35.0 species per relevé. Altogether, 149 species were recorded in the 12 relevés of the core dataset (Fig. 4.42), with 5 red data species (excluding those classified as not threatened), 3 of them endemic to the complex.

### Acid Sand Proteoid Fynbos

This most prominent, characteristic and best surveyed formation of the Acid Sand Fynbos Complex is predominantly situated on hilltops and steeper slopes, with its largest patch on Swartkransberg (Fig. 4.43). Making up 65.7 ha (3.9 per cent of the reserve), it is characterized by the absence of species that have their center of distribution in the Alkaline Sand Fynbos Complex.

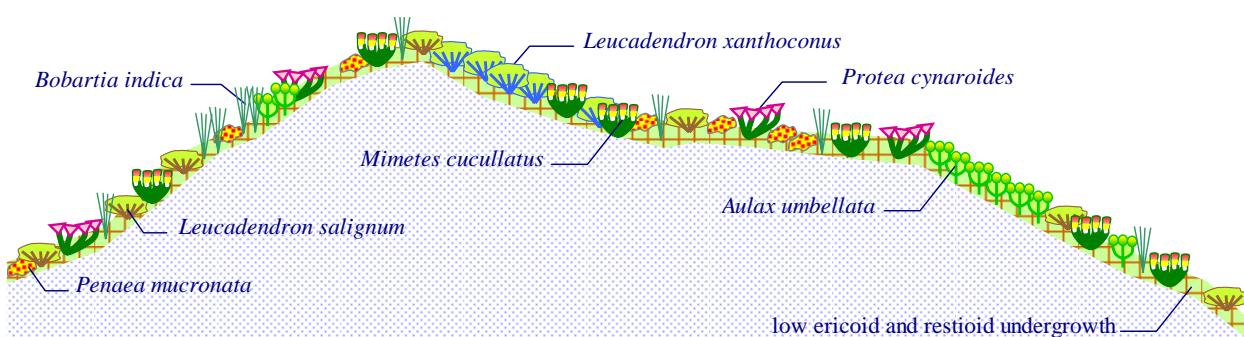
Based on the 5 relevés 29, 30, 33, 64 and 68, the CCA indicated an association with high elevation, shallow, rocky and acid (pH 5.2 - 5.6) soils with low levels of all nutrients except K, and N-facing slopes. The formation can be structurally characterized by a low to medium dense proteoid layer usually less than 1.5 m high, including several of the acidophilous Proteaceae (Fig. 4.1) with a changing composition. There is usually no clear dominance of one species but *Mimetes cucullatus* and *Leucadendron salignum* are the most common, joined by *Aulax umbellata*, *Leucadendron tinctum*, *L. spissifolium*, *L. xanthoconus*, *Protea acaulos*, *P. cynaroides*, *P. longifolia* and *P. speciosa*. The most conspicuous among the lower shrubs are *Penaea mucronata* and *Leucospermum prostratum*. Several smaller species of *Erica* and further ericoid shrubs can form a sparse to medium, low height

Fig. 4.42 (top): Plant collection from the Acid Sand Fynbos Complex - from left to right and from top to bottom:  
*Mimetes cucullatus*, *Leucadendron salignum*,  
*Leucadendron tinctum*, *Aulax umbellata* and *Penaea mucronata*.

Fig. 4.43 (upper middle): Acid Sand Proteoid Fynbos at the Southern slope of Swartkransberg (11/2004).

Fig. 4.44 (lower middle): Acid Sand Proteoid Fynbos: Dense canopy of *A. umbellata* (11/2004).

Fig. 4.45 (bottom): Schematic profile across the Acid Sand Proteoid Fynbos. Designed by the author.



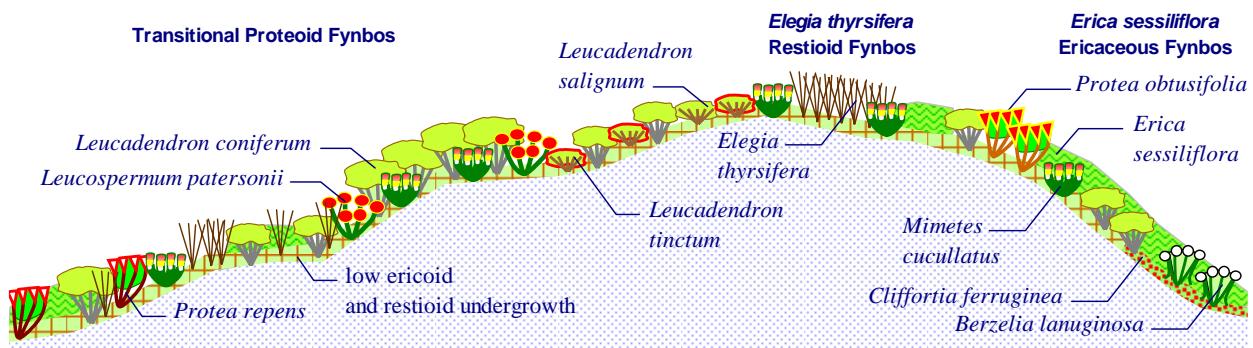


Fig. 4.46 (top): Schematic profile across an intermix between *Erica sessiliflora* Ericaceous Fynbos, Transitional Proteoid Fynbos and *Elegia thrysifera* Restioid Fynbos. Designed by the author.

Fig. 4.47 (middle): The carnivorous *Drosera capensis*, a common element of the damp slopes covered by *E. sessiliflora* Ericaceous Fynbos (10/2004).

Fig. 4.48 (bottom): *E. sessiliflora* Ericaceous Fynbos, in the left foreground *Leucadendron xanthoconus* (11/2004).

ground layer. The restioid component is variable but *Elegia juncea* in particular can become a considerable structural dominant in places where it grows well, such as on the NW slope of Swartkransberg. A large number of geophytes may grow on acid sand. Most of them are only conspicuous when flowering, like eg. *Aristea capitata* or *Watsonia stenosiphon*. The large *Bobartia indica* is the only element of this group that is conspicuous throughout the year, forming extensive stands in some places.

Some of the non-sprouting Proteaceae, especially *Aulax umbellata* (Fig. 4.44) and *Leucadendron xanthoconus*, may gain dominance in some places with ground covers of well beyond 50 per cent (Fig. 4.45). The largest patch of *A. umbellata* occurs on the SE slope of Swartkransberg, two smaller patches were spotted on N-facing slopes on Steynsbos. *L. xanthoconus* forms extensive canopies on the S slope of Swartkransberg. However, a recognition of these patches as separate formations is not supported.

### ***Erica sessiliflora* Ericaceous Fynbos**

On damp, S-facing slopes and in valleys, the Acid Sand Fynbos is joined by several elements indicating moist conditions, such as *Berzelia lanuginosa*, *Cliffortia ferruginea*, *Drosera capensis* (Fig. 4.47) and *Psoralea arborea*. Structurally dominant is *Erica sessiliflora*, which can be up to 1.5 m high and can attain cover values of over 75 per cent (Fig. 4.48). *Mimetes cucullatus*, *Leucadendron coniferum* and *E. glabella* are common. The formation includes an area of 55.2 ha (3.2 per cent of the entire Grootbos Nature Reserve).



The largest patch occurs on the S slope of a mountain on the Steynsbos property, but extended canopies of *E. sessiliflora* also occur on the N slope of Swartkransberg, indicating that the species can also cope with less moist conditions. The moisture indicators as mentioned above are lacking in these places. Transitions to the *Protea repens* Proteoid Fynbos, the Transitional Proteoid Fynbos, the *Elegia thrysifera* Restioid Fynbos and even *Protea obtusifolia* Proteoid Fynbos are manifold.

The formation is represented by one relevé of the core dataset (69). It represents some of the characteristic features of the formation, and also some problems: The soil is deeper and less rocky than in the Acid Sand Proteoid Fynbos, the resistance is higher, but the

Fig. 4.49 (top): The transition between Alkaline Sand Fynbos and Acid Sand Fynbos at the S slope of Swartkransberg (10/2004).

Fig. 4.50 (bottom): *Elegia thrysifera* Restioid Fynbos on Tygerboom (11/2004).

affinities to the Alkaline Sand Fynbos Complex become obvious not only through the CCA. Although the pH is as low as 5.9, *Protea obtusifolia* plays a major role on this relevé, as it is located in a place where Bredasdorp Limestone and Table Mountain Sandstone alternate in a fine-grained pattern.

### Transitional Proteoid Fynbos

45.9 ha (2.7 per cent of the reserve's surface, excluding the *Erica sessiliflora* Ericaceous Fynbos and the *Elegia thrysifera* Restioid Fynbos) support a mixture of species centered in the Alkaline Sand Fynbos Complex, and species centered in the Acid Sand Fynbos Complex. The transitional character is well indicated by the CCA where the relevés of the core dataset representing the formation (31, 37, 44) show similar patterns to those of the Acid Sand Proteoid Fynbos, but shifted towards the center and thus less extreme. The pH, however, does not exceed 6.0. Various subtypes of this formation are present on the reserve.

The dense stands of *Leucadendron coniferum* covering vast areas of neutral sands do not open abruptly to make open space for the Acid Sand Fynbos (Fig. 4.49). In many places, a gradual decrease of size and of cover of *L. coniferum* can be observed on the middle slopes. The lower parts of this transition zone are structurally similar to the Neutral Sand Fynbos but acidophilous proteoids, usually *Mimetes cucullatus*, indicate the acidic conditions.

Damp ravines on the S slope of Swartkransberg support a thicket-like vegetation with high cover of *Olea capensis*. Since *Leucadendron coniferum* and *Mimetes cucullatus* are common as well and further thicket species are missing these few patches were included in the fynbos and not in the thicket. However, more sampling is necessary to clarify the issue.

Another transition zone exists between *P. obtusifolia* Proteoid Fynbos and Acid Sand Fynbos, leading to very complex situations with *Protea obtusifolia* and *Aulax umbellata* growing almost together, but representing completely different soil nutrient regimes. The major difference to the transition described above is that it is not based on a gradual decrease of soil depth and pH-value, but on a fine-grained mosaic of limestone ridges and Table Mountain Sandstone. Extremely complex situations prevail at the W slope of a mountain on Steynsbos, where *Leucadendron coniferum*, *Leucospermum patersonii* and *P. obtusifolia* coexist with some of the acid sand proteoids.



### *Elegia thrysifera* Restioid Fynbos

Although representatives of the Restionaceae are present all over the reserve, fynbos dominated by large restios is not very abundant. Three relatively large spots are dominated by *Elegia thrysifera* and *Thamnochortus erectus*. Two of them are situated along the transition from Neutral to Acid Sand Proteoid Fynbos, the third is surrounded by ecosystems indicating rather alkaline soil conditions (Fig. 4.50). Since no relevé of the core dataset was available and thus no soil analysis either and the formation was clearly assigned to the Acid Sand Fynbos Complex in the classification for the extended dataset, it should be included here. However, further research is necessary to clarify the question of whether it also grows on more alkaline soils or whether its distribution is driven by completely different variables.

Both *E. thrysifera* and *T. erectus* can grow up to two meters high and are structurally dominant with shifting composition. Proteoids are abundant but not dominant. Most common are *Leucadendron coniferum*, *Leucospermum patersonii* and partly *Mimetes cucullatus*. In some places, *Helichrysum patulum* and *Morella quercifolia* appear in the formation as conspicuous elements.

At the N slope of Swartkransberg, the formation creates a mixture with the *Erica sessiliflora* Ericaceous Fynbos.

## 5 Discussion

### The problems of vegetation research in the Fynbos Biome

The distinction of the Fynbos Biome in an Alkaline and an Acid Sand Fynbos Complex seems sufficiently supported by the classification and the ordinations. In contrast, the division of those complexes into proper communities is problematic for certain reasons. Most sub-complex vegetation units are based on one or maximum two dominant species which give the landscape a very characteristic face. Nevertheless, the classic concept of plant communities as an association of several characteristic species which differentiates it from other communities should not be applied to those entities. They should rather be considered as variations of the Acid Sand Fynbos and the Alkaline Sand Fynbos. It is obvious that the Clementian View of nature is applicable for the distinction of those two complexes while this way of considering nature fails for the sub-complex divisions and the Gleasonian view is more applicable. Some more problems concerning the recognition of a single species as differential for a community will be discussed below.

In the Forest Biome, both Milkwood Scrub Forest and Afromontane Forest contain a number of species occurring predominantly there and, therefore, legitimizing the status of the two complexes as plant communities but they also contain species present in both of them, underlining a common character.

More sampling would be necessary to give more confident information about the Wetland Biome.

The problem discussed above has already been addressed by various authors. Simmons (unpublished) referred to a number of previous phytosociological studies on the Cape Peninsula to underline the difficulties of separating sufficiently distinctive plant communities mirroring environmental variables. The floristic and structural complexity of fynbos ecosystems and also the influence of fire are specified as the major reasons leading to those methodical problems. The high beta- and gamma-diversity would lead to a high degree of floristic "noise" and make a distinction of meaningful species associations difficult. Furthermore, both structural and floristic properties of a given site would often mirror the fire history rather than other factors and would therefore be highly variable over time. Despite the fact that some

successful phytosociological studies have been carried out in the fynbos, they are problematic and better-suited for small-scale studies. Floristic studies of patches of few square kilometers may, however, only have limited predictive value for larger areas. This would mean that the results of this study could hardly be applied to a more extended area such as, for example, the Agulhas Plain.

Structural approaches are better applicable to larger units since the high gamma-diversity may cause very different species compositions among sites with similar conditions. In order to establish the plant communities of the reserve in a fynbos-wide system it is necessary to refer to structural classifications.

### The vegetation units of Grootbos Nature Reserve in the context of the Fynbos Biome

Various authors have tried to classify the habitat types and the plant communities of the Fynbos Biome in the previous decades - some regarding the entire region, others only considering smaller entities. In particular the Cape Peninsula has gained a lot of attention (Taylor 1983, Cowling et al. 1996, Privett et al. 2001). Several studies based on transects across mountain ranges are also available, such as the Southern Langeberg (McDonald et al. 1996) or the Cederberg (Lechmere-Oertel & Cowling 2000). However, no comparable studies have been set up on the Agulhas Plain.

Cowling & Heijnis (2001) have tried to identify so-called Broad Habitat Units for the entire Fynbos Biome, based on environmental variables. However, the authors stress that their units are no vegetation types per se but a surrogate for them. The Broad Habitat Units show good correlation with previous studies. Sixteen primary and 102 secondary units in four biomes (Fynbos, Succulent Karoo, Thicket and Forest) were recognized. The secondary units are based on geographic localities and have no major importance in regard to the reserve. Fynbos and Forest Biomes occur on the reserve. Among the primary units, Fynbos/Thicket Mosaic, Limestone Fynbos, Mountain Complexes and Afromontane Forest are present on the reserve. Fynbos/Thicket Mosaic and Limestone Fynbos together may largely correspond to the Alkaline Sand Complex while the mountain complexes may be identical with the Acid Sand

Complex of Grootbos Nature Reserve. No Milkwood Forest and Wetland were recognized by Cowling & Heijnis, probably due to the limited extent of those vegetation types.

Moll et al. (1984) described the major vegetation categories in and adjacent to the Fynbos Biome. They introduced three levels of generalization. The highest level comprises of Cape Fynbos Shrublands, Mosaic of Cape Fynbos Shrublands and Subtropical Elements (Dune Fynbos), Afromontane Forest, Cape Transitional Small-leaved Shrublands (Renosterveld), Cape Transitional Large-leaved Shrublands and Subtropical Transitional Thicket. Only the former three types are relevant to the reserve. The Dune Fynbos corresponds to the Dune Asteraceous Fynbos, being part of the Alkaline Sand Complex together with the Limestone Fynbos type of the Lowland Fynbos (part of the Cape Fynbos Shrublands). According to Cowling & Heijnis (2001: 23), the Dune Fynbos would be better considered as fynbos community described above due to the fact that the vast majority of the species - and also endemics - have their center of distribution in the fynbos. The position of *Protea repens* Proteoid Fynbos and Neutral Sand Proteoid Fynbos remain unclear, as well as remains the subdivision of Limestone Fynbos not specified by Moll et al.

The Mountain Fynbos of Moll et al. (1984), part of the Cape Fynbos Shrublands, is likely to correspond to the Acid Sand Fynbos Complex of this study. Moll et al. separate three types of mountain fynbos: Wet Mountain Fynbos, Mesic Mountain Fynbos and Dry Mountain Fynbos. The *Erica sessiliflora* Ericoid Fynbos established in this study may be assigned to Wet Mountain Fynbos while the Acid Sand Proteoid Fynbos and the Transitional Proteoid Fynbos may be considered as Mesic Mountain Fynbos. The situation is less clear for the *Elegia thrysifera* Restioid Fynbos as large restioids can gain dominance in both dry and wet Mountain Fynbos. Due to the fact that it is partly intermixed with *E. sessiliflora* Ericoid Fynbos, it may instead be assigned to the Wet Mountain Fynbos.

Mustart et al. (2003) reviewed the vegetation units of Southern Overberg. He distinguished between Acid Sand Proteoid Fynbos, Limestone Proteoid Fynbos, Neutral Sand Proteoid Fynbos, Ericaceous Fynbos, Dune Asteraceous Fynbos, Forest and Thickets, Wetlands and some more units not relevant to Grootbos Nature Reserve.

Acid Sand Proteoid Fynbos may largely correspond to the Acid Sand Fynbos Complex of this study. Mustart et al. (2003: 21) emphasize that several different communities may be separated according to different habitat settings. The *Erica sessiliflora* Ericoid Fynbos may correspond to the Ericaceous Fynbos of Mustart et al. (2003: 25).

According to these authors, Neutral Sand Proteoid Fynbos is associated with partly leached sands deriving from a calcareous substrate. For the Neutral Sand Proteoid Fynbos established in this study this is not necessarily the case. It is situated at the base of acid sand mountains, and the neutral sands may rather derive from downward wind-blown alkaline dune sands than from upwards as indicated by the topography, by Privett (pers. comm.) and by H. Lutzeyer (pers. comm.). At the upper edge of the formation, where *Leucadendron coniferum* intermixes with Acid Sand elements (Transitional Proteoid Fynbos of the Acid Sand Complex), only a shallow layer of wind-blown sand is supposed to cover the rocks of Table Mountain Sandstone supporting the latter species. Also from a floristic point of view the Neutral Sand Proteoid Fynbos of this study corresponds only partly to the community described by Mustart et al. (2003: 24). The characteristic species, *Protea susannae*, is absent from the reserve and the diversity of proteoids is low, limited to *Leucadendron coniferum* and *Leucospermum patersonii*. Limestone Proteoid Fynbos may largely correspond to the *Protea obtusifolia* Proteoid Fynbos of this study although also here the diversity of Proteoids is low, only including *P. obtusifolia*, *Leucadendron coniferum* and sometimes *Leucospermum pattersonii*, which are transitional to the Neutral Sand Proteoid Fynbos. Mustart et al. (2003) do not refer at all to communities comparable with *Erica coccinea* Ericoid Fynbos and *Thamnochortus fraternus* Restioid Fynbos. The same is true for *Protea repens* Proteoid Fynbos. Dune Asteraceous Fynbos like described by Mustart et al. (2003: 26f) largely corresponds to the Dune Asteraceous Fynbos of this study. Forest and thicket like those considered by Mustart et al. correspond well to the Forest Biome on the reserve, with thickets in rocky kloofs and river valleys, a few forest-like patches of *Sideroxylon inerme* and some isolated patches of true forest (Afromontane Forest). The wetlands described by the mentioned author are partly related to the wetlands on the reserve.

Campbell (1986) has reviewed data dealing with the plant communities of montane fynbos, largely corresponding to the Acid Sand Fynbos Complex of this study. He distinguished between Asteraceous, Restioid, Ericaceous and Proteoid Fynbos, in addition to some more types which were not relevant to the Grootbos Nature Reserve. Each type is further subdivided according to the moisture regime of the habitat. Campbell (1986: 8) only considers a community as proteoid if it has more than 10 per cent cover of seed-regenerating, medium-height to high proteoids (for a discussion concerning various reproduction strategies see below). That means that species like *Leucadendron salignum* and *Mimetes cucullatus*, being very common on the reserve, do not help in the recognition

of a community as proteoid. According to Campbell, large parts of the Acid Sand Proteoid Fynbos established in this study should instead be recognized as Asteraceous Fynbos. In contrast, the Transitional Proteoid Fynbos would correspond to Campbell's concept of Proteoid Fynbos. However, it is impossible to assign the Transitional Proteoid Fynbos to one of the series (mesotrophic, dry, mesic, wet), because they are largely distinguished by certain dominant overstory proteoids not occurring on the reserve.

The *Erica sessiliflora* Ericoid Fynbos of this study largely corresponds to Campbell's (1986) Wet Ericaceous Fynbos even though the partly high cover of proteoids also allows a recognition as Proteoid Fynbos. The prominence of Bruniaceae (*Berzelia lanuginosa*) and Penaeaceae (*Penaea mucronata*), however, clearly supports a recognition as Wet Ericaceous Fynbos. In contrast, it is problematic to relate the *Elegia thrysifera* Restioid Fynbos of this study to one of Campbell's series of Restioid Fynbos although it can be clearly assigned to this type. The sites of this formation may represent a series of Mesic Restioid Fynbos with a higher share of ericaceous Ericaceae (mainly *E. sessiliflora*) to Dry Restioid Fynbos. It has to be taken into account that Campbell's Restioid Fynbos is concentrated at elevations much higher than the restioid fynbos on Grootbos Nature Reserve.

Some ravines on the S slope of Swartkransberg with high cover of *Olea capensis* may show some similarities with Campbell's (1986) Closed Scrub Fynbos. However, more sampling at those sites would be necessary to establish a separate unit.

In his review on the Fynbos Biome, Kruger (1979) distinguished between Mountain Fynbos and Coastal Fynbos, a separation which is largely consistent with that in the Acid Sand Fynbos Complex and the Alkaline Sand Fynbos Complex in this study. He divided the Mountain Fynbos into an upper zone with ericoid and restioid vegetation, and a lower zone (applicable to the reserve) with tall proteoid shrubs. However, the types of Mountain Fynbos described by Kruger show only a weak correspondence to the vegetation of Grootbos due to the predominantly open character of the Acid Sand Fynbos Complex on the reserve. As some of the authors above, Kruger emphasizes the major role of *Protea repens* in the mountain fynbos which forms dense, tall stands together with *P. neriiifolia*. On the reserve, *P. repens* forms dense, tall, stands, too, but they have clearly been assigned to the Alkaline Sand Complex by both the classification and the ordination. However, its position partly at the upper edge of the Alkaline Sand Complex may indicate a certain transitional character.

Regarding Coastal Fynbos, Kruger (1979: 49ff) differentiated between two types of distribution: the

Western type (ranging eastwards to Danger Point) dominated by ericoids and a lower stratum of restioids, which - in contrast to the Eastern type - lacks a proteoid overstorey. Furthermore, Kruger distinguished between fynbos of coastal sands and fynbos on limestone. The Dune Asteraceous Fynbos of the reserve may correspond to fynbos of coastal sands of the Western type. The notion of fynbos on limestone not only includes the proteoid type but takes the common ericoids and the restioid *Thamnochortus fraternus* into account as well.

### Fire succession

As already discussed in chapter two, fire is considered one of the most important variables in determining not only the structure but also the floristic composition of the fynbos. Kruger (1979: 52) provides an overview of post-fire succession in mountain fynbos which shall be used to discuss succession on Grootbos Nature Reserve. He distinguishes five phases of succession (Fig. 5.1).

The **immediate post-fire** phase in the first year after a fire is characterized by resprouting of all species capable of vegetative reproduction, by an intense reproductive response of geophytes to the fire event as well as by the presence of annuals. These characteristics were obvious in Transitional Proteoid Fynbos on the N slope of Witkransberg in October 2004 after a fire event in the previous autumn (Fig. 5.2). The overstorey shrub *Leucadendron coniferum* was entirely killed, remaining only as dense stands of standing dead. Small individuals of the resprouting Proteaceae *Mimetes cucullatus* were omnipresent. Large patches were covered in red by the geophyte *Watsonia stenosiphon* (Iridaceae, Fig. 5.3). The genus *Watsonia* is well-known for its clustered flowering after fire although its reproduction is not always coupled with such events. There was a high cover of grasses. Non-sprouting Proteaceae were completely absent.

The **regenerating** phase, lasting from two years to four or five years after a fire, is characterized by graminoid herbs attaining dominance and being joined by opportunistic shrubs setting their seeds and dying. Kruger (1979) mentioned *Aspalathus* spp., *Othonna quinquedentata* and *Euryops abrotanifolius* as examples. Larger proteoid shrubs also start to emerge from the canopy and resprouting shrubs reach maturity (Fig. 5.4 and 5.5). Since two larger fires occurred on the reserve in 2000 and 2001 respectively, the patterns described by Kruger could clearly be observed in spring 2004. The lower and rather flat slopes were partly occupied by dense thickets of *Aspalathus microphylla*, a clear indicator for fire. Steep, rocky slopes showed a high abundance of *Aspalathus ciliaris* and *Othonna quinquedentata*, sometimes joined by clusters of the large

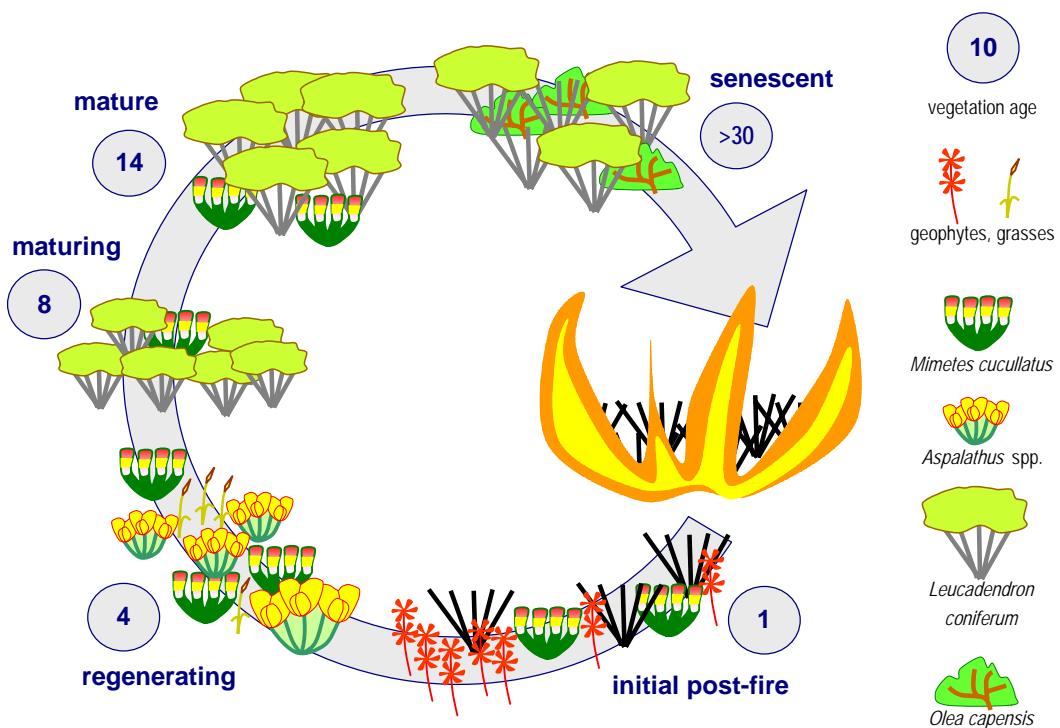


Fig. 5.1 (top): Fire cycle in the Acid Sand Fynbos of Grootbos, according to observations by the author and to Kruger (1979). Designed by the author.

Fig. 5.2 (middle): Transitional Fynbos during the immediate post-fire phase on the N slope of Witkransberg. In the foreground mature stands of Neutral Sand Proteoid Fynbos, the reddish color above the limit of standing dead of *L. coniferum* is caused by *Watsonia stenosiphon* (11/2004)

Fig. 5.3 (bottom): *Watsonia stenosiphon* on the N slope of Witkransberg (10/2004).

hemiparasitic shrub *Thesium strictum* (Fig. 5.6). The latter species composition showed no major difference between similar slopes in limestone and Table Mountain Sandstone, indicating that soil depth may play a more important role for the composition of fynbos in the early stages of succession than the chemical properties of the substrate. However, *Mimetes cucullatus* and *Euryops abrotanifolius* were only observed on sandstone slopes. The life form of graminoid herbs mentioned by Kruger (1979) was largely represented by the grass *Pseudopentameris macrantha* which contributed extensively to the cover on steep, rocky slopes. It was very abundant on a site burned in 1997 and again in 2001 - supporting the thesis that short fire intervals (up to four years) favor grasses (Privett, pers. comm.).

The high abundance of fabaceous ericoids in the regenerating stage is connected with the low nitrogen status of the soil after fire (Privett pers. comm.). Fabaceous species have the ability to catch nitrogen from the air due to a symbiosis with nitrogen-fixing

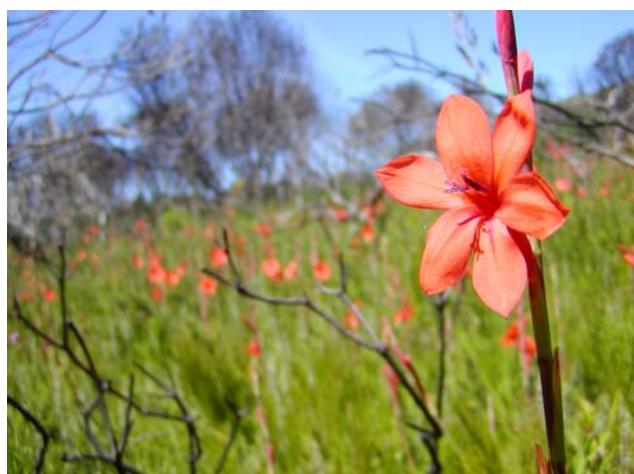




Fig. 5.4 (top): Three years old Transitional Proteoid Fynbos on Platrug, with young *Leucospermum patersonii* and mature *Mimetes cucullatus* (10/2004).

Fig. 5.5 (middle): Three years old Acid Sand Fynbos with *Aspalathus ciliaris*, *Helichrysum patulum* and a high cover of grasses. The large individuals of *Leucadendron coniferum* in the background have survived the fire of 2001 (11/2004).

Fig. 5.6 (bottom): Limestone slope burned in 2001 with *Pseudopentameris macrantha* (left) and *Thesium strictum* (right, 11/2004).

*obtusifolia* Proteoid Fynbos on the reserve were passing this stage at the time of the survey because their habitats burned in 1996. However, in particular the former formation shows features valid for the mature phase (see below) due to litter accumulation and sparse undergrowth.

The **mature phase** spans between about ten and thirty years after the previous fire event. Tall shrubs attain their full, rounded shape and reach their maximum flowering activity. Lower reseeding shrubs, for example various species of *Erica*, begin to die. No more germination takes place. Litter accumulates and suppresses the lower strata so that they are reduced in importance. Large parts of the Acid Sand Complex of the reserve were in this stage at the time of the survey because the previous fires date back to 1990 and 1992 respectively. The canopy was open in many places but the described patterns apply in sites dominated by *Leucadendron coniferum*. Although not a part of the mountain fynbos, the vast closed canopies of the Neutral Sand Proteoid Fynbos, built up entirely by *L. coniferum* (Fig. 4.32), may represent an ideal example of the mature phase of fynbos as described by Kruger (1979).

The **senescent phase** begins about thirty years after the previous fire event. Tall shrubs show accelerated mortality leading to an opening of the canopy. Some regeneration from seeds occurs. On relatively moist and fertile sites the immigration of forest precursors takes place. Due to prescribed fires as a tool in fire management the distribution of senescent fynbos is limited on the reserve. Some S-facing slopes of the Neutral Sand Proteoid Fynbos show an invasion by forest and thicket species like *Euclea racemosa* and their rather moist character is underlined by the presence of the fern *Asplenium adiantum-nigrum*. However, these sites also burned in 1990 according to the available records and the canopy of *L. coniferum* does not provide a senescent impression.

Comparing the characteristic fire cycle of mountain fynbos with that of the Lower Chaparral of California (Fig. 2.9), some differences are obvious. The dominant reseeders of the Chaparral, especially *Ceanothus* spp., are short-lived, being replaced by the resprouting

bacteria. As soon as the nitrogen status of the soil has been improved (low nitrogen is characteristic for fynbos anyway) the fabaceous species perish. *Aspalathus ciliaris*, for example, has been characterized as a long-living fire ephemeral maturing already in the second year (Van Wilgen & Forsyth 1992: 65).

The **maturing phase** lasts until about ten years after the previous fire and is characterized by all species attaining maturity and tall shrubs developing their ascending branch habit. Although not actually part of the mountain fynbos the majority of the *Protea repens* Proteoid Fynbos and also a considerable share of *P.*

*Adenostoma fasciculatum* in the mature phase. In the fynbos, the reseeders appear after the same period as in California but may maintain dominance until senescence. Resprouters - often emerging in the first year after a fire - are rather small, also among the Proteaceae, and only keep dominance where larger shrubs are missing.

In the Alkaline Sand Fynbos Complex of the reserve the succession patterns are supposed to differ considerably from the Acid Sand Fynbos Complex. A major reason for that may be the lack of resprouting Proteaceae and the total lack of Proteaceae in the Dune Asteraceous Fynbos. A site on Steynsbos, burned in 2000, did not differ considerably from sites burned in 1992 from a floristic point of view during spring 2004. However, the canopy was very low, with the restioid *Ischyrolepis eleocharis* playing an important role in some places, as well as *Pelargonium betulinum* and to a lesser extent *Eriocephalus racemosus* (Fig. 4.27). The sites do not lack thicket species (*Euclea racemosa*, *Olea exasperata*) but an ericoid overstorey common in older dune fynbos (mainly built up by *Otholobium bracteolatum*) was absent.

Species commonly found together in the Dune Asteraceous Fynbos can show clearly different fire-related life histories. While *Passerina vulgaris* is considered a pioneer species (senescence and mortality have been observed in only 13 years old stands), *Metalasia muricata* should be considered as early successional thicket species - indicated by low seed densities, long distance seed dispersal by wind and high germination success (Pierce 1987: 51, 53). The statements regarding *P. vulgaris* are supported by observations by the author on Platrug where twelve year old stands provided an extremely senescent impression. This, however, may also be caused by other factors.

A belt of Limestone Fynbos was affected by the 2000 fire. Due to the quite disturbed status of the place (the NE part of Steynsbos), connected with intense clearing of *Acacia cyclops*, it was difficult to provide confident information about the fire succession in Limestone Fynbos, also because it is not clear which of the three limestone formations would be dominant during maturity. Among the species of the regenerating phase, *Aspalathus ciliaris* played the major role. Regarding the Proteaceae, *Protea obtusifolia*, *Leucadendron coniferum* and *Leucospermum patersonii* were present at low abundance. One patch at the transition to the *P. repens* Proteoid Fynbos was occupied by restioid fynbos dominated by *Thamnochortus erectus*. The same was true for a patch on Platrug burned in 2001. Some places at the transition between Alkaline Sand Fynbos and Acid Sand Fynbos hit by the fires 2000 and 2001, respectively, supported dense mats of *Aspalathus microphylla* (relevés 67, 122,

171). The classification indicated connections with the Neutral Sand Proteoid Fynbos but in the CCA it became obvious that the habitat at least of relevé 67 shows close similarities to the *Protea repens* Proteoid Fynbos. The relevés have therefore been classified as post-fire regenerating *P. repens* Proteoid Fynbos, but more research would be necessary to clarify whether this is reasonable or not.

It was not possible to discuss fire succession in the Neutral Sand Proteoid Fynbos because the latest fires there dated back to 1990 and 1992 at the time of the survey so that the whole stand had reached maturity. As mentioned above, some patterns valid for the Acid Sand Fynbos may be applicable.

According to Van Wilgen & Forsyth (1992: 68), no fynbos community is favored by a certain fire regime, but all communities are maintained with fire intervals in between 10 and 20 years.

The vegetation analyses in this study are based on sites in the maturing and mature phases, as are most analyses for the fynbos. Since the fire intervals peak between 10 and 30 years those investigations give the impression of describing climax vegetation at the end of succession. In a strong ecological sense the whole fynbos can be considered as a series of successional stages, leading to forest if no disturbances occur for a certain period.

### Fynbos and forest

Certain studies indicate that most habitat types covered by fynbos potentially support forest under the given climatic and edaphic conditions (compare Cowling et al. 1997a for a review). This is in line with a statement by Manders et al. (1992: 106), that fynbos and forest are in fact not discrete, unconnected vegetation types, but are connected along a continuous gradient; a statement that is supported if one looks at some S-exposed valleys embedded in Neutral Sand Proteoid Fynbos of Grootbos Nature Reserve. Some of the most extreme sites are covered in Afromontane Forest but others support Valley Thicket, indicating very low fire frequencies or intensities but still the occurrence of fires. Very large and extensively branched individuals of *Leucadendron coniferum* are mixed with typical forest elements like *Chionanthus foveolatus*, *Olea capensis* ssp. *macrocarpa*, *Rapanea melanophloeos* and *Sideroxylon inerme*. The undergrowth comprises mainly of forest species, climbers are very common. Ferns are common as well and exposed sites are colonized by members of the Crassulaceae and *Heliophila linearis* var. *reticulata*.

Fire as frequent disturbance factor is considered to be the main variable preventing or stopping forest development. If, for some reason, a site of fynbos escapes the fire cycle discussed above for a period of

certain decades, patches of initial forest may develop and, as soon as having attained a certain size, lose its fire prone character and serve as fire-free islands which can develop into forest patches without further disturbance. Therefore, a permanent race between fire interval and forest development is taking place in the fynbos biome which in most cases is won by the fire. However, patches of forest are distributed all over the Fynbos Biome.

Potential forest species are omnipresent in the fynbos, on Grootbos Nature Reserve especially in the Alkaline Sand Complex. Already in four year old Alkaline Sand Fynbos of Steynsbos, elements like *Euclea racemosa*, *Olea capensis*, *Olea exasperata* or *Rhus* spp. contribute a considerable proportion of cover and biomass to the ecosystems. According to Cowling (1987: 3), they all produce diaspores suitable for long-distance dispersal (e.g. bird-dispersed fleshy fruits), enabling the quick colonization of new sites. Seed banks are absent and no specific adaptations for recruitment after fires have been observed. The species occupy rather moist sites and increase in abundance when fire is excluded (Fig.



Fig. 5.7 (top): Forest elements in sheltered ravines and on rocky slopes on a S-facing slope in the Tygerboom Kloof (10/2004).

Fig. 5.8 (bottom): Dense stands of *Acacia cyclops* in an area burned in 2001 (10/2004).

### 5.7).

Since those species are quite slow-growing they require long fire-free periods to grow to a stage at which they are fire-resistant and can form the cores of forest patches. True forest species like *Rapanea melanophloeos* or *Sideroxylon inerme* show similar features as the shrubs mentioned above but they cannot invade young fynbos because their seeds require more sheltered places than the seeds of the shrubs.

Cowling et al. (1987: 3) emphasize the similarities between the mentioned shrubs and some elements of the Californian Chaparral like *Cercocarpus betuloides*, *Heteromeles arbutifolia*, *Prunus ilicifolia* or *Rhamnus* spp., that have the same reproductive strategies and the same responses to habitat and fire incidence.

All of the mentioned above is only true for indigenous trees and forests. As emphasized by Manders et al. (1992: 105f), the behaviour of alien trees is quite the reverse. The immediate post-fire conditions are favorable for most of them so that they can easily colonize burned sites. Regarding Grootbos Nature Reserve, *Acacia cyclops* has recently provided clear support for the afore-mentioned statement because it reinvaded a cleared site at the E edge of Platrug and Steynsbos burned in 2001, partly forming dense, almost impenetrable thickets there (Fig. 5.8).

The results of the geostatistical analysis show a higher share of forest compared to the vegetation map (Fig. 4.8 and 4.10). Patches of Milkwood Scrub Forest are suggested to be dispersed all over the lower parts of the reserve, especially in S-facing sites. The large patch adjacent to the Forest Lodge (NW-facing) was not recognized. Afromontane Forests were placed on steep, S- and SE-facing slopes, mainly outside the borders of the reserve. In fact, these slopes largely support mountain fynbos. Within the reserve the Afromontane Forest was predicted well.

The reasons for the mispredictions may be manifold. Several factors have to be taken into account:

- environmental variables not connected to topographic surrogates may be significant
- the models for the advanced topography may be insufficient
- the accuracy of the mapped vegetation units may be insufficient - in rugged terrain like the forest valley, small errors may also bias the results considerably.
- randomness may play a prominent role for the establishment of forest patches
- the results may be theoretically correct but anthropogenic influences could have promoted fynbos

The latter point may be of some importance for the Milkwood Scrub Forest since *Sideroxylon inerme* provides valuable timber in an otherwise forest-poor environment and the soil is suitable for agriculture (compare chapter 4). Some places were cultivated in the past and they have been abandoned too recently to allow potential patches of Milkwood Scrub Forest to reestablish. The distribution of Afromontane Forest appears to be explained by limited solar irradiation rather than by wind protection or flow accumulation, as already indicated by the CCA. One would expect a higher importance particularly of the wind exposition. Insufficient modeling may partly explain this phenomenon. However, some sheltered ravines along the N slope of Swartkransberg were predicted as Afromontane Forest although they were fed into the Analysis as Transitional Proteoid Fynbos. In fact they are dominated by dense thickets of *Olea capensis* (compare chapter 4).

The author believes that the role of randomness - or stochasticity - should not be underestimated as an explanatory variable for the distribution of forests. As discussed above, a certain set of conditions has to be fulfilled to allow the establishment of pockets of thicket and their succession to forests. It should be reiterated that the major inhibitor of forest establishment, fire, is a stochastic process as well.

In the CCA, the relevés of the Forest Biome were discriminated from the fynbos and wetlands by soils being extraordinarily rich in certain nutrients. One should be careful when using those chemical variables as explanators since they are influenced by the forests themselves as their nutrient cycle is supposed to differ completely from that of the fynbos.

### **Fire-related reproduction strategies and vegetation structure**

Fynbos ecosystems are considered as resilient as long as they are exposed to intermediate fire intervals (about 10 to 20 years), as investigations in the Jonkershoek Mountains indicated (Van Wilgen & Forsyth 1992: 68). Nevertheless, a number of studies have shown that it is problematic to base communities on non-sprouting members of the Proteaceae family. Especially *Protea repens* and *P. nerifolia* have gained attention (e.g. Van Wilgen & Forsyth 1992) probably due to their broad distribution. The former species also plays a prominent role on the reserve. It is serotinous, meaning that seeds remain in the canopy until a fire occurs. Then they are released and germinate. Though this reproduction strategy helps the species to reinhabit the site quickly after a fire the problem is that it can lead to local extinction. *P. repens* produces seeds from the age of three years and it has a maximum lifespan of 35 years. If a fire event occurs



Fig. 5.9: *Leucadendron xanthoconus*, one of the reseeding Proteaceae of Grootbos Nature Reserve, achieving high cover in some patches of the Acid Sand Proteoid Fynbos (11/2004).

before four years or if the site remains fire-free for more than 35 years, the species may face local extinction. The second problem for serotinous species is their sensitivity to the fire season. Germination usually occurs in autumn to ensure favorable conditions for the seedling. If the site happens to burn in spring, the released seeds are highly prone to consumption by small mammals during the whole summer.

As emphasized by Van Wilgen & Forsyth (1992: 63), serotinous species are not very numerous but they often dominate ecosystems by contributing up to 89 per cent of the aboveground biomass and 53 per cent of the belowground biomass in the Swartboskloof (Jonkershoek). The same patterns are true for *P. repens* in the *P. repens* Proteoid Fynbos of Grootbos. *Leucadendron coniferum*, dominating large areas of the Neutral Sand Proteoid Fynbos, is serotinous as well and may occupy an even larger proportion of the biomass in some places of the reserve (estimation by the author). Less pronounced but similar patterns may be applicable to the *Protea obtusifolia* Proteoid Fynbos.

Richardson & Van Wilgen (1992: 279) used the term "drifting clouds of species abundance", referring to the very unstable distribution of reseeders over a number of decades (or fire intervals). Privett et al. (2001) reported this phenomenon when re-analysing the vegetation of the Cape of Good Hope Nature Reserve and comparing the results with the survey of Taylor (1983). They observed a turnover of about forty per cent of all species in a given plot. Similar patterns of behavior are known for *Leucadendron xanthoconus*. This species occurs in the Acid Sand Fynbos of Grootbos Nature Reserve. Its distribution is rather limited but where it occurs, it contributes a considerable share of cover and biomass (Fig. 5.9). According to the above these patches may shift from fire interval to fire

interval and are therefore difficult to be considered as a separate formation. The same is true for the serotinous Proteaceae *Aulax umbellata*. In contrast to *L. xanthoconus* it is widespread all over the Acid Sand Proteoid Fynbos but several clusters of abundance (compare App. 4) may be subjected to shifting from fire interval to fire interval.

One important exception from the rule that Proteaceae have the exclusive right for serotiny in the fynbos (compare chapter 2) is the only serotinous Ericaceae, *Erica sessiliflora*, which can - like the mentioned Proteaceae - attain high cover values, dominating a formation of the Acid Sand Fynbos.

Resprouters are less common in the Fynbos Biome than in other mediterranean biomes (e.g. Cowling et al. 1997a: 112) but there are nevertheless many species with the ability to resprout. However, most of the dominant taxa contributing the majority of biomass and cover are serotinous reseeders. In the Jonkershoek Mountains resprouters are associated with rather moist sites, but can not clearly be discriminated from reseeding species along a suite of environmental gradients as they can be in the Californian Chaparral (Smith et al. 1992: 121f). Furthermore, resprouters are associated with short fire intervals when reseeding species can not grow to maturity. The latter is especially true for grasses. On the reserve, *Pseudopentameris macrantha* attains high cover in a site of Acid Sand Fynbos burned in 1997 and again in 2001.

Resprouting Proteaceae show a slower population growth after a fire than reseeding members, as shown by Le Maitre (1992) for *Protea nerifolia* and *P. nitida*, and hardly attain dominance in fynbos ecosystems due to their slow dynamics. In contrast they do not face as a high risk of local extinction as reseeding - and among them especially serotinous - species do.

Resprouting Proteaceae are limited on the reserve: *Protea cynaroides*, *P. speciosa*, *Leucadendron salignum* and *Mimetes cucullatus* and maybe *Leucospermum prostratum* are the only ones. Their distribution patterns are in line with the results reviewed above. They are omnipresent over the Acid Sand Fynbos Complex but never attain high covers, always showing a rather patchy distribution of small clusters of plants (each cluster probably deriving from one single genetic individual). For a detailed discussion of the importance of reseeding and resprouting for evolution the author refers to chapter two.

In the geostatistical analysis a considerable share of Neutral Sand Proteoid Fynbos was predicted as *Protea repens* Proteoid Fynbos. This phenomenon may be connected to the problems discussed above. The significantly higher resistance of soils supporting *P. repens* Proteoid Fynbos may be another explanation for the poor prediction as resistance was not included in

the geostatistical analysis. However, most of the other points mentioned in connection to the fynbos/forest-boundary may apply as well. The Neutral Sand Proteoid Fynbos was generally very poorly predicted, indicating that it is not well-defined by topography.

### Biodiversity

Fig. 5.10 represents the floristic diversities of the vegetation units of the reserve on the complex level. Although fynbos and forest are connected along a continuum, as discussed above, they constitute completely different species pools. Less than ten taxa occur in both biomes together, Acid Sand Fynbos and Afromontane Forest share no taxa at all. In contrast the complexes within each biome share a considerable amount of their taxa. Wetland shares only a few taxa with the other biomes, but the low diversity of the wetland may contribute to this phenomenon.

Although the Alkaline Sand Fynbos hosts more taxa (200) than the Acid Sand Fynbos (149), the diversity of the latter is more than four times higher if normalized to the area (0.63 and 0.14 taxa per ha respectively). Even though this ratio may be of limited value it confirms the general patterns obtained from the relevé data. The phenomenon of the high floristic diversity in the fynbos has already been discussed in chapter 2.

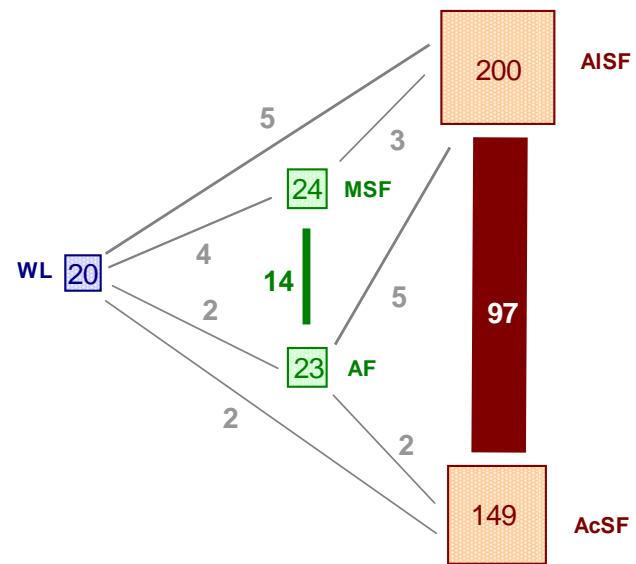


Fig. 5.10: Number of taxa in the different vegetation complexes of the reserve and floristic relationships (WL = Wetland, MSF = Milkwood Scrub Forest, AF = Afromontane Forest, AISF = Alkaline Sand Fynbos, AcSF = Acid Sand Fynbos. Designed by the author.

### Human influences

The available record of utilization of Grootbos Nature Reserve by humans is rather poor. However, since the reserve consists of several pieces of land called farms it is likely that some kind of cultivation took place on most of the reserve. This hypothesis is supported by the aerial imagery which clearly shows structures indicating cultivation in the past. This is especially true for a patch in the N part of Platrug with parallel structures most likely connected to the growth of crops (Fig. 5.11). Less clear, but nevertheless obvious circular structures are present in the vicinity of the Garden Lodge. The presence of the grass *Stenotaphrum secundatum* in some places (particularly at the bottom of Tygerboom Kloof) indicates cattle grazing in the not so far past. However, large parts of the reserve do not carry traces in the landscape indicating cultivation. It may be that these areas have never been used or that they have been used extensively a long time ago, so that several fire cycles have eliminated the traces. It is unlikely that the higher parts of the reserve where the Table Mountain Sandstone is exposed have ever experienced cultivation.

When the Grootbos property was bought by the Lutzeyer family in 1995 it was partly covered by alien vegetation. Especially the slope below the Garden Lodge carried a dense thicket of *Acacia cyclops*. Parts of the Mountain Fynbos were invaded by *Hakea suaveolens*. Intense efforts of alien clearing have reduced the presence of introduced plants to a minimum. However, on the recently bought properties, especially Steynsbos, *A. cyclops* is widespread in the Alkaline Sand Fynbos Complex (compare App. 4). The species is patchily distributed with single plants, small clumps or larger patches all over the lower and mid elevations of



Fig. 5.11: Parallel patterns on Platrug, indicating former cultivation (11/2004).

the farm. The highest densities of *A. cyclops* were observed in the E part of the property at the Steynsbos-Platrug border where a fire occurred in 2001. Clearing efforts were carried out before, but after the fire the species reestablished itself and vigorously invaded parts of the burned site, constituting dense canopies in 2004 particularly along the base of the limestone ridge E of the small patch of Milkwood Scrub Forest (Fig. 5.7).

*Acacia cyclops* has also invaded some places in the Acid Sand Fynbos Complex of Steynsbos, but to much lesser extent than the Alkaline Sand Complex. Another *Acacia* species occasionally encountered on this property is *Acacia mearnsii* which is concentrated in one patch at the N edge. *A. saligna* is less common at Grootbos but still present, as well as *A. longifolia*. The mountain fynbos is predominantly alien-free. However, some clumps of *Pinus pinaster* occur, most of them on Steynsbos, the largest on the slope N of the dam.

## 6 Conclusions

### Fynbos and remote sensing - a review

The interpretation of color aerial images in order to delimit different plant communities or vegetation units in the fynbos is highly problematic. This is especially true for numerical methods but also for manual interpretation. A combination of various reasons seems to be responsible for those difficulties.

The available images were taken in May, a period of the year with reduced biological activity and thus poor accentuation of the land surface. Images taken in spring may supply better information. In addition, infrared images would allow a more meaningful interpretation than color images due to the reflection properties of chlorophyll (compare chapter 3).

The texture and the color of different units of fynbos are often quite similar. Tall proteoid vegetation can usually be distinguished from open heathlands, the former may even be interpreted as forest. However, within these two groups the distinction of meaningful subgroups was hardly possible. In addition, some vegetation units comprise of both tall shrublands and open heathlands. The situation is even more difficult with vegetation units with low cover because there the substrate contributes a major share to the reflection properties. Thus it was not at all possible to separate Acid Sand Proteoid Fynbos from *Thamnochortus fraternus* Restioid Fynbos.

Furthermore, aerial images may represent the stage of post-fire succession rather than the actual vegetation units. The short turnover period of fynbos ecosystems as a response to the high fire frequency implicates that images become out-dated within a few years, and the vegetation found in a certain place in the terrain may be very distinctive from the vegetation represented by the image at the same site.

The Milkwood Scrub Forest was clearly separated from the fynbos by the numerical interpretation. This was not the case for the Afromontane Forest due to intense shading. Without shading the Afromontane Forest should be clearly distinguishable too. Also renosterveld and succulent karroo biome types should be distinguishable due to their different activity of life processes (Privett, pers. comm.), provided the availability of infrared aerial or satellite imagery.

As a consequence it can be concluded that numerical remote sensing techniques are expected to be useful

for the identification of different biome types of Southern South Africa. Their usefulness for the identification of fynbos units, however, is very limited.

### The Vegetation of Grootbos Nature Reserve

The recognition of a Forest and a Fynbos Biome is in line with existing vegetation classification systems for the mediterranean part of South Africa. Although, when considered on a broader scale, the Fynbos Biome covers the whole area (compare chapter 2), the forest may be considered as an extrazonal biome within the fynbos. The status of the wetland unit is less clear, but because their relationships both to forest and to fynbos are limited, it appears necessary to consider it as a separate biome despite its limited distribution. Also Cowling et al. (1997b) treat wetlands as biome in their account of the vegetation of Southern Africa.

The separation of fynbos into two broad complexes is supported by various authors as well, only the nomenclature differs. The Acid Sand Fynbos Complex is part of the Mountain Fynbos recognized by most of the authors while the Alkaline Sand Fynbos Complex belongs to a type referred to as Coastal Fynbos, or is a combination of Dune Fynbos (Coastal Sands Fynbos) and Limestone Fynbos (Moll et al. 1984, Kruger 1979), Dune Asteraceous Fynbos, Limestone Fynbos and Neutral Sand Proteoid Fynbos (Mustart et al. 2003) or Fynbos/Thicket Mosaic and Limestone Fynbos (Cowling & Heijns 2001). The subdivisions provided by these authors are largely supported by the classification and ordination carried out in this study. For the Mountain Fynbos, existing subdivisions are hardly applicable to Grootbos Nature Reserve. This is mainly due to the high floristic and structural diversity among different mountain ranges throughout the fynbos biome. In addition, the mountains of the reserve attain only very limited elevations compared with the major mountain ranges most of the studies referred to. The *Erica sessiliflora* Ericaceous Fynbos could be related to the Wet Ericaceous Fynbos (Campbell 1986) or to the Ericaceous Fynbos (Mustart et al. 2003).

The recognition of vegetation units for the reserve was based on the TWINSPLAN classification (biome level and complex level), the ordination results and the presence of characteristic species (formation level). The latter introduced some degree of subjectivity into

the study, but it was necessary to attain units that are easily recognizable in the field to be suitable for management issues. Although the author is aware of the problems of using reseeding Proteaceae as indicators for the recognition of communities (and also vegetation units) he had to follow this approach in some cases in order to attain the objective specified above (Neutral Sand Proteoid Fynbos, *Protea obtusifolia* Proteoid Fynbos and *P. repens* Proteoid Fynbos).

### Implications for the management

The problematics connected with serotiny were discussed in detail in the previous chapter. To avoid local extinction of the major serotinous species of the reserve (*Leucadendron coniferum*, *Protea obtusifolia* and *P. repens*), suitable management techniques have to be applied. The ecosystems have to be burned at reasonable ages and during the right season (late summer or autumn). Further attention has to be directed towards the protection of the ecosystems of fires approaching them from outside during unsuitable vegetation age or unsuitable season.

According to the CCA the red-data species are concentrated to habitats with rather extreme conditions. In order to protect those species particular emphasis has to be put on the conservation of such habitats, especially Limestone Fynbos and Acid Sand Proteoid Fynbos. The latter deserves attention due to its high species diversity as well.

Measures to control introduced species, especially *Acacia cyclops*, are essential for the maintenance of near-natural ecosystems. Also in future it will be necessary to apply chemical (poisoning) and biological methods, but also manual clearing to cope with this major threat to biodiversity.

The general conservation objectives and activities of Grootbos Nature Reserve have been specified in an explicit Management Plan (Grootbos Nature Reserve 2002).

### Needs for further research

Grootbos Nature Reserve has been intensively surveyed during this study. However, the time window available for the field survey was limited and no study can answer all possible questions on a topic. Most results provide new problems to be resolved. Various questions were answered by the study but at least as many remained unanswered and a large number arose.

Some ecosystem types were studied more intensively than others. Since the author's local knowledge of the

area was limited in the beginning of the study not all vegetation units were sampled and analyzed as one would wish afterwards. A big question remains in connection with the fynbos types dominated by the large restioids *Elegia thyrsifera* and *Thamnochortus erectus*. No soil samples were taken from sites at these locations and their assignment to the Acid Sand Fynbos may be revised by further studies. The status of the dry sub-formation of the Neutral Sand Proteoid Fynbos remains completely unclear. Little attention has been put on the *Erica sessiliflora* Ericaceous Fynbos as well as on the *Erica coccinea* Ericoid Fynbos. To a lesser extent the wetlands are also under-sampled as they appear to constitute a complex system with several subdivisions and transitions to other vegetation units.

The remaining units were largely surveyed to a sufficient extent but further sampling would doubtlessly mean a gain of information to refine the existing knowledge. The internal patterns (sub-formations) of the Acid Sand Proteoid Fynbos and the Transitional Proteoid Fynbos would be of particular interest.

Sites in the immediate post-fire phase have been completely disregarded and sites in the regenerating phase appear to be underrepresented in the dataset. However, to gain more detailed knowledge about fire succession, sampling and analysis of these sites would be necessary.

Since the vegetation-environment relationships were based on spatial coincidence between the species and certain soil attributes, the results can only provide hypotheses for future research directed towards the explanation of the observed phenomena.

To enable calculated measures against alien plant species, a more accurate map of their distribution is essential. Recent imagery or detailed field work would be necessary. A spatial dataset was set up a couple of years before this survey but due to the quick dynamics of alien plant invasions it is out-dated. In this survey the mapping of alien plants was not a major objective and the dataset should be considered as a rough estimation.

As discussed in detail above, not only the introduced species are subjected to rapid changes but also the near-natural or even natural fynbos. Therefore, continuous monitoring is essential to keep informed what is going on in the ecosystems of the reserve. Only with this knowledge, suitable management techniques can be applied in order to conserve the biodiversity of the species and ecosystems of Grootbos Nature Reserve.

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## Lists of figures and tables

### Figures

All photographs are from the archive of the author if not mentioned otherwise. All maps of Grootbos Nature Reserve have been designed by the author using the software ArcGIS, based on own research and topographic layers obtained from contour data provided by the General Directory of Survey and Mapping in Mowbray.

#### Front cover

Forest valley, dry Neutral Sand Proteoid Fynbos with *Leucospermum patersonii* in the foreground and Afromontane Forest in the background (10/2004).

#### Back cover

From top to bottom: *Mimetes cucullatus* (11/2004), *Protea obtusifolia* (10/2004), *Leucospermum prostratum* (10/2004), *Leucadendron tinctum* and *Aulax umbellata* (10/2004).

#### First page

*Erica magnisylvae*, discovered first on Grootbos Nature Reserve (10/2004).

#### Introduction

Fig. 1.1: Grootbos Nature Reserve is located on the slopes above the Walker Bay, SE of Cape Town (map reproduced from the "Reise-know-how" map "South Africa").

Fig. 1.2: The farms making up the reserve.

Fig. 1.3: The facilities of the Garden Lodge, Walker Bay in the background. The visible dunes belong to the Walker Bay Nature Reserve (10/2004).

Fig. 1.4: The Witkraansberg (451 m) is one of the highest points of the reserve (11/2004).

Fig. 1.5: Grootbos Nature Reserve from a bird's eye view. The underlying digital elevation mode was obtained from contour lines, further details regarding terrain modelling are discussed in chapter 3.

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Adapted from Cowling et al. (1997a).

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## Methods

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Fig. 4.22: Schematic profile across the wetlands and thickets of the forest valley. Designed by the author.

Fig. 4.23: *Pteris dentata* Fernland in the forest valley (10/2004).

Fig. 4.24: *Gunnera perpensa* Wetland in the forest valley (10/2004).

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Fig. 4.26: Dune Asteraceous Fynbos with a young individual of *Otholobium bracteolatum* (foreground), *Metalasia muricata* (background and the thicket species *Olea capensis* ssp. *capensis* (11/2004).

Fig. 4.27: Four year old Dune Asteraceus Fynbos dominated by *Eriocephalus racemosus* and *Ischyrolepis eleocharis* (10/2004).

Fig. 4.28: Dune Asteraceous Fynbos plant collection (thicket species excluded) - from left to right and from top to bottom: *Ischyrolepis eleocharis*, *Erica irregularis*, *O. bracteolatum*, *Anthospermum aethiopicum*, *Metalasia brevifolia*, *Oedera capensis*, *M. muricata*.

Fig. 4.29: Schematic profile across the Dune Asteraceous Fynbos. Designed by the author.

Fig. 4.30: Schematic profile across the Neutral Sand Proteoid Fynbos. Designed by the author.

Fig. 4.31: Neutral Sand Proteoid Fynbos leaf collection - from left to right and from top to bottom: *Thamnochortus erectus*, *Phyllica dodii*, *Leucadendron coniferum*, *Leucospermum patersonii*, *Erica lineata*

Fig. 4.32: Large canopy of *L. coniferum*, Acid Sand Fynbos in the foreground (11/2004).

Fig. 4.33: The forest valley with dense canopies of *L. coniferum* at the top and dry Neutral Sand Fynbos on the opposite slope (10/2004).

Fig. 4.34: Schematic profile across the *Protea repens* Proteoid Fynbos. Designed by the author.

Fig. 4.35: Plant collection from the *P. repens* Proteoid Fynbos - from left to right and from top to bottom: *Willdenowia teres*, *P. repens*, *Cliffortia ilicifolia*, *Aspalathus salteri*, *Dipogon lignosus*, *Phyllica disticha*, *Diosma subulata* var. *subulata*.

Fig. 4.36: The Steynsbos Valley is largely covered in *P. repens* Proteoid Fynbos, disrupted by patches of Dune Asteraceus Fynbos and Limestone Fynbos (view from Swartkransberg, 11/2004).

Fig. 4.37: *P. repens* Proteoid Fynbos, Swartkransberg in the background (11/2004).

Fig. 4.38: Collection of the limestone fynbos Proteoid Fynbos - from left to right and from top to bottom: *Cullumia squarrosa*, *Indigofera brachystachya*, *Erica coccinea* var. (yellow), *Thamnochortus fraternus* and *Protea obtusifolia*.

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Fig. 4.40: Transition between *Protea obtusifolia* Proteoid Fynbos and *Erica coccinea* Ericoid Fynbos in the Steynsbos Valley (11/2004).

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Fig. 4.42: Plant collection from the Acid Sand Fynbos Complex - from left to right and from top to bottom: *Mimetes cucullatus*, *Leucadendron salignum*, *Leucadendron tinctum*, *Aulax umbellata* and *Penaea mucronata*.

Fig. 4.43: Acid Sand Proteoid Fynbos at the S slope of Swartkransberg (11/2004).

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Fig. 4.45: Schematic profile across the Acid Sand Proteoid Fynbos. Designed by the author.

Fig. 4.46: Schematic profile across an intermix between *Erica sessiliflora* Ericaceous Fynbos, Transitional Proteoid Fynbos and *Elegia thrysifera* Restioid Fynbos. Designed by the author.

Fig. 4.47: The carnivorous *Drosera capensis*, a common element of the damp slopes covered by *E. sessiliflora* Ericaceous Fynbos (10/2004).

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Fig. 4.49: The transition between Alkaline Sand Fynbos and Acid Sand Fynbos at the S slope of Swartkransberg (10/2004).

Fig. 4.50: *Elegia thrysifera* Restioid Fynbos on Tygerboom (11/2004).

## Discussion

Fig. 5.1: Fire cycle in the Acid Sand Fynbos of Grootbos, according to observation by the author and to Kruger (1979). Designed by the author.

Fig. 5.2: Transitional Fynbos during the immediate post-fire phase on the N slope of Witkransberg. In the foreground mature stands of Neutral Sand Proteoid Fynbos, the reddish color above the limit of standing dead of *L. coniferum* is caused by *Watsonia tenosiphon* (11/2004)

Fig. 5.3: *Watsonia stenosiphon* on the N slope of Witkransberg (10/2004).

Fig. 5.4: Three years old Transitional Proteoid Fynbos on Platrug, with young *Leucospermum patersonii* and mature *Mimetes cucullatus* (10/2004).

Fig. 5.5: Three years old Acid Sand Fynbos with *Aspalathus ciliaris*, *Helichrysum patulum* and a high cover of grasses. The large individuals of *Leucadendron coniferum* in the background have survived the fire of 2001 (11/2004).

Fig. 5.6: Limestone slope burned in 2001 with *Pseudopentameris macrantha* (left) and *Thesium strictum* (right, 11/2004).

Fig. 5.7: Forest elements in sheltered ravines and on rocky slopes on a S-facing slope in the Tygerboom Kloof (10/2004).

Fig. 5.8: Dense stands of *Acacia cyclops* in an area burned in 2001 (10/2004).

Fig. 5.9: *Leucadendron xanthoconus*, one of the reseeding Proteaceae of Grootbos Nature Reserve, achieving high cover in some patches of the Acid Sand Proteoid Fynbos (11/2004).

Fig. 5.10: Number of taxa in the different vegetation complexes of the reserve and floristic relationships (WL = Wetland, MSF = Milkwood Scrub Forest, AF = Afromontane Forest, AISF = Alkaline Sand Fynbos, AcSF = Acid Sand Fynbos. Designed by the author.

Fig. 5.11: Parallel patterns on Platrug, indicating former cultivation (11/2004).

## Tables

Tab. S.1: Summary of the vegetation units recognized in this study. The Forest biome is shaded green, the Wetland Biome blue and the Fynbos Biome red. The numbers in brackets added to the complex names are the average species numbers of the complexes on the 50 mts<sup>2</sup> level, the environmental data account for the average for each unit. The numbers close to the diagnostic species (column "criteria") are the pseudospecies levels of the TWINSPAN-classification for the extended dataset.

Tab. 2.1: Prediction of the species diversity of Grootbos Nature Reserve according to different area-species models (A = area in km<sup>2</sup>, n = sample size, S = number of species). Data compiled from Cowling (1997c).

Tab. 2.2: The quantitatively most important families of the Cape Floristic Region and of Grootbos Nature Reserve (a = number of species, b1 = number of endemic species, b2 = percentage of endemic species, c = ranking according to the number of species, d = number of genera, e = number of endemic genera, f = ranking according to number of genera, g = percentage of the species within each family compared with the total species number). There are no endemic genera at Grootbos, the only endemic species is *Erica magnisyrae*. Data compiled from the Grootbos species list (App. 1.1) and Goldblatt & Manning (2000).

Tab. 3.1: Environmental variables recorded for the relevés. a = core dataset (sampling 1997), b = core dataset (sampling 2004), c = extended dataset (2004, with soil sampling), d = extended dataset (2004,

without soil sampling). Content partly reproduced from Privett et al. (unpublished).

Tab. 3.2a and b: Growth forms and leaf forms assigned to the species of Grootbos Nature Reserve.

Tab. 4.1: Correct predictions in per cent for different levels of vegetation units and different combinations of topographic variables (adv = advanced variables, bas = basic variables, alt = elevation and advanced variables, all = all variables).