

Spatial Patterning and Demography in Strandveld Succulent Karoo:
Implications for Biodiversity Management.

by
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Thesis presented in fulfilment of the requirements for the degree of Master of Science at the
University of Stellenbosch



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December 2004

Declaration

I, the undersigned, hereby declare that the work contained in this thesis, unless otherwise specified, is my own original work and that I have not previously in its entirety or in part submitted it at any university for a degree.

Summary

This thesis focuses on the effects of vegetation resting on biodiversity and community dynamics at Rocherpan Nature Reserve (32° 36'S, 18° 18'E) in the semi-arid coastal strip of the Succulent Karoo known as Strandveld. As a whole, the Succulent Karoo has an extraordinary high level of phyto diversity with high levels of endemism. This is particularly true for succulent shrubs belonging to the groups Mesembryanthemaceae, Crassulaceae and Asteraceae.

The thesis begins with an investigation into effects that vegetation resting has on plant diversity. The aim was to determine if resting affected biodiversity levels and if so, which plant groups are affected and why. Through a numerical approach, it was determined that with resting overall species richness remained the same. However, different plant life forms responded to resting differently. With increased resting, abundance of succulent shrubs decreased, while richness of annuals increased.

The second aspect under investigation was to determine how resting the vegetation affected community dynamics. The aim was to understand how vegetation structure and interspecific associations changed with resting and to apply these findings to known community models. Through an autocorrelation approach, it was found that horizontal patterning of long-lived woody species, that formed distinctive vegetation clumps, did not change with resting, while differences were found in woody matrix species and succulent species. These changes in structure were investigated further through a study on the demography of specific species. Demography of woody species associated with vegetation clumps did not change with vegetation resting, while significant changes were observed for woody matrix species and succulent species. In longer rested vegetation, woody matrix species showed a greater range in size class distribution (i.e. had both very large and smaller plants) with the tendency towards larger plant sizes. Succulents on the other hand, had a smaller range in size class distribution with a tendency towards larger plants. For all species investigated there were low seedlings counts. It was concluded that succulent shrub populations were 'mature' and continued resting could result in local extinction of some species due to the lack of regeneration. The overall lack of seedlings was attributed to a saturated establishment environment. Implications for conservation management were discussed.

Opsomming

Hierdie tesis fokus op die gevolge van plantegroei op biodiversiteit en gemeenskapsdinamika by die Rocherpan Natuurreservaat (32° 36'S, 18° 18"O) in die halfdor kusstrook van die Sukkulente Karoo, bekend as die Sandveld. In die geheel gesien het die Sukkulente Karoo 'n buitengewone hoë vlak plantdiversiteit met hoë vlakke endemie. Dit is veral waar vir sukkulente struik wat tot die groepe Mesembryanthemaceae, Crassulaceae en Asteraceae behoort.

Hierdie tesis ondersoek eerstens die gevolge wat plantegroei op plantdiversiteit het. Die doel was om te bepaal of die biodiversiteitsvlakke beïnvloed het en indien wel, watter plantegroeie en waarom. Deur middel van 'n numeriese benadering is bepaal dat die algehele diversiteit, numeries gesproke, met plantegroei dieselfde gebly het. Verskillende plantlewensvorme het egter verskillend gereageer. Met toenemende rus het die diversiteit van sukkulente struik afgeneem, terwyl die diversiteit van jaarplante verhoog het.

Die tweede aspek wat ondersoek is, was om te bepaal hoe die plantegroei die dinamika van die omgewingsgemeenskap beïnvloed het. Die doel was om te verstaan hoe die struktuur van die plantegroei en die interspesifieke assosiasies verander het met rus en om dan hierdie bevindinge toe te pas op bekende gemeenskapsmodelle. Deur middel van 'n outokorrelasie-benadering is gevind dat die horisontale patrone van meerjarige houtagtige spesies wat in duidelik-uitkenbare plantegroeigroeiperings voorkom, nie met rus verander het nie. Veranderinge is egter wel in die houtagtige matriksspesies en die sukkulente spesies waargeneem. Hierdie veranderinge in struktuur is verder ondersoek deur 'n studie te maak van die demografie van spesifieke spesies. Daar is gevind dat die demografie van houtagtige spesies geassosieer met plantegroeigroeiperings nie met plantegroei verander het nie, maar beduidende veranderinge is waargeneem in die geval van houtagtige matriksspesies en sukkulente spesies. By plantegroei wat langer gerus het, het die houtagtige matriksspesies 'n wyer verspreiding in klasgroottes vertoon (d.i. daar was baie groot plante én kleiner plante) met 'n gemiddelde afname in plantgrootte. Sukkulente, aan die ander kant, het 'n kleiner verspreiding in klasgroottes vertoon met 'n neiging tot groter plante. Vir al die spesies wat ondersoek is, was daar lae saailingtellings. As gevolg van die "volwassenheid" van die populasies van sukkulente struik, sou voortdurende rus, weens die gebrek aan regenerasie,

kon lei tot die plaaslike uitwissing van sommige spesies. Die algemene gebrek aan saailinge is toegeskryf aan die versadigde vestigingsomgewing. Die implikasies vir natuurbewaringsbestuur word bespreek.

Acknowledgements

At the end of the day this thesis would not have been possible without the collaborative efforts of several people and organisations. On the top of list are my co-supervisors, Dr. Karen Esler and Prof. Sue Milton. Their experience, guidance, motivation and love of the topic have been exceptional, not to mention constructive comments to improve all chapters.

A special thank you to Annelise le Roux (Western Cape Nature Conservation Board), who managed to do the impossible in identifying plant specimens collected from field trips. Also to WCNCB who made accommodation available for the duration of the study.

To Penelope Furness, who sorted out logistics for field trips as well as aided with field work

Lastly, but not least, this research was funded by BIOTA (Biodiversity Monitoring Transect in Africa) under sub project S06.

Contents

| | |
|--|-----------|
| Summary | iii |
| Opsomming | iv |
| Acknowledgements..... | vi |
| Chapter 1: General Introduction and Study Site Description..... | 1 |
| 1.1 Introduction | 1 |
| 1.2 Thesis Overview | 2 |
| 1.2.1 Thesis Structure | 2 |
| 1.2.2 Thesis Rationale | 3 |
| 1.2.2.1 Known Community Dynamics | 3 |
| 1.2.2.2 The Importance of Biodiversity..... | 4 |
| 1.2.2.3 Key Conservation Management Question | 5 |
| 1.2.3 Research Objectives | 6 |
| 1.3 Study Area: Rocherpan Nature Reserve | 6 |
| 1.3.1 Location | 6 |
| 1.3.2 Vegetation..... | 6 |
| 1.3.3 Land Use History..... | 8 |
| 1.3.4 Climate | 8 |
| 1.3.5 Topography, Geomorphology and Soils..... | 9 |
| 1.4 Overall Approach and Methods..... | 9 |
| 1.5 References | 12 |
| Chapter 2: Quantifying the Differences in Plant Diversity Between Medium Rested and Long Rested Strandveld Succulent Karoo | 17 |
| 2.1 Abstract..... | 17 |
| 2.2 Introduction | 17 |
| 2.3 Materials and Methods | 19 |
| 2.3.1 Study Area | 19 |
| 2.3.2 Plot Layout | 20 |
| 2.3.3 Diversity Indices..... | 21 |
| 2.3.4 Abundance Model | 22 |
| 2.3.5 Life Form Analysis | 22 |
| 2.4. Results | 23 |
| 2.4.1 Richness, Dominance and Evenness | 23 |
| 2.4.2 Life Form Analysis | 25 |
| 2.5 Discussion..... | 26 |
| 2.6 References | 29 |
| Chapter 3: Quantifying the Differences in Spatial Patterning and Species Association Between Medium Rested and Long Rested Strandveld Succulent Karoo | 33 |
| 3.1 Abstract..... | 33 |
| 3.2 Introduction | 33 |
| 3.3 Materials and Methods | 35 |

| | | |
|-------|-------------------------------------|----|
| 3.3.1 | Study Area | 35 |
| 3.3.2 | Sample Design..... | 36 |
| 3.3.3 | Horizontal Pattern Analysis..... | 36 |
| 3.3.4 | Interspecific Association | 37 |
| 3.3.5 | Clump, Matrix and Gap Analysis..... | 38 |
| 3.4 | Results | 38 |
| 3.4.1 | Horizontal Pattern Analysis..... | 38 |
| 3.4.2 | Interspecific Association | 43 |
| 3.4.3 | Clump, Matrix and Gap Analysis..... | 45 |
| 3.5 | Discussion..... | 49 |
| 3.6 | References | 52 |

Chapter 4: Quantifying the Difference in Shrub Demography Between Medium Rested and Long Rested Strandveld Succulent Karoo and its Implications Conservation Management.....55

| | | |
|-------|--------------------------------------|----|
| 4.1 | Abstract..... | 55 |
| 4.2 | Introduction | 55 |
| 4.3 | Materials and Methods | 56 |
| 4.3.1 | Study Area | 56 |
| 4.3.2 | Species Selection & Plot layout..... | 57 |
| 4.4. | Results | 58 |
| 4.5 | Discussion..... | 62 |
| 4.6 | References | 64 |

Chapter 5: General Conclusions and Management Recommendations67

| | | |
|-----|------------------|----|
| 5.1 | References | 69 |
|-----|------------------|----|

Appendix 1:

Graphical representation of sub-transects in Medium Rested and Long rested sites in Strandveld Succulent Karoo.

Appendix 2:

Plant species list for Medium Rested Vegetation (MRV) and Long Rested Vegetation (LRV) with the total cover measured on each transect and growth form used in analysis.

CHAPTER 1: GENERAL INTRODUCTION AND STUDY SITE DESCRIPTION

1.1 Introduction

The Succulent Karoo is an astonishing winter rainfall desert. In an area covering 82 500 km² at least 2 750 vascular plants occur, of which approximately 50% are endemic (Low & Rebelo 1996, Cowling et al. 1999a). Comparatively, this is four times the number of species for the equivalent sized areas in North American winter rainfall deserts (Cowling et al. 1999b). These exceptional levels of biodiversity pose several challenges to researchers, conservation managers and livestock farmers. For conservation managers, species will tend to be lost from areas under their jurisdiction despite the best conservation efforts. This is due to the often highly fragmented nature of conservation areas, inappropriate land use adjacent to reserves and lack of information for management decisions (Walker 1992, Main 1992). It is imperative that conservation managers understand the driving forces of community dynamics in order to make informed decisions when altering or maintaining community dynamics for biodiversity purposes. For the researcher, the challenge is to identify and describe the relative importance of the 'key dynamics' that maintain biodiversity and to turn these into appropriate biodiversity conservation strategies for the short, medium and long term. Currently, overgrazing, particularly by small stock on communally managed lands is considered to pose a substantial threat to the biodiversity of the Succulent Karoo (Cowling & Pierce 1999). Studies into the effects of varying grazing intensities on the Succulent Karoo vegetation have focused primarily on quantifying the differences in biodiversity and population dynamics in actively grazed areas (Todd & Hoffman 1999, Carrick 2001, Riginos & Hoffman 2003). Such studies have highlighted that although there are general decreases in shrub canopy cover, overall species richness generally remains unchanged because the loss of certain shrub species is compensated for by an increase in species richness of pioneer species for example, *Galenia africana* (Aizoaceae) and annuals (Carrick 2001).

The long term changes in plant diversity and population dynamics in vegetation rested from grazing have been understudied in the Succulent Karoo. At Rocherpan Nature Reserve, two adjoining areas of the reserve have been rested from domestic grazing for 34 years and 11 years. This provided an opportunity to investigate the post grazing dynamics in the

Succulent Strandveld – the coastal vegetation of the Succulent Karoo. The primary aim of this thesis is two-fold. Firstly, to determine the relative differences in floristic diversity, population structure and community structure between the two areas rested for different lengths of time and secondly, to relate known community models to the observed community patterns to determine which model appropriately describes the community dynamics of the Strandveld Succulent Karoo.

1.2 Thesis Overview

1.2.1 Thesis Structure

This thesis is divided into 5 chapters. This first is a general introduction that includes the motivation for the thesis, research objectives and a study area description. The three data chapters (Chapters 2, 3 & 4) are written as stand-alone research papers, hence some repetition in terms of study area description and methods. The introduction highlights the concern of the conservation managers that a portion of the reserve tended to be dominated by *Lebeckia multiflora* (Fabaceae) as a result of post grazing resting. Chapter 2 quantifies the difference in plant diversity between Succulent Strandveld rested from domestic stock grazing for 34 years compared to vegetation rested for 11 years. A quantitative approach was employed using the comparison of well-known diversity indices that describe aspects of diversity. In Chapter 3, the difference in spatial patterning and species associations of dominant shrubs is presented. Here the focus is on quantifying the relative differences in vegetation pattern and species association between the two sites that have been rested from grazing for different periods. The aim was to determine if the proposed community models of Yeaton & Esler (1990) and Eccles (2000) were appropriate to this system (community models are summarised below). In chapter 4, the original concern about woody species dominance is addressed through a study of the demography of key shrub species. In the concluding chapter, (Chapter 5) the results from this study are contextualised within a management environment with the aim of addressing how to optimise species diversity at the study site, Rocherpan Nature Reserve.

1.2.2 Thesis Rationale

1.2.2.1 Known Community Dynamics

Contemporary understanding of community dynamics of the Succulent Karoo originates from two general models. The first is a deterministic cyclic succession model that is driven by ‘nurse plant’ interactions (Yeaton & Esler 1990). This model was developed at the Tierberg Karoo Research Centre located in the south-eastern region of the Succulent Karoo (Low and Rebelo 1996). The area receives an average annual rainfall of 170 mm with March to May (autumn months) being the wettest. The average maximum temperature in January (the hottest month) is about 35°C.

The key aspects of the deterministic cyclic succession model are that a pioneer guild of succulent shrubs comprised of *Brownanthus ciliatus* and *Ruschia spinosa* (Mesembryanthemaceae) colonise open areas. These succulents then act as facilitators, through the provision of shade and protection from browsing, for the establishment of a woody shrub guild comprising of *Pteronia pallens* and *P. empetrifolia* (Asteraceae). The woody shrubs then replace the succulents through competition and persist until they die due to drought, browsing or senescence. The loss of the woody shrubs through animal activities (digging and burrowing), drought or senescence, then creates openings that allows for the establishment of the succulent shrubs.

The second model follows a non-deterministic (stochastic) approach (Cowling et al. 1999a, Esler et al. 1999, Eccles 2000). This model was developed at the Groen River Research Area located in the Succulent Strandveld, the western coastal margin of the Succulent Karoo. The area receives an average annual rainfall of around 140 mm with June to August (winter months) being the wettest. Dew and fog events contribute additional moisture (Desmet & Cowling 1999). The average maximum temperature in January (the hottest month) is about 20°C.

In this model, the importance of competition and environmental heterogeneity are played down. Key aspects of this model are that both the succulent and woody shrubs are short lived (Jürgens et al. 1999) which results in regular gap formation. This, coupled with a variety of seed dispersal mechanisms (wind and water) and weak competitive interactions,

produces randomly assembled vegetation communities. Dominant plant species within these communities include *Pteronia onobromoides* (Asteraceae), *Zygophyllum morgsana* (Zygophyllaceae), *Stoeberia utilis* (Mesembryanthemaceae) and *Lebeckia multiflora* (Fabaceae).

In addition to these two general Succulent Karoo based models, the dynamics of dune thicket formation needs to be considered. Many species of the Succulent Strandveld are of subtropical origin with wide distributional ranges (Cowling et al. 1997) and include amongst other species *Rhus spp.* (Anacardiaceae), *Maytenus spp.* (Celastraceae), *Euclea spp.* (Ebenaceae) and *Olea spp.* (Oleaceae). Unlike sun establishing succulents, these species require shade for establishment, tend to be very long lived resprouters, are strong competitors and are dependant on birds for seed dispersal. Where these species occur in clumped thickets, a distinctive plant assemblage is supported (Dean et al. 1999).

1.2.2.2 The Importance of Biodiversity

The maintenance of optimal biodiversity is a key function of conservation managers as plant and animal species are currently being lost at rates 100 times higher than expected (Wilson 1988). Arguments put forward to justify the stemming of this ‘sixth extinction’ encompass two broad perceptions.

The first argument is based on ethical grounds and is the foundation for “Deep Ecology” (Nations 1988). It questions if humans have the right to destroy species and provokes that all species have the right to exist without human interference. This philosophy stems from many traditional cultures that have coexisted with local fauna and flora through mutual respect for them (Primack 1998). The claim that biodiversity has intrinsic value has been successful in the conservation of certain ‘high-profile’ species but has had little impact on the global scale.

In the context of ecosystem complexity and stability, the role of diversity is not clear (Schwartz et al. 2000). During the 1950’s and 1960’s it was hypothesised that ecosystems that harboured more species were more stable than species-poor ecosystems (e.g. MacArthur 1955). The reasoning followed that the more species diverse the ecosystem was,

the greater the number of alternate energy pathways that existed and that these alternate pathways would aid ecosystem resilience to disturbance and allow recovery back to a normal state (Pimm 1993). This is aligned with Ehrlich and Ehrlich (1981) who introduced the ‘rivet hypothesis’ where each species contributes a small but significant proportion to ecosystem integrity. However with the realisation of ‘keystone’ (Paine 1966) or ‘fusewire’ (Scarff & Bradley 2002) species, some authors advocate that loss of certain species within ecosystems may be more important than the loss of others, since their absence results in dramatic changes to the ecosystem, including the loss of several other species. Bond (1993) highlighted the need to identify and conserve ‘keystone species’ within an ecosystem although the identification of these species may be problematic.

Other authors (Walker 1992, Grime 1998, Schwartz et al. 2000, Fridley 2001, Loreau et al. 2001, Duffy 2002) question the degree to which species redundancy occurs within an ecosystem with the general conclusion that the number of species required to maintain biochemical pathways will be lower than that currently observed (Walker 1992, Lawton & Brown 1993, Woodward 1993). However, one area where there is support for the maintenance of the full complement of diversity is that of long-term ecosystem adaptability (Walker 1992, Grime 1998). Here a precautionary argument is followed where the redundant or rare species of the present times may important species in the future. Another is that some of the most species diverse ecosystems have high functional redundancy e.g. tropical forests (Hubbell & Foster 1986), Fynbos (Cowling et al. 1992) and Succulent Karoo (Cowling et al. 1994). This challenges the concept of the classic ‘niche-assembled’ community where community structure is determined by segregation along a structural axis (Cody 1991). Hubbell & Foster (1986) conclude that “species in these systems coexist not in spite of, but because of being functional equivalent generalists”. This allows for the development of mutualisms and hence ecosystem process maintenance (Boucher 1982, Cowling et al. 1999a).

1.2.2.3 Key Conservation Management Question

Management decisions to change or alter a system for the benefit of diversity need to be based on contemporary understanding ecosystem processes, as well as have the availability of resources to successfully manipulate these processes in field. Such a need for current

information was requested by the managers of Rocherpan Nature Reserve (detailed description follows below). At Rocherpan Nature Reserve, the key management concern was the perceived decline in plant species diversity in a portion of the reserve (Wessels & Hanekom 1997). The area under question was incorporated into the reserve in 1990 and had previously been utilised for livestock grazing. The perception was that area tended to be dominated by Leguminous shrubs, namely *Lebekia multiflora* and it was thought that these 'fast-growing' shrubs had become dominant, at the expense of other species, during post grazing resting. This perception arose after visual comparison with an adjacent area that had been rested from domestic grazing for 34 years. Although no management strategy had been engaged to enhance plant diversity in the area that had been rested for 11 years, it was felt by reserve management that recovery was not 'adequate' and a variety of rejuvenation techniques needed to be considered.

1.2.3 Research Objectives

The objectives of the research were three-fold:

1. To determine if the perceived difference between the veld rested for 11 years and that rested for 34 years was measurable and significant;
2. To determine the natural vegetation processes maintaining biodiversity
3. To provide management with guidelines on appropriate methods for biodiversity conservation.

1.3 Study Area: Rocherpan Nature Reserve

1.3.1 Location

Rocherpan Nature Reserve is located approximately 180 km north of Cape Town and 35 km north of the Berg River (32° 36'S, 18° 18'E) on the west coast of South Africa. The reserve is bounded by farmlands to the north, east and south and the Atlantic Ocean in the west (Figure 1.1). The present size of the reserve covers some 914 hectares.

1.3.2 Vegetation

Rocherpan Nature Reserve occurs near the south-western boundary of the Succulent Karoo Biome and falls within the Strandveld Succulent Karoo veld type (Low & Rebelo 1996).

The formal approximations of the coverage of Strandveld Succulent Karoo (referred to as Strandveld) extend from the Berg River Mouth in the south to Alexander Bay in the north covering some 4 000 km² (Low & Rebelo 1996; Cowling et al. 1999a). Overall, Strandveld is poorly conserved, with only 0.4% falling under conservation management and it is the least conserved veld type of the Succulent Karoo Biome (Low & Rebelo 1996). The Succulent Strandveld is dominated by scattered low to medium shrubs including the leaf succulent Mesembryanthemaceae (especially *Ruschia* spp. and *Stoebaria utilis*) and Euphorbiaceae as well as evergreen and deciduous shrubs including *Euclea* (Ebenaceae), *Rhus* (Anacardiaceae), *Chrysanthemoides*, *Pteronia*, *Eriocephalus*, *Othonna* (Asteraceae) and *Lebeckia* (Fabaceae). Geophytes are well represented and include *Albuca*, *Lachenalia* (Hyacinthaceae), *Babiana* and *Gladiolus* (Iridaceae). Grasses occur in scattered patches and include *Stipagrostis*, *Cladoraphis* and *Odyssea*. Restionaceae species (*Willdenowia*) become more dominant where Strandveld is associated with Sand Plain Fynbos.

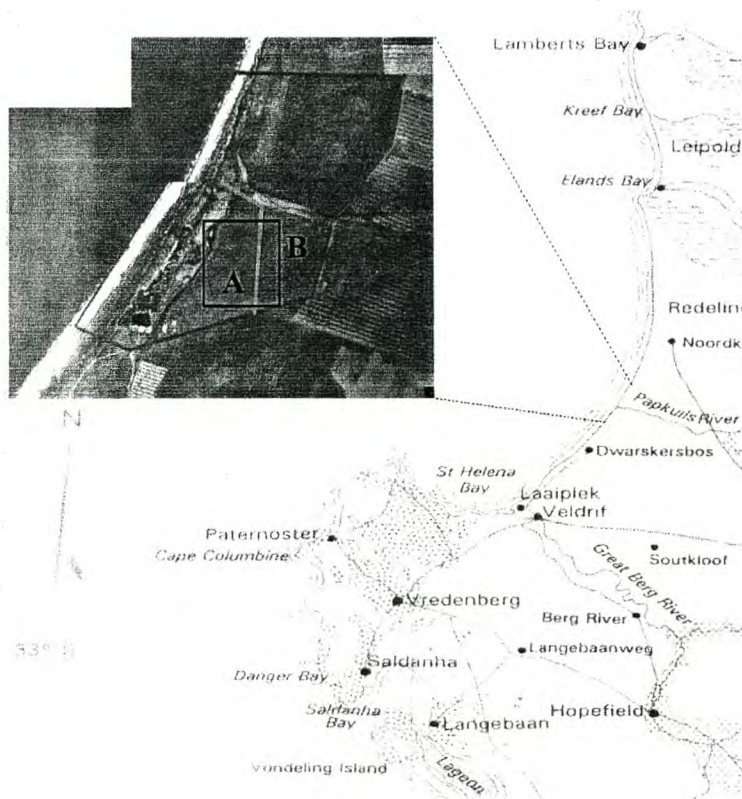


Figure 1.1 Location of Rocherpan Nature Reserve on the west coast of South Africa, with the two study sites 'A' in the 34 year rested vegetation and 'B' in the 11 year rested vegetation. The square that transverses the two sites denotes the BIOTA Grid. Aerial pictures courtesy of Western Cape Nature Conservation Board and the west coast back drop redrawn from Manning & Goldblatt (1996)

Rocherpan has approximately 20% of the same species found in studies in the Port Nolloth to Alexander Bay area (Desmet 1996), some 300 km north and approximately 40% similarity with dominant, woody species found in the Groen River area (Eccles 2000) some 150 km north. The main differences in plant species composition between Rocherpan and the other areas further north is the absence further north of species with a paleotropical origin such as *Euclea spp.* (Ebenaceae) and *Rhus spp.* (Anacardiaceae), as well as the absence of fynbos elements such as *Willdenowia spp.* (Restionaceae).

1.3.3 Land Use History

Prior to the establishment of the reserve in 1967, the area was used for light goat, sheep and cattle grazing since circa 1840 (Wessels & Hanekom 1997). The first portion of the reserve (394 ha) was proclaimed in 1967 as a nature reserve with a second portion (520 ha) proclaimed in 1990. Currently Western Cape Nature Conservation Board manages the reserve as a 'natural recovery' system.

1.3.4 Climate

The reserve is located within the winter-rainfall region of southern Africa. The area receives an average annual rainfall of 230 mm with the wettest seasons being June, July and August. As with the rest of the Strandveld Succulent Karoo, thick coastal fog contributes significantly to total precipitation (Desmet & Cowling 1999). The average annual rainfall for Rocherpan is 260 mm and is on average 100 mm more than that reported in studies in the same vegetation type further north (Desmet 1996, Eccles et al. 1999), indicating a strong north-south precipitation gradient along the coast. Frost occurs on average 10 days a year. The dominant wind direction is southerly to southeasterly in summer and the rain bears northwesterly in winter. Hot, dry berg winds can occur throughout the year but are most common in mid to late summer. Temperatures in the area are moderated proximity to the Atlantic Ocean but maximum temperatures over summer (November-February) can exceed 35°C (mean Max: January- February = 36.9°C).

1.3.5 Topography, Geomorphology and Soils

Aeolian deposited tertiary to residual sands (Wessels & Hanekom 1997) are characteristic of both the 34 and 11 year rested vegetation (hereafter referred to as Long Rested Vegetation – LRV and Medium Rested Vegetation – MRV). For each site, seven 1 kg soil samples were collected from the 0-10 cm soil layer and analysed for texture, pH, resistance, macroelements (sodium, calcium, magnesium, silica, phosphorus and nitrogen) and trace elements (boron, copper, manganese and zinc). All soil analyses were conducted by BEM-Lab Analytical Laboratories, Somerset-West, South Africa (methods following Sparks et al., 1996). Soil samples were saturated with de-ionised water and electrical resistance measured in a standard USDA soil cup, and their pH read from a KCl-soil mixture (10 g soil and 25 ml solution with deionized water with 1 M KCl). Samples for soil moisture were collected from both sites at 10 cm below soil surface in both in the wettest season (July) and the driest (February) for comparison. Soil depth (depth to an impenetrable subsoil horizon) was also recorded by means of a steal dropper.

Soils tend to be slightly reddish to white and well sorted (Figure 1.2). Soils were characterised by a shallow A horizon and a deep B horizon (> 2 meters). In the region an impenetrable calcrete layer 50 cm to 1 m below the soil surface is often found, but where soil depth was tested in this study, the calcrete ‘dorbank’ was not found within the tested depth of 2 meters. Soil chemistry did not differ between the two sites. Soils were composed of mainly calcium (60%), silica (20%) and magnesium (15%) with organic carbon being very low at *circa* 1% (Figure 1.3). Soil moisture in the wettest season was also found to be very low and ranged between <0.2% to 3%. During the driest month soil moisture for all samples was <0.1%. Overall, the only differences in soil composition between the two sites was that of pH, where the LRV had slightly lower pH levels of 5.0 when compared to the MRV which had an average pH of 5.5 (Figure 1.4).

1.4 Overall Approach and Methods

As part of the Biodiversity Monitoring Transect Analysis in Africa (BIOTA) program, a fixed 1 km by 1 km grid was positioned at Rocherpan and formed the framework within which all sampling occurred (Figure 1.1). The grid covered both the older portion of the reserve that was established in 1967 and has been rested from grazing for 34 years and the

more recent acquisition in 1990, which has been rested from grazing for 11 years. In terms of naming convention, sampling sites in the vegetation rested for 34 years will be called 'Long Rested Vegetation' (LRV), while sample sites in the vegetation rested for 11 years will be called 'Medium Rested Vegetation' (MRV).

Two 1000 meter line transects, one in the LRV and one in the MRV, were placed within the BIOTA grid, running in a north-south direction, 100 meters apart. Each transect consisted of 20 sub-transects measuring 50 meters in length and coincided with the 50 m x 50 m plots within the BIOTA grid. For each sub-transect a tape measure was laid out over the vegetation, and intercept cover as well as plant height was recorded. All sub-transects were placed in a continuous fashion so that a single continuous transect could be reconstructed for analysis. The beginning of each sub-transect was marked with 40 cm steel peg to allow for relocation.

It is acknowledged that the sample design suffers from pseudo-replication. However this was unavoidable. Due to disturbed land surrounding Rocherpan Nature Reserve, it was not possible to replicate across browsing gradients with similar histories and resting periods. Also, as the focus for conservation management was quantifying the differences between the two rested sites within the reserve, it was decided that by using the proposed methods, this would be achieved. Further, Oksanen (2001) put forward the argument that unreplicated tests of 'strong and critical predictions' would be more instructive than well-replicated tests of weakly defined predictions. Following this thinking, each chapter in this thesis has specific predictions that are investigated.

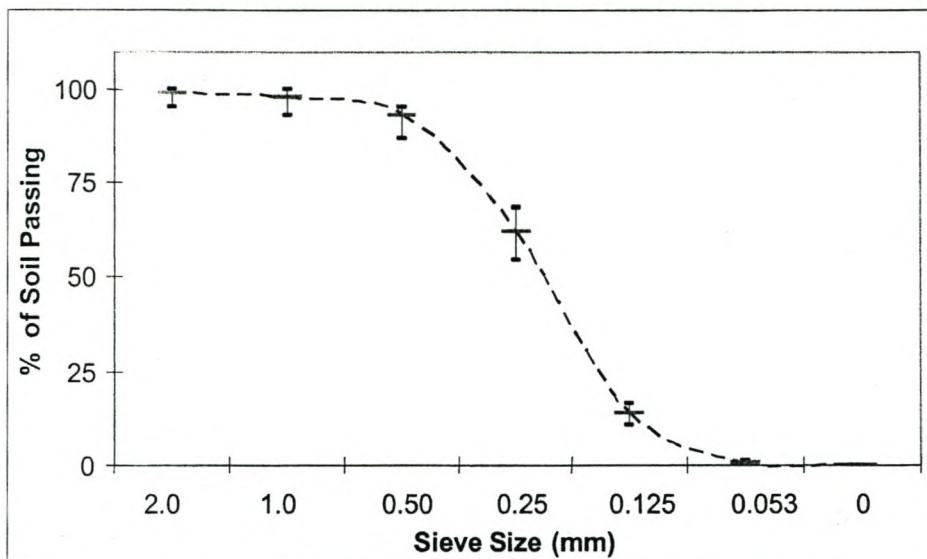


Figure 1.2. The percentage of soil passing through standard sieves show that soils were composed of uniform sand with 80% of soil particles between 0.5 mm and 0.1 mm in size. Error bars show the range for all soils samples while the broken line depicts the mean. (n= 14).

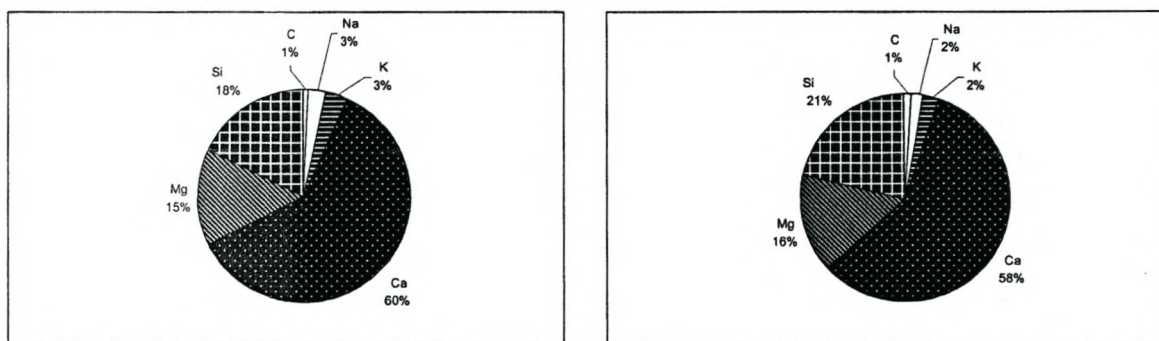


Figure 1.3. Elemental composition of soils in the MRV (A) and LRV (B) were very similar with the majority of the soils being composed of calcium (60%) silica (20%) and magnesium (15%), while organic carbon was low at 1%.

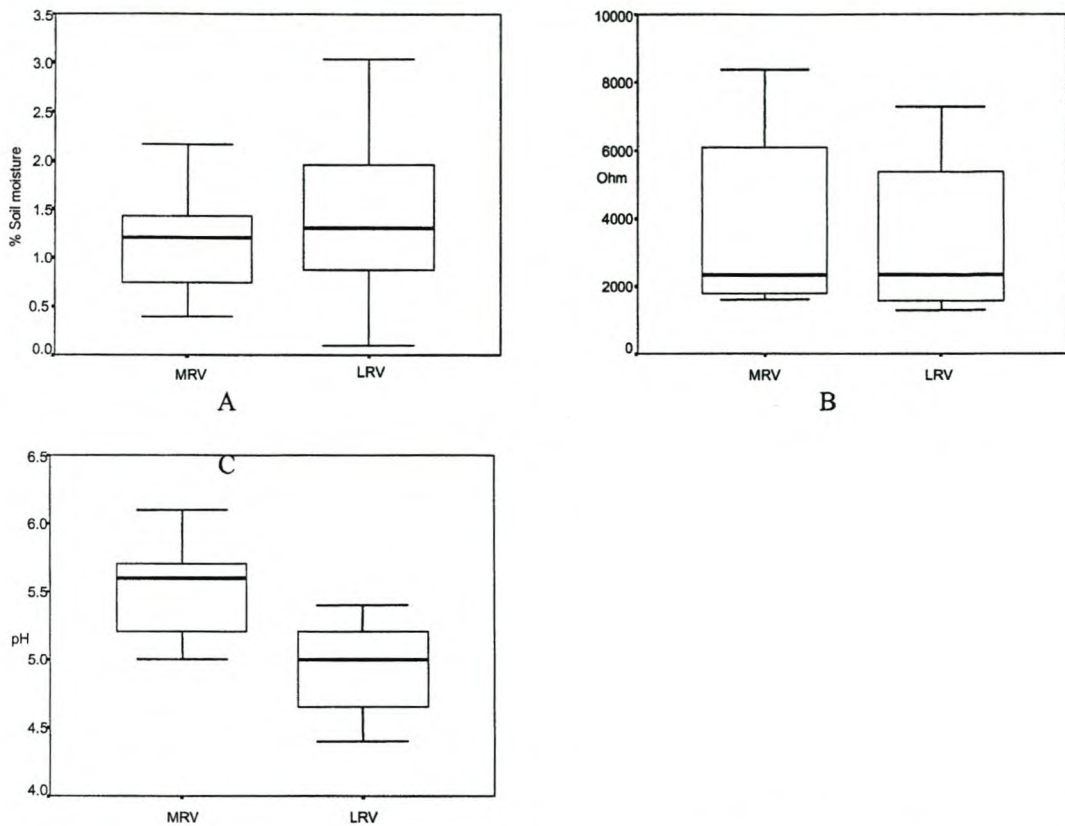


Figure 1.4. Box and whisker plots showing similarity of mean soil moisture and resistance (A & B), while overall pH (C) was lower in the LRV with an average of 5.0

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CHAPTER 2: QUANTIFYING THE DIFFERENCES IN PLANT DIVERSITY BETWEEN MEDIUM RESTED AND LONG RESTED STRANDVELD SUCCULENT KAROO

2.1 Abstract

Species diversity was compared across an historic fence line separating vegetation that had been rested from grazing for 34 years and vegetation that had been rested from grazing for 11 years in the Strandveld Succulent Karoo. Diversity, as measured by the Shannon index, was significantly different between the two sites with higher diversity being recorded in the area rested for 34 years. Several other diversity indices supported this observation. Life form analysis revealed that the diversity difference could be attributed to changes in species richness of annuals and lower abundance of Non Dwarf Leaf Succulents in the area, rested for 34 years. This could be interpreted as the Non Dwarf Leaf Succulents becoming senescent under condition of no large scale grazing disturbance. These results are discussed further in terms of biodiversity management in the area.

2.2 Introduction

One of the unique aspects of the succulent-dominated communities in the Succulent Karoo, South Africa, is the prevalence of relatively short-lived shrubs (Cowling et al. 1999, Eccles et al. 1999, Esler et al. 1999, Jürgens et al. 1999, Eccles 2000), which results in 'rapid' population turnover, local gap creation and weak competitive interactions. Coupled with regular (Jürgens et al. 1999) and random (Esler et al. 1999) seedling recruitment, this creates general neighbourhood uncertainty. The mutualistic and general positive interactions result in randomly assembled vegetation clumps that are characteristic of these systems, particularly in the Strandveld Succulent Karoo (Eccles et al. 1999, Eccles 2000). These processes occur within a relatively homogenous abiotic environment and it has been proposed (Eccles et al. 1999, Jürgens et al. 1999, Eccles 2000) that the extraordinary levels of plant diversity in the region are largely due to this unique set of abiotic and biotic conditions (Cowling et al. 1999).

These community processes align well with two hypothesis on the maintenance of species diversity at the local scale. The first is the dynamic equilibrium model (Huston 1979, 1994) which stems from the general intermediate disturbance hypothesis. Of relevance to the Succulent Karoo is that this model predicts that local community diversity will be highest if

the intensity of disturbance is low and this is mirrored by a low rate of competitive displacement. The second is Hubbell's (2001) description of 'dispersal assembled' communities where the expected abundance of a species depends only on the local community size and the abundance of the species in the meta-community and that recruitment into the local community is essentially a random process brought about by differing dispersal and life-history traits (Tilman 1994). Thus the processes of local immigration into the community from the meta-community and local extinction largely determine local diversity. Thus when investigating changes in diversity under different management regimes, it is helpful to attempt to identify the processes that are responsible for the change.

A key management issue at Rocherpan Nature Reserve was the perceived decline in plant diversity in a portion of the reserve (Wessels & Hanekom 1997). The area under question was 520 ha of land that had been incorporated into the reserve in 1990 and had previously been utilised for domestic livestock grazing since *circa* 1840. The area tended to be dominated by Leguminous shrubs, namely *Lebeckia multiflora* and it was thought that these 'fast-growing' shrubs had become dominant, at the expense of other species, during post grazing resting. This perception was based on visual comparisons with an adjacent area (394 ha) within the reserve, that had been incorporated in 1967 and had been used for domestic grazing since *circa* 1840. Although no management strategy to enhance plant diversity in the area that had been rested for 11 years had been engaged, it was felt by reserve management that recovery was not 'adequate' and a variety of rejuvenation techniques needed to be considered.

The first step to address concerns of management was to quantify the difference in plant species diversity between the vegetation that had rested for a long period, 34 years (referred to in the text as Long Rested Vegetation – LRV) and the vegetation that had rested for medium period, 11 years (Medium Rested Vegetation – MRV). Here a numerical approach was adopted where a range of related diversity indices (Hill 1973) were calculated. Several ecologists (Hurlbert 1971, Hill 1973, Pielou 1975, Connor & McCoy 1979, Magurran 1988, Tokeshi 1993) highlight concern with the derivation of a single numerical relationship when trying to characterise the complexities of diversity from community samples. The reason for this concern (as reviewed by Tokeshi 1993) has been two fold. First, there is a general lack of understanding of how species abundance and diversity models are affected by inherent sampling problems at differing spatial scales. Second, is the need to relate the numerical findings to the possible mechanistic processes that may be involved.

Specific predictions on how diversity should change in the context of proposed community processes can be proposed (models reviewed in Chapter 1 and see Yeaton and Esler 1990, Cowling et al. 1997, Cowling et al. 1999, Dean et al. 1999, Esler et al. 1999, Eccles 2000). In the Yeaton and Esler model, pioneer succulent shrubs colonise open areas and are then replaced by woody shrubs through competition, while the model proposed by Cowling et al. (1999) plays down competition and emphasises random recruitment and mutual interactions. Where sub tropical thicket species (e.g. *Rhus spp.*, *Maytenus spp.* and *Euclea spp.*) are able to establish in the shade of vegetation clumps, these will result in the establishment of a distinctive vegetation association (Dean et al. 1999).

Prediction 1. The Long Rested Vegetation (LRV) should be more speciose than the Medium Rested Vegetation (MRV) and the rate at which species are accumulated along the transect should be higher. The reason is that the lack of dominance of *Lebeckia multiflora* in the LRV should allow the other species from the meta-community to occupy these sites thus accounting for higher diversity.

Prediction 2. In the MRV, the decrease in diversity should be accompanied by an increase in abundance of the most dominant species. This is because available sites should be occupied at random from the meta-community; the most abundant species would occupy relatively more of these sites.

Prediction 3. Overall dominance-diversity patterns should be different between the two vegetation successional stages, with the LRV having a more even distribution of species due to the lack of dominance (Whittaker 1965).

2.3 Materials and Methods

2.3.1 Study Area

Rocherpan Nature Reserve is located approximately 180 km north of Cape Town and 35 km north of the Berg River (32° 36'S, 18° 18'E) on the west coast of South Africa. The reserve is bounded by farmlands to the north, east and south and the Atlantic Ocean to the west (Figure 1.1). The present size of the reserve covers some 914 hectares. Rocherpan Nature Reserve occurs near the south-western boundary of the Succulent Karoo Biome (Low and Rebelo 1996) and falls within the Strandveld Succulent Karoo veld type (known as Strandveld). The

area receives predominantly winter rainfall with an estimated average annual of 260 mm. Fog and dew are a regular occurrence and may contribute significantly to the total precipitation received (Desmet & Cowling 1999). Temperatures in the area are moderated by the Atlantic Ocean but maximum temperatures over summer (November-February) can exceed 35°C (mean Max: January-February = 36.9°C). The coolest months are between June to August with mean minimum temperatures of 3.3°C recorded. Frost occurs on average 10 days per year. Wind plays an important role in the climate of the area. Hot, easterly berg winds can occur throughout the year and have very high evaporative demands (Desmet & Cowling 1999) while rain bearing northwesterly prevails during winter. Soils are aeolian deposited tertiary to residual sands (Wessels & Hanekom 1997) with a shallow A horizon and a deep (>2 m) B horizon.

The vegetation is dominated by scattered low to medium shrubs including the leaf succulent Mesembryanthemaceae (especially *Ruschia* spp. and *Stoebaria utilis*) and Euphorbiaceae as well as evergreen and deciduous shrubs including *Euclea* (Ebenaceae), *Rhus* (Anacardiaceae), *Chrysanthemoides*, *Pteronia*, *Erioccephalus*, *Othonna* (Asteraceae) and *Lebeckia* (Fabaceae). Geophytes are well represented and include *Albuca*, *Lachenalia* (Hyacinthaceae) *Babiana* and *Gladiolus* (Iridaceae). Grasses occur in scattered patches and include *Stipagrostis*, *Cladoraphis* and *Odyssea*. Restionaceae species (*Willdenowia*) become more dominant where Succulent Strandveld is associated with Sand Plain Fynbos.

2.3.2 Plot layout

Two line transects, one in the LRV and one in the MRV, covering a distance of 1 000 meters, were placed parallel to each other a distance of 100 meters apart. Each transect consisted of 20 sub-transects measuring 50 meters in length. For each sub-transect, a tape measure was laid out over the vegetation, and intercept cover as well as plant height was recorded. All sub-transects were placed in a continuous fashion so that a single continuous transect could be reconstructed for analysis. Individual species abundance was taken as its sum total of cover as measured on the transect.

2.3.3 Diversity Indices

Three community traits of species richness, dominance and evenness were investigated (Table 2.1). Hill (1973) presented a unified concept of how three popular diversity indices, viz. Simpson's index, Shannon's index and total species number are related. As each of these indices expresses different traits of a community's relative abundance, it is recommended that the full series of indices should be presented.

Indices emphasising species richness included species richness (S) and the Q-statistic (Kempton & Taylor 1976). Species richness (S) was the total number of species found on each transect. Species accumulation curves were calculated by randomising the order of 20 sub transects and calculating the average number of species encountered over set distances on each transect and over 10 iterations in order to remove sampling bias. Due to the problems of numerical interpretation of the curves (Connor & McCoy 1979), only visual interpretation is presented. The Q-statistic measures the inter-quartile slope of the cumulative species to species abundance curve and gives an indication of community diversity with no weighting towards either the very abundant or rare species (Magurran 1998).

Table 2.1. Equations for diversity indices

| Index Name | Equation | Emphasis |
|-------------------|--|----------|
| Species Richness | S | Richness |
| Q statistic | $\frac{0.5S_{25} + \sum S_i + 0.5S_{75}}{\log(N_{25} / N_{75})}$ | Richness |
| Shannon (H') | $-\sum p_i \ln p_i$ | Evenness |
| Simpson (d) | $\sum \left(\frac{n_i(n_i - 1)}{N(N - 1)} \right)$ | Evenness |
| Hill Evenness (E) | $\frac{(1/d) - 1}{e^{H'} - 1}$ | Evenness |

N , total number of individuals; N_i , number of individuals belonging to species i ; p_i , proportion of species i among total individuals ($= N_i/N$); n , standardised sample size; S_{25} , S_{75} , number of species in the 25% and 75% quartiles, respectively; N_{25} , N_{75} , number of individuals in the 25% and 75% quartiles, respectively.

Indices that emphasise community species dominance and evenness include the Shannon-Wiener index (Zar 1984), the Simpson's dominance index (Hill 1973, Ludwig & Reynolds 1988) and the modified Hill's ratio (Hill 1973, Alatalo 1981). The Shannon index of diversity

(H') determines the average degree of 'uncertainty' that an individual will be chosen at random from a collection of species (Zar 1984, Ludwig & Reynolds 1988, Magurran 1988). Variance on H' is calculated and significant differences between the two samples tested with a t -test (Magurran 1988). In order to standardise the units (species) with the other diversity indices, $e^{H'}$ is also calculated which can be interpreted as the number of equally common species. The Simpson's dominance index (d) gives the probability of two individuals being drawn at random being the same species and decreases with increasing diversity. The reciprocal ($1/d$) is the number of very common species from a collection. The Hill's evenness ratio (E) ranges from 0 to 1 and approaches 0 as a single species becomes more dominant.

2.3.4 Abundance Model

To determine dominance-diversity patterns, sequential dominance data were plotted (Whittaker 1965). Two proposed uses of this relationship are to illustrate the dominance differences in successional systems (e.g. Huston 1994, Bazzaz 1996) and to monitor the changes to a community under environmental stress (e.g. Kempton 1979). However, Tokeshi (1993) notes that although it may be tempting to relate changes in abundance models to changes in community disturbance, this may not necessarily be justified. This is due to some 'disturbed' communities showing similar abundance models to 'undisturbed' communities, even though the actual number of species present has changed. Thus there is a need to establish benchmark abundance models against undisturbed communities first before comparison between disturbed communities. As a suitable undisturbed site could not be found in this study, a precautionary approach was adopted and only visual interpretation of abundance models was made between sites.

2.3.5 Life Form Analysis

Plants were assigned to one of the following categories based on growth form and life history: Annual Herb; Dwarf Leaf Succulent (leaf succulents < 0.3 m); Geophyte; Graminoid (grasses); Non-Dwarf Leaf Succulent (leaf succulents > 0.3 m); Non-Succulent Perennial (Perennial not succulent and not shrubs); Non-Succulent Shrub; Stem Succulent. Significant differences between the number of species falling into these categories between sites was tested with a Mann-Whitney U test.

2.4. Results

2.4.1 Richness, Dominance and Evenness

A total of 117 species were encountered from both transects with 104 species recorded in the LRV and 100 species in the MRV (Table 2.2, see Appendix 2 for species list). Of the 117 species recorded, 87 species (76%) were common to both transects. Seventeen species (15%) were exclusive (i.e. species only recorded on one transect) to the LRV while 13 species (11%) were exclusive to the MRV. The log plot (Figure 2.1) of the average number of species accumulated showed that the MRV had on average, less species per sampled distance between 10 and 1000 meters. This is confirmed by the Q-statistic, which scored a higher value for the LRV (LRV: 19.1; MRV: 16.6).

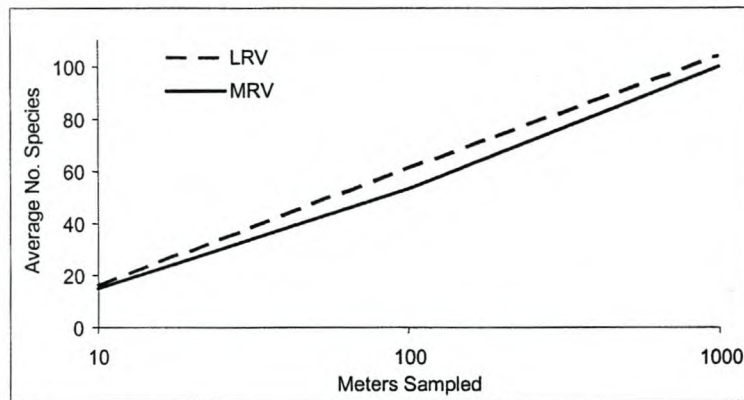


Figure 2.1 Plot of log distance to average species number showing that Long Rested Vegetation (rested for 34 years – LRV) had a greater average rate of species accumulation than the Medium Rested Vegetation (rested for 11 years – MRV) in Strandveld Succulent Karoo.

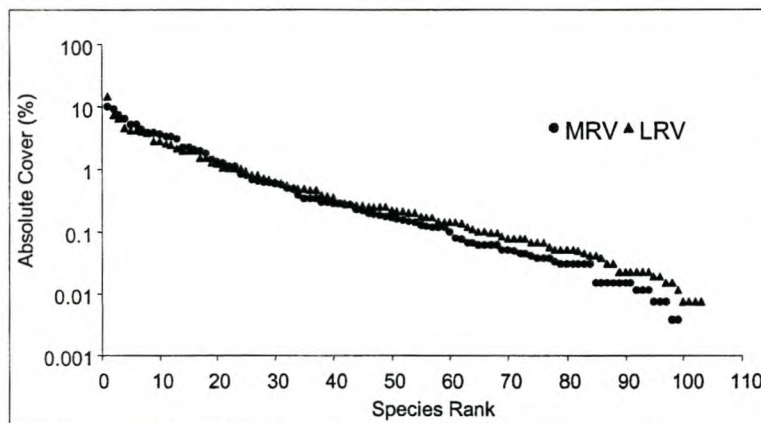


Figure 2.2 Dominance-diversity patterns for Medium Rested Vegetation (Rested for 11 years - MRV) and Long Rested Vegetation (rested for 34 years - LRV) in Strandveld Succulent Karoo. Dominance was taken as the absolute cover for a species as measured on the transects.

Table 2.2 Summary of diversity indices between Long Rested Vegetation (rested for 34 years - LRV) and Medium Rested Vegetation (rested for 11 years - MRV) in Strandveld Succulent Karoo.

| | Species (S) | Shannon (H') | $e^{H'}$ | Simpson $1/d$ | Hill's E | Q Statistic |
|-----|-------------|--------------|----------|---------------|----------|-------------|
| LRV | 104 | 3.5337* | 34.25 | 19.76 | 0.56 | 19.1 |
| MRV | 100 | 3.4517* | 31.55 | 21.10 | 0.66 | 16.6 |

* $t = 17.556$; $df = 39$; $p < 0.001$

Table 2.3 Exclusion of growth forms from diversity analysis between the Long Rested Vegetation (LRV) and Medium Rested Vegetation (MRV) showing that with the exclusion of Annuals or Non Dwarf Leaf Succulents, there was no significant difference between the LRV and MRV as tested by a t -test ($n = 40$).

| Growth form excluded from transect analysis | Number of Species Removed | | Shannon Index (H') | | t -test | p |
|--|---------------------------|-----|--------------------|--------|-----------|--------|
| | MRV | LRV | MRV | LRV | | |
| Annuals | 29 | 31 | 3.3346 | 3.3183 | -3.677 | N.S |
| Geophytes | 15 | 15 | 3.3454 | 3.4378 | 20.566 | <0.001 |
| Non Dwarf Leaf Succulents | 9 | 10 | 3.3283 | 3.3332 | 0.863 | N.S |
| Non Succulent Shrubs | 24 | 23 | 3.0571 | 3.2222 | 24.693 | <0.001 |

The MRV had a slightly higher number of very abundant species (Simpson's Index $1/d$) (MRV: $1/d = 21.1$; LRV: $1/d = 19.8$) while the LRV tended to have more common species (LRV: $H' = 3.533$; $e^{H'} = 34.3$; MRV: $H' = 3.451$; $e^{H'} = 31.6$) with the difference being significant (Table 2.2). The Hill's evenness ratio (E) was slightly lower in the LRV (LRV: $E = 0.567$; MRV: $E = 0.659$), but both sites showed an overall lack of dominance by a few species.

Visual inspection of the dominance-diversity plots based on percentage cover for each species (Figure 2.2) showed very little difference between the two vegetation types in terms of diversity, dominance and evenness. *Willdenowia incurvata* (Restionaceae) dominated both the MRV and LRV (LRV: 14% cover; MRV: 10% cover, Table 2.4). In the LRV, the non-succulent shrubs *Eriocephalus kingesii* and *Pteronia onobromoides* (Asteraceae), were the next most abundant, while in the MRV, *Senecio aloides* (Asteraceae) and *Tetragonia fruticosa* (Aizoaceae) were the next most abundant. Overall, the absolute abundances of the 15 most common species were very similar between the two samples with only 3 species (*W. incurvata*, *S. aloides* and *P. onobromoides*) having cover differences greater than 3% between the two sites (Table 2.4).

Table 2.4 Ranked species cover of MRV (medium rested vegetation) and LRV (long rested vegetation). The last column shows the percentage difference for each species when comparing cover between the two sites. In both vegetation types *W. incurvata* (Wi) was the most abundant with a 3.9% difference in cover between the two sites.

| MRV | | LRV | | Cover Difference | |
|--------------|----------------------|--------------|----------------------|------------------|-------------|
| Species Code | Percentage Cover (%) | Species Code | Percentage Cover (%) | Species Code | Percent (%) |
| Wi | 10.2 | Wi | 14.1 | Sa | 7.0 |
| Sa | 9.2 | Ek | 7.4 | Wi | 3.9 |
| Tf | 7.5 | Po | 6.5 | Po | 3.2 |
| Ek | 6.5 | Tf | 4.6 | Tf | 2.9 |
| Rg | 5.3 | Sl | 4.2 | Hs | 2.7 |
| Er | 5.2 | Er | 4.2 | Su | 2.3 |
| Su | 4.3 | Rg | 4.0 | Rg | 1.3 |
| Sl | 3.9 | Ev | 3.9 | Zm | 1.3 |
| Hs | 3.8 | Zm | 2.8 | Er | 1.0 |
| Zm | 3.7 | Pd | 2.8 | Ek | 0.9 |
| Ev | 3.4 | Oc | 2.6 | Oc | 0.8 |
| Po | 3.3 | Lm | 2.5 | Lm | 0.7 |
| Lm | 3.1 | Sa | 2.2 | Ev | 0.5 |
| Cd | 2.2 | Su | 2.0 | Pd | 0.5 |
| Pd | 2.2 | Eb | 2.0 | Sl | 0.4 |
| Eb | 2.0 | Pe | 1.9 | | |
| Rb | 2.0 | Cd | 1.5 | | |
| Oc | 1.8 | Rb | 1.5 | | |
| Ci | 1.5 | Ed | 1.3 | | |
| Hy | 1.3 | Hy | 1.2 | | |

Species Codes: Cd- *Chaetobromus dregeanus*, Ci- *Chrysanthemoides incana*, Eb- *Euphorbia burmannii*, Ed- *Ehrharta delicatula*, Ek- *Eriosephalus kingesii*, Er- *Euclea racemosa*, Ev- *Ehrharta villosa*, Hs- *Hermannia sp.*, Hy- *Helichrysum sp.*, Lm- *Lebeckia multiflora*, Oc- *Othonna cylindrica*, Pd- *Pteronia divaricata*, Pe- *Pharnaceum exiguum*, Po- *Pteronia onobromoides*, Rb- *Rushia breuibractata*, Rg- *Rhus glauca*, Sa- *Senecio aloides*, Sl- *Salvia lanceolata*, Su- *Stoeberia utilis*, Tf- *Tetragonia fruticosa*, Wi- *Willdenowia incurvata*, Zm- *Zygophyllum morgsana*.

2.4.2 Life Form Analysis

Comparison of the number of species for each growth form between each site showed non significant results for all growth forms except for that of annuals. Overall, annuals had the largest number of species (MRV = 29; LRV = 31) for a growth form followed by non-succulent shrubs (MRV = 24; LRV = 23). However the non-succulent shrubs contributed the most to the cover from each site (MRV = 36% total cover; LRV = 40% total cover) while annuals covered less than 10% total cover in both sites (Figure 2.3). Exclusion of either the annuals or the Non Dwarf Leaf Succulents from the transects resulted in the differences in diversity between the transects being non significant (Table 2.3).

Table 2.5 The mean (\pm SE) number of species per 50 meter sub transect within 9 growth form categories as well as the mean number of species per 50 meters sub transect within the Medium Rested Vegetation (MRV) and Long Rested vegetation (LRV). Results of the Mann-Whitney test are given.

| Growth Form | MRV | LRV | <i>P</i> (n= 20) |
|--|------------------|------------------|------------------|
| Annuals | 2.65 \pm 0.33 | 4.45 \pm 0.46 | <0.005 |
| Dwarf Leaf Succulent | 0.45 \pm 0.14 | 0.85 \pm 0.17 | NS |
| Geophyte | 2.25 \pm 0.35 | 2.65 \pm 0.21 | NS |
| Graminoid | 2.80 \pm 0.21 | 3.45 \pm 0.17 | NS |
| Non Dwarf Leaf Succulent | 5.00 \pm 0.31 | 4.50 \pm 0.29 | NS |
| Non succulent perennial | 3.55 \pm 0.27 | 3.00 \pm 0.26 | NS |
| Non Succulent Shrub* | 9.80 \pm 0.44 | 8.95 \pm 0.34 | NS |
| Stem Succulent | 1.35 \pm 0.11 | 1.45 \pm 0.11 | NS |
| No. Spp per 50m Transect | 27.85 \pm 1.12 | 29.30 \pm 0.73 | NS |
| * Sub division on fruit type | | | |
| Non Succulent Shrub – Fleshy Fruit | 4.75 \pm 0.28 | 4.40 \pm 0.34 | NS |
| Non Succulent Shrub – Non Fleshy Fruit | 5.05 \pm 0.30 | 4.55 \pm 0.22 | NS |

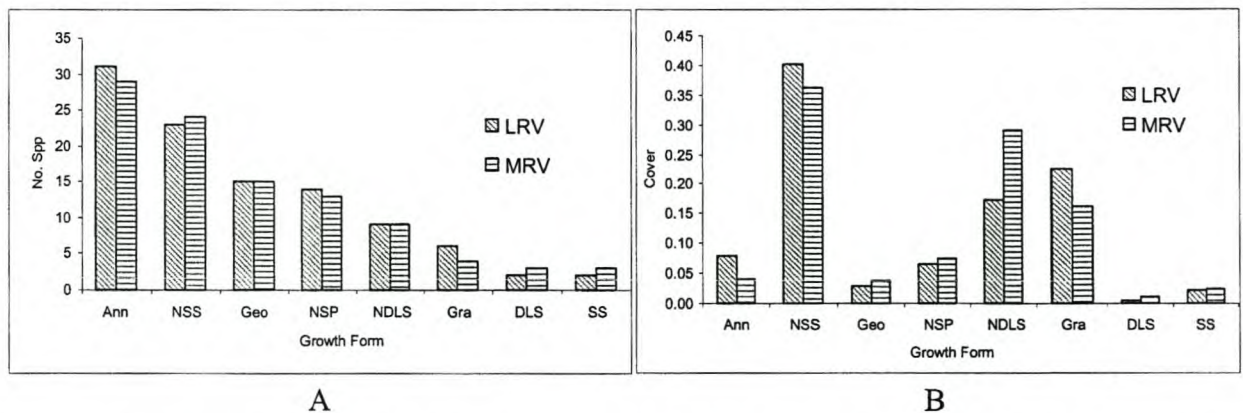


Figure 2.3. Total number of species of each growth form (A) and the proportion of cover of each growth form (B) for the Medium Rested Vegetation (MRV) and the Long Rested Vegetation (LRV). Growth form codes: Annual herbs (Ann); Dwarf Leaf Succulent (DLS); Geophytes (Geo); Graminoid (Gra); Non-Dwarf Leaf Succulent (NDLS); Non-Succulent Perennial (NSP); Non-Succulent Shrub (NSS); Stem Succulent (SS).

2.5 Discussion

The results from this study show that the management perception that the Medium Rested Vegetation (MRV) at Rocherpan is lacking in species richness is unfounded. Despite

differences in sampling methods, plot size and shape, the total species richness of 117 species from a 0.2 ha sample are in this study compares favourably to other studies in the Succulent Karoo. Cowling et al. (1989) for example reported a maximum of 115 (mean = 75) species in 0.1 ha plots; Desmet (1996) reported 117 species in over plots totalling 2 hectares and Todd & Hoffman (1999), 272 species in plots totalling 0.8 ha. At the local scale, species richness differed by only 4 species, although the LRV did have on average slightly more species per 50 meters sampled (Table 2.5). Evidence for similarity between the sites can be seen from the absolute abundances of species (Table 2.4) where only 3 of the 87 species common to both sites had differences in absolute abundance greater than 3%.

The expected dominance of *Lebeckia multiflora* in the MRV (as suggested by reserve management) was not found. In terms of overall dominance, *L. multiflora* was ranked 12 and 13 in the LRV and MRV respectively, with the difference in cover between the two sites less than 1%. An unexpected result was the overall dominance of *W. incurvata*, in both the MRV and LRV. This species is associated more with Sand Plain Fynbos on acidic soils (Low & Rebelo 1996). Other studies (e.g. Desmet 1996, Eccles 2000) did not record this species. Thus it is possible that this site is unique as it could be situated in the ecotone between the northern boundary of the Fynbos and Succulent Karoo Biomes. The possibility of this area being an eco-tone needs to be considered by reserve management when strategies aimed at rejuvenation are considered.

There are three possible reasons for the apparent difference in species richness between the two sites. These are sampling inadequacies, initial conditions and system dynamics. Species diversity indices are sensitive to the number of species present and the relative number of rare species in the collection (Hill 1973, Ludwig & Reynolds 1988). The line intercept method is a relatively very fine measurement technique in terms of measurement of species richness when compared to plot based methods and may tend to underestimate rare species or growth forms, e.g. geophytes. This may in turn result in the inability of the indices to detect differences between the two sites (chance of a Type II error). To compensate for this, this study does not rely on the diversity indices alone, but also reports on relative abundance and growth form analysis. Results from relative abundance and growth form analysis agree with the observation of an overall lack of difference in species richness between the two sites. Thus although the chance of committing a Type II error was reduced, it will only be totally eliminated through plot based sampling.

The second hypothesis to account for the equality in species richness between the two sites relates to the relative difference at the beginning of the resting periods, or initial resting conditions. Domestic grazing in the area commenced around 1840 (Wessels & Hanekom 1997), so the relative long term changes resulting from grazing could overshadow the short term trends in resting for both sites. A third possibility relates to internal system dynamics of the MRV. Although for only hypothetical reasoning can be engaged here, it can be postulated that over the last 11 years the random and mutual interactions in the MRV have readjusted to match that of the LRV. However, due to the relatively short resting period of 11 years, this readjustment of system processes seems unlikely.

The diversity results gained from the two sites are of importance to conservation managers. They illustrate that the Succulent Strandveld Karoo is a complex system that results from interactions between at least 35 woody and succulent shrubs, 30 annual species and a number of geophytes. As the number or types of interactions between all of these main species may never be quantifiable, efforts to manipulate the system to enhance species diversity should be considered with care. Particular attention needs to be given to the ecotonal properties of the area as a single specific treatment (e.g. fire) is likely to favour a certain sub-set of species. This is due to particular life history characteristics of different shrub species (e.g. resprouters versus reseeders) that may result in a shift in overall dominance of life forms. Lastly, manipulation treatments need to be undertaken in conjunction with long-term conservation goals for the area. Without specific goals, such treatments are likely to be haphazard at best.

The most interesting dynamic is the difference in cover of non-dwarf leaf succulents (NDLS) between the two sites despite an equal number of species comprising this growth form (Figure 2.3). These species generally have short life spans (Jürgens et al. 1999) and require open spaces for germination (Milton 1995). The reduced cover of the NDLS in the vegetation that has been rested for 34 years (LRV) may indicate that the succulent shrub population is senescing. However, the loss of cover of the NDLS is countered by an increase in cover of annuals and woody shrubs. Thus it seems that the lack of disturbance in the Long Rested Vegetation has negatively impacted the abundance of succulent shrubs whilst overall species richness has remained the same.

Milewski (2002) suggests that, amongst other possibilities, herbivore browsing and infrequent cool fires could be important in terms biodiversity maintenance within the Strandveld. Currently, the total exclusion of large herbivores from the area is unnatural. Before human settlement, the area would have been utilised by eland (*Taurotragus oryx*), ostrich (*Struthio camelus*) and black rhinoceros (*Diceros bicornis*) (Skead 1980). With the onset of human settlement (circa 1840) cattle, sheep and goat grazing replaced indigenous species. Currently, the lack of large herbivore activity is likely to disadvantage the relatively short lived succulents, as gaps created by trampling and browsing would be absent, thus reducing overall site availability for seedling establishment (Milton 1995).

In terms of fire, Cowling et al. (1997) reports that fire exclusion in coastal dune fynbos allows for the establishment and subsequent domination by thicket vegetation (*Rhus spp.*, *Maytenus spp.* and *Euclea spp.*) of the dune fynbos. This process can be applied conceptually to the Succulent Strandveld Karoo, where patches of thicket vegetation could establish and eventually replace the succulent flora in the absence of disturbance. The extent to which fire may be important in reducing thicket cover to allow the establishment of succulents in this vegetation type is not known and requires further investigation.

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CHAPTER 3: QUANTIFYING THE DIFFERENCES IN SPATIAL PATTERNING AND SPECIES ASSOCIATION BETWEEN MEDIUM RESTED AND LONG RESTED STRANDVELD SUCCULENT KAROO

3.1 Abstract

Differences in vegetation patterning and species association was compared across an historic fence line separating vegetation that had been rested from grazing for 34 years and vegetation that had been rested from grazing for 11 years in the Strandveld Succulent Karoo. At both sites there was an overall tendency for clumped patterning at small scales (15 meters) as well as at larger scales (80 meters) when all species were pooled. Analysis of interspecific association at three spatial scales revealed a majority of non-significant associations. Species that were involved in significant positive interactions could be separated into three specific associations, viz. *Euclea racemosa* clump associations, vegetation matrix and *Willdenowia incurvata* mono-specific stands. These results are contextualised within the known community dynamics of the Succulent Karoo.

3.2 Introduction

A focus on vegetation spatial patterns allows inference of underlying community processes (e.g. Watt 1947, Paine 1966, Phillips & MacMahon 1981, Huston 1994, Bazzaz 1996, Yeaton & Esler 1990, Eccles et al. 1999). This is due to the basic assumption that observed patterns are underlined by some physical process. However, identifying the overriding process can be difficult, as a number of different processes can result in the same observed patterning (Cale et al. 1989, Dale 1999). Arid systems have been observed to be composed of a two-phase mosaic structure where patches of high vegetation cover are separated by a low cover matrix (Aguiar & Sala 1999). Vegetation models and studies generally view this patch mosaic pattern as different stages of an event driven cycle (Watt 1947, Yeaton & Esler 1990, Wiegand et al. 1995).

Within the Succulent Karoo, two such vegetation models have been proposed to explain observed clump-matrix pattern. The first is a deterministic cyclic succession model that is driven by 'nurse plant' interactions (Yeaton & Esler 1990, Esler 1993, Esler & Cowling 1993, Silvertown & Wilson 1994, Holmgren et al. 1997). This model was developed in vegetation

from the south eastern part of the Succulent Karoo. The key aspects of this model are that 1) a pioneer guild colonises open sites, 2) these plants then act as facilitators for the establishment of secondary colonisers, 3) these secondary colonisers often replace the pioneers through competition and 4) the secondary colonisers will persist until they die. Such communities can be considered as classical ‘niche-assembled’ communities that are composed of members with specific requirements based on their specific adaptations (Hubbell 2001) and where competition between members is a major factor in shaping the community.

The second model follows a non-deterministic (stochastic) approach (Cowling et al. 1999, Esler et al. 1999, Jürgens et al. 1999, Eccles 2000), which was developed in the north western part of the succulent Karoo. In this model, the importance of competition and environmental heterogeneity are played down. Key aspects of this model are 1) short perennial life spans that result in 2) regular gap formation and 3) weak competitive interactions that produce 4) randomly assembled vegetation clumps. Such communities can be considered as ‘dispersal-assembled’ communities where random interactions are dominant (Hubbell 2001).

Particular to the Succulent Strandveld Karoo, is the possibility that subtropical thicket (*Rhus spp.*, *Maytenus spp.* and *Euclea spp.*) species can invade and alter the overall vegetation dynamics (Cowling et al. 1997), especially when fire is infrequent. This is due these species being competitive, long-lived, woody resprouters that can replace the shorter-lived succulent species. Where these species have become established, they are likely to support a distinctive vegetation association (Dean et al. 1999).

At Rocherpan Nature Reserve, two areas that have been rested from livestock grazing for 11 and 34 years, showed little overall difference in plant species richness (Chapter 2). It was managements’ perception (Wessels & Hanekom 1997) that the area rested for 11 years (termed Medium Rested Vegetation – MRV) was dominated Leguminous shrubs, namely *Lebeckia multiflora*, and that succulent shrubs in the area rested for 34 years (termed Long Rested Vegetation – LRV) were being replaced by woody shrubs (Chapter 2). In order to determine if this process was a feature of the Strandveld Succulent Karoo (known as Strandveld), the dominant community process in the area needed to be identified (viz. deterministic competition or stochastic mutualism). The approach taken in this study was to gain a static picture of the vegetation structure of the two areas and then apply inferential techniques against key predictions of each model:

Prediction 1: Vegetation clumping. Both models assume that there is vegetation aggregation at the small (< 1 m) to medium scales (1 – 4 m) as a result of either net facilitation or mutualism. Lack of distinctive clumps would render both models invalid.

Prediction 2: Clump membership. A key difference between the two models is that clump membership in the stochastic model is random thus the occurrence of randomly assembled communities would support the stochastic model.

Prediction 3: Competition levels. In the ‘nurse-plant’ model, strong competitive effects assumed to be measured by regular patterning in adult plants are key. A presence of strong regular patterning would lend support to this model.

Prediction 4: Membership of gaps. In the deterministic model, gaps in the vegetation are first occupied by succulent shrubs while the stochastic model allows for gaps to be occupied by both succulent and woody species. Thus if gaps are occupied by succulent shrubs this would lend support to the deterministic model.

3.3 Materials and Methods

3.3.1 Study Area

Rocherpan Nature Reserve is located on the west coast of South Africa, approximately 180 km north of Cape Town and 35 km north of the Berg River (32° 36'S, 18° 18'E) and covers an area of 914 ha. The reserve is bounded by farmlands to the north, east and south and the Atlantic Ocean in the west. The Reserve occurs near the south western boundary of the Succulent Karoo Biome (Low and Rebelo 1996) and falls within the Strandveld Succulent Karoo veld type (known as Strandveld). The area receives predominantly winter rainfall with an estimated average annual total rainfall of 260 mm. Fog and dew are a regular occurrence and may contribute significantly to the total precipitation received (Desmet & Cowling 1999). Temperatures in area are moderated by the Atlantic Ocean but maximum temperatures over summer (November-February) can exceed 35°C (mean Max: January- February = 36.9°C). The coolest months are between June to August with mean minimum temperatures of 3.3°C being recorded. Frost occurs on average 10 day per year. Wind plays an important role in the climate of the area. Hot, easterly berg winds can occur throughout the year and have very high evaporative demands (Desmet & Cowling 1999) while rain-bearing northwesterly prevails during winter. Soils are aeolian deposited tertiary to residual sands (Wessels & Hanekom 1997) with a shallow A horizon and a deep (>2 m) B horizon.

The vegetation is dominated by scattered low to medium shrubs including the leaf succulent Mesembryanthemaceae (especially *Ruschia* spp. and *Stoebaria utilis*) and Euphorbiaceae as well as evergreen and deciduous shrubs including *Euclea* (Ebenaceae), *Rhus* (Anacardiaceae), *Chrysanthemoides*, *Pteronia*, *Eriocephalus*, *Othonna* (Asteraceae) and *Lebeckia* (Fabaceae). Geophytes are well represented and include *Albuca*, *Lachenalia* (Hyacinthaceae), *Babiana* and *Gladiolus* (Iridaceae). Grasses occur in scattered patches and include *Stipagrostis*, *Cladoraphis* and *Odyssea*. Restionaceae species (*Willdenowia*) become more dominant where Succulent Strandveld is associated with Sand Plain Fynbos.

3.3.2 Sample Design

Two line transects, one in Succulent Strandveld vegetation rested for 34 years (LRV) and one in the same vegetation type rested for 11 years (MRV), covering a distance of 1 000 meters, were placed parallel to each other a 100 meters apart. Each 1 000 meter transect was composed of 20, 50 meter sub-transects placed end to end. For each plant species falling directly on the transect line, its start distance and end distance was recorded as well as its height on the transect.

3.3.3 Horizontal Pattern Analysis

In order to analyze spatial vegetation patterns, species canopy cover over sequential 1 meter intervals was calculated from each of the 1 000 meter line transects. This produced a base data set consisting of 1 000 continuous sample units (line segments) containing species cover measured in centimetres. Pattern analysis was conducted using an auto-correlation procedure known as the two-term local quadrat variance (TTLQV) (Hill 1973, Ludwig & Reynolds 1988, Dale 1999). This procedure entails calculating the variance as the average of the square of the difference between the 'quadrants' of all possible adjacent pairs of a specific 'quadrant' size (Equation. 3.1, Figure 3.1). In terms of this study, 'quadrant' is defined as a 1 meter segment of the line transect. Quadrat size was sequentially increased by increments of 1, so that average block variance could be plotted as a function of quadrat size. Peaks in the variance plots are interpreted as clumping at a spatial scale of twice the quadrat size. As recommended by Hill (1973), Ludwig & Reynolds (1988) and Dale (1999), quadrat size was not increased beyond 10% of the total number of quadrats.

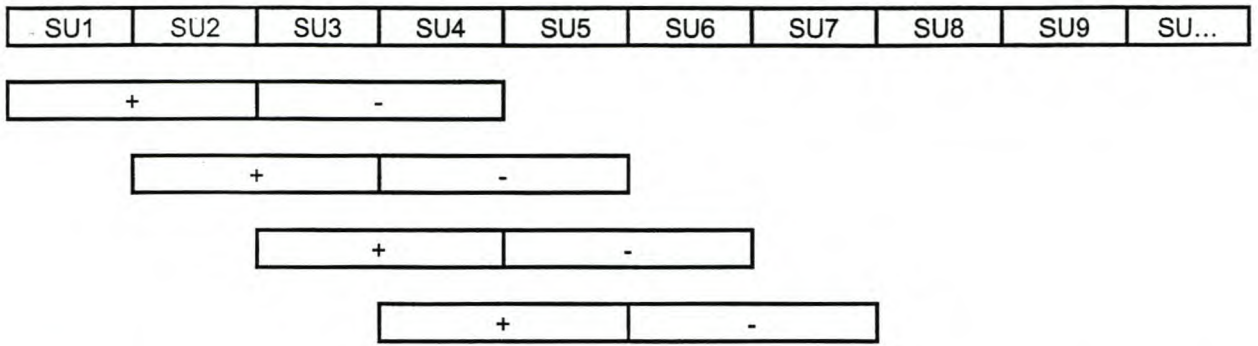


Figure 3.1 In the two-term local quadrat variance (TTLQV) variance is calculated as the average of the square of the difference between the block totals of all possible adjacent pairs of block size b (In this example $b=2$). The values of in the quadrants of the '+' are added together and then the values of the '-' blocks are then subtracted. The differences are squared and then averaged over all positions. Size of b is increased incrementally to a maximum of 10% of the sample size. SU = Sample Unit.

$$V(b) = \sum_{i=1}^{n+1-2b} \left(\sum_{j=i}^{i+b-1} x_j - \sum_{j=i+b}^{i+2b-1} x_j \right)^2 / 2b(n+1-2b) \text{ (Dale 1999)}$$

(Eq. 3.1, see Figure 3.1 for explanation)

For each transect, all species were pooled to determine overall vegetation patterns within the MRV and LRV. For individual species analysis, only species that had a frequency of greater than 10% over the entire length of the transect were considered (N= 15 species), since frequencies less than this gave erroneous results. Confidence limits for complete spatial randomness were estimated by using random permutations of the quadrant data based on 100 simulations for each analysis. The type of spatial pattern present was determined by departure from the random confidence limits. Where this departure was below the random limits, this indicated spatial regularity, while departures above the limits indicated spatial clumping.

3.3.4 Interspecific Association

For the 15 species analysed, interspecific association was determined at the individual, neighbour and neighbourhood levels between species pairs. Individual associations were defined as plants within the canopy and directly adjacent to the individual; neighbours were defined as plants between 1 – 2 meters from the individual (thus not directly within the space of an individual, but 'close-by') and the neighbourhood plants as those between 2 – 4 meters from the individual (based on an average clump size of 4 – 5 meters). Plants greater than 5 meters from the individual were not considered to have an association with that plant. The association of each species with the pool of remaining 14 species was also determined for the above scales. Analysis entailed replacing cover data from the base data set with

presence/absence data then computing a standard 2x2 contingency table. Due to the problems of pair wise analysis from multi-species collections (Silvertown & Wilson, Dale 1999), a supercritical chi-squared test was performed (Zar 1984, Ludwig & Reynolds 1988, Silvertown & Wilson 1994). Significance was tested at $P < 0.05$ where $\chi^2 > 12.46$ and the degrees of freedom = 1. As per the χ^2 table nomenclature, the direction of the association was determined positive if $ad > bc$ and negative if $ad < bc$.

To determine the strength of the association between each species pair, the Jaccard Index (JI) (Ludwig & Reynolds 1988) was calculated. This index ranges from 0 (species are never found together) to 1 (species always occur together). In order to better visualise these associations, a bi-plot of the principle coordinate analysis (Ter Braak 1987) of the JI symmetry matrix was produced for quadrat sizes of 1 and 10 meters. Associations with $\chi^2 > 12.46$ were indicated on the bi-plots with connecting lines.

3.3.5 Clump, Matrix and Gap Analysis

In order to investigate the relative proportion of matrix to clumps in each site, each transect was divided into 1 meter segments as assigned to 1 of 3 classes: Clump; Matrix or Gap. Clumps were defined as those sections of the transects that were occupied by groupings of woody and succulent shrubs; matrix species included non-woody perennials and woody and succulent shrubs that did not occur in clumps; and gaps were defined as areas occupied exclusively by annuals open space or seedlings.

3.4 Results

3.4.1 Horizontal Pattern Analysis

When considering all individuals in the community, the overall patterning between the two sites was remarkably similar (Figure 3.2). A small shallow peak, just bordering the confidence limits, indicates the presence of vegetation clumping at ≈ 15 meters, with a second clumping association at ≈ 80 meters (Table 3.1).

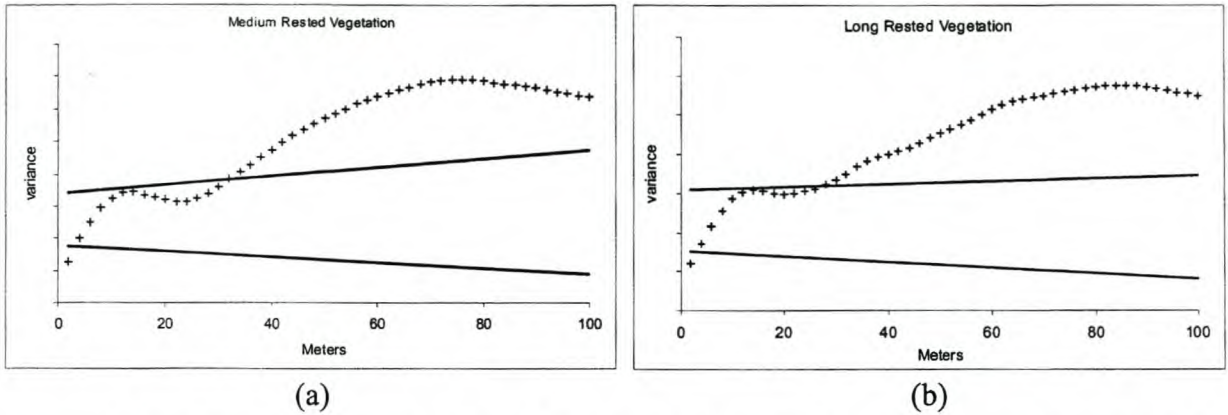


Figure 3.2 Overall variance patterns for the Medium Rested Vegetation (a) and Long Rested vegetation (b) where the broken line represents the variance as determined by Two Term Local Quad variance method and the solid lines represent the estimated random confidence limits assuming a random pattern.

Of the 117 species measured on the transects, 15 species had a frequency of more than 10% with all of these 15 species occurring in both sites. Overall these 15 species contributed to 90% of the pattern in the MRV and 70% in the LRV. Over a distance of 100 meters, 5 species showed distinctive clumping in both sites, with a further 6 species showing a distinctive clumped patterning in one of the two sites. Four species showed no distinctive clumping formation in either of the two sites (table 3.1). Comparative individual species patterns between the two vegetation types reveals overall similarity especially for the relatively long-lived species such as *Euclea racemosa*, *Stoeberia utilis*, *Rhus glauca* and *Pteronia onobromoides*. Some spatial patterning did differ at the species level between sites where it tended towards clumping in at one site, but random in the other, e.g. *Euphorbia burmannii* tended to be clumped in the MRV, but not the LRV while *Salvia lanceolata* showed clumping in the LRV, but not in the MRV. Most notable from all dispersion patterns was the lack of pattern regularity for all species beyond the 1 meter scale.

Table 3.1. Occurrence distances (in meters) of vegetation clumping in the Medium Rested Vegetation (MRV) and the Long Rested Vegetation (LRV) for: all species pooled; species with a frequency > 0.1 pooled and individual species with a frequency > 0.1. Dashes indicate no clumping pattern present. Species codes: Cd- *Chaetobromus dregeanus*, Eb- *Euphorbia burmannii*, Ek- *Eriocephalus kingesii*, Er- *Euclea racemosa*, Ev- *Ehrharta villosa*, Lm- *Lebeckia multiflora*, Pd- *Pteronia divaricata*, Po- *Pteronia onobromoides*, Rg- *Rhus glauca*, Sa- *Senecio aloides*, Sl- *Salvia lanceolata*, Su- *Stoeberia utilis*, Tf- *Tetragonia fruticosa*, Wi- *Willdenowia incurvata*, Zm- *Zygophyllum morgsana*.

| | Spp. | All Spp. | All Spp > 10% | Er | Su | Pd | Tf | Rg | Ek | Ev | Sl | Cd | Zm | Wi | Eb | Po | Sa | Lm |
|-------------------|------|----------|---------------|----|----|----|----|---------|----|----|----|----|----|----|----|----|----|----|
| Clump Spacing (m) | LRV | 15, 90 | 15, 90 | 40 | 20 | 25 | 35 | 30, 100 | 30 | 35 | 20 | 30 | - | - | - | - | - | - |
| | MRV | 15, 80 | 15, 80 | 50 | 30 | 50 | 15 | 20, 80 | - | - | - | - | 30 | 30 | 15 | - | - | - |

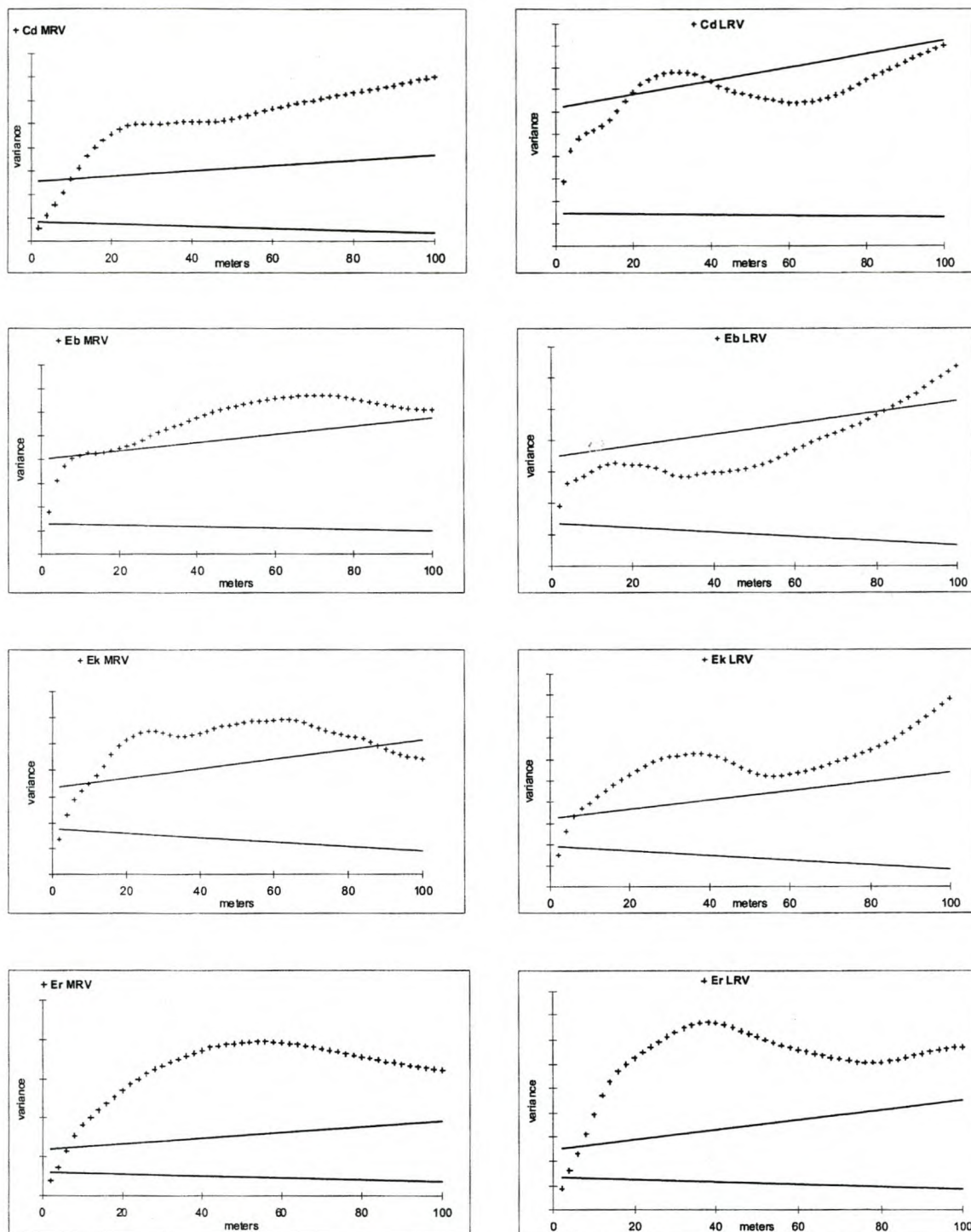


Figure 3.3 Overall variance patterns for the Medium Rested Vegetation (MRV) and Long Rested vegetation (LRV) where the broken line represents the variance as determined by Two Term Local Quad variance method and the solid lines represent the estimated random confidence limits assuming a random pattern. **Species codes:** Cd- *Chaetobromus dregeanus*, Eb-*Euphorbia burmannii*, Ek- *Eriocephalus kingesii*, Er-*Euclea racemosa*, Ev- *Ehrharta villosa*, Lm- *Lebeckia multiflora*, Pd- *Pteronia divaricata*, Po- *Pteronia onobromoides*, Rg- *Rhus glauca*, Sa- *Senecio aloides*, Sl- *Salvia lanceolata*, Su- *Stoebertia utilis*, Tf- *Tetragonia fruticosa*, Wi- *Willdenowia incurvata*, Zm- *Zygophyllum morgsana*.

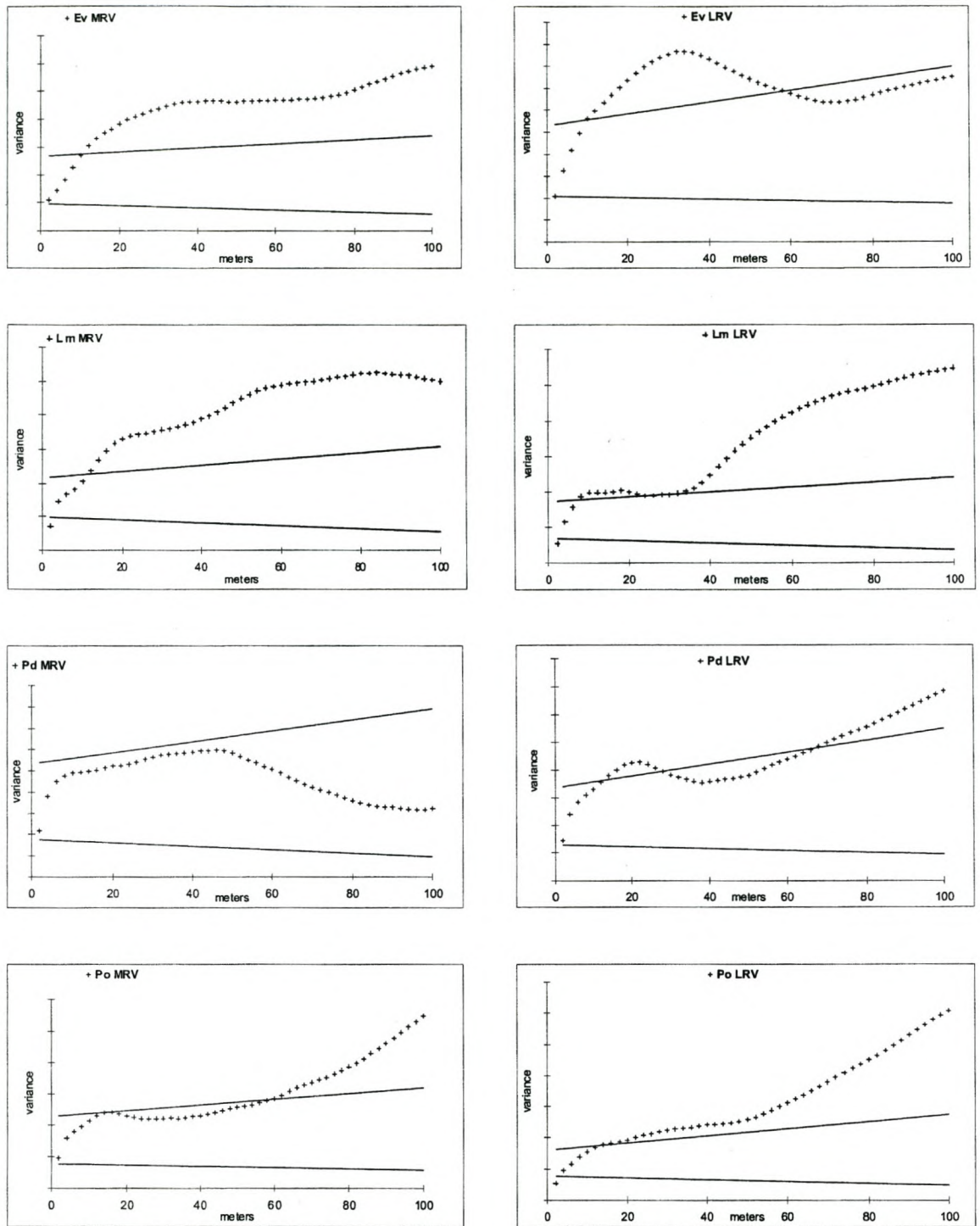


Figure 3.3. Continued...

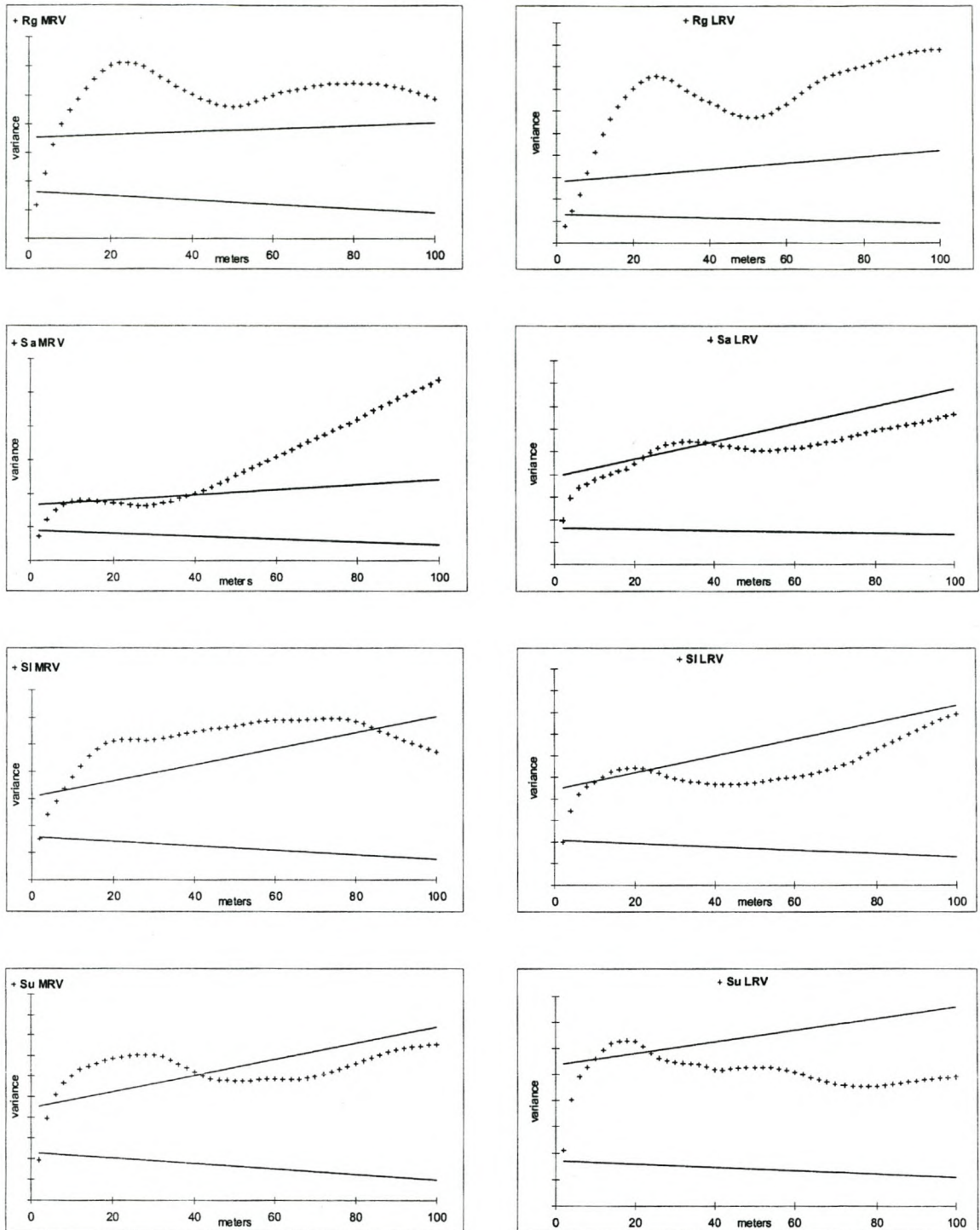


Figure 3.3. Continued...

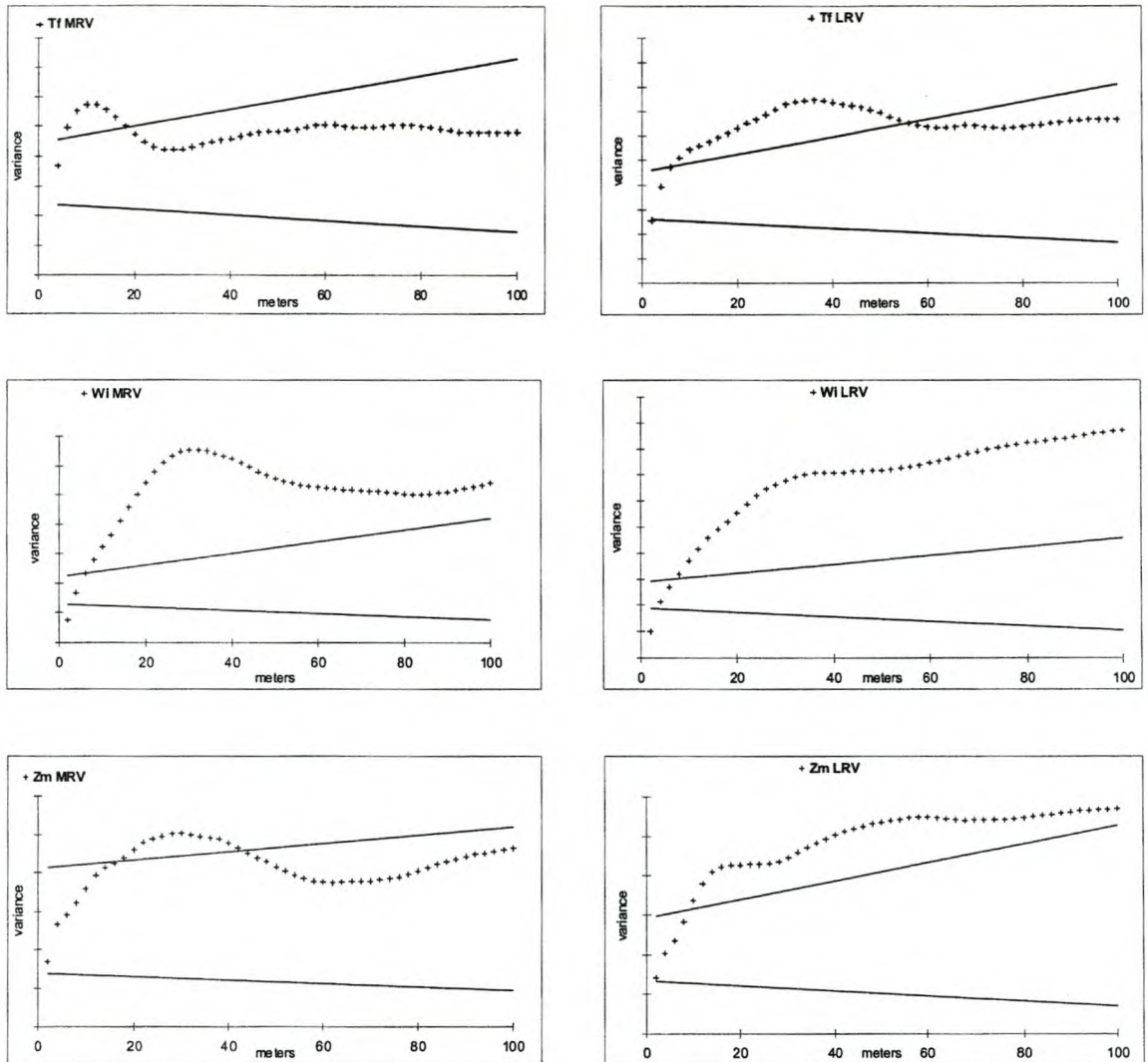


Figure 3.3. Continued.

3.4.2 Interspecific Association

Between the MRV and the LRV there was no overall difference in the trend of species associations at the individual, neighbour and neighbourhood scales. At the three scales the majority of all interactions were either non-significant positive or non-significant negative. At the individual scale, the LRV had 11 significantly negative associations compared with 5 for the MRV. Of these associations, 3 were common to both sites. The number significant positive associations at the individual level, were 7 for the MRV and 5 for the LRV. These groupings of associations tended to hold for all scales and the significance of this is described below. Overall association between species was non-significant.

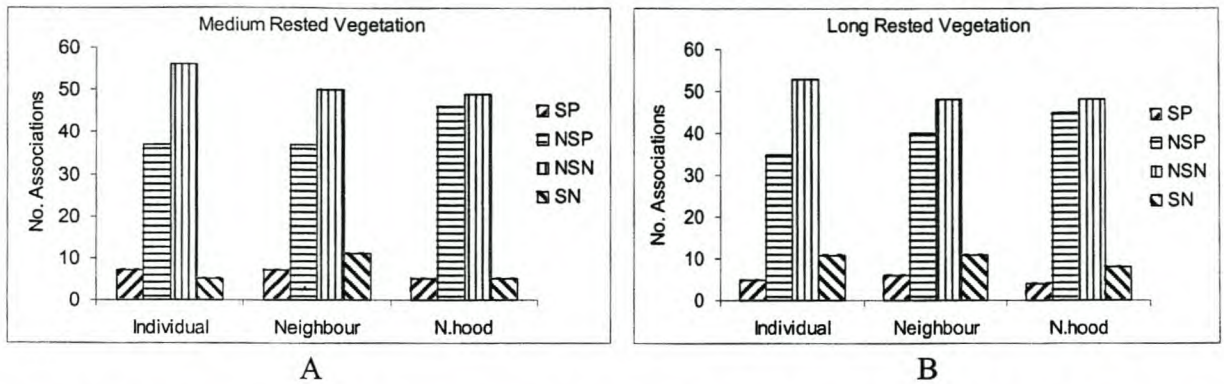


Figure 3.4 The number and type of associations the found for the 15 species in the MRV (A) and LRV (B) where SP- Significantly Positive, NSP- Non Significantly Positive, NSN- Non Significantly Negative, SN- Significantly Negative at the Individual, Neighbour and Neighbourhood scales as determined by χ^2 analysis. Interactions were considered significant at the 5% level where $\chi^2 > 12.46$.

Three specific associations were common to both the LRV and the MRV. The first association was that of species grouped with *Euclea racemosa* in clumps and included *Tetragonia fruticosa*, *Zygophyllum morgsana*, *Stoeberia utilis* and *Rhus glauca* as principle members and *Senecio aloides*, *Salvia lanceolata* and *Pteronia divaricata* as secondary members. The matrix portion of the vegetation can be separated into two distinctive associations. The more dominant of the two associations were the *Willdenowia incurvata* stands that tended to form monospecific stretches. Although *W. incurvata* was negatively associated with 11 species in the MRV and 9 in the LRV, *Euphorbia burmannii* was significantly positively associated with it in both vegetations at all scales. The remainder of the matrix was divided between the significantly negatively associated (in the LRV) *Pteronia onobromoides* and *Erioccephalus kingesii*. Individual species χ^2 values can be viewed in Table 3.2 (a-f) at the individual, neighbour and neighbourhood scales.

Overall the Jaccard Index ranged between 0 and 0.29 for all interactions indicating a prevalence of weak associations. For the MRV, the overall Jaccard Index for 15 analysed species at the individual, neighbour and neighbourhood scales were 0.06, 0.09 and 0.12 respectively, while in the LRV the Jaccard Index for the same scales were 0.05, 0.08 and 0.11. Bi-plots (Figure 3.5 a-f) of the Jaccard Index reveal the clustering of positive associations among species in the *Euclea* clumps (*Euclea racemosa*, *Zygophyllum morgsana* and *Tetragonia fruticosa*) as well as the general even dispersion of the other species.

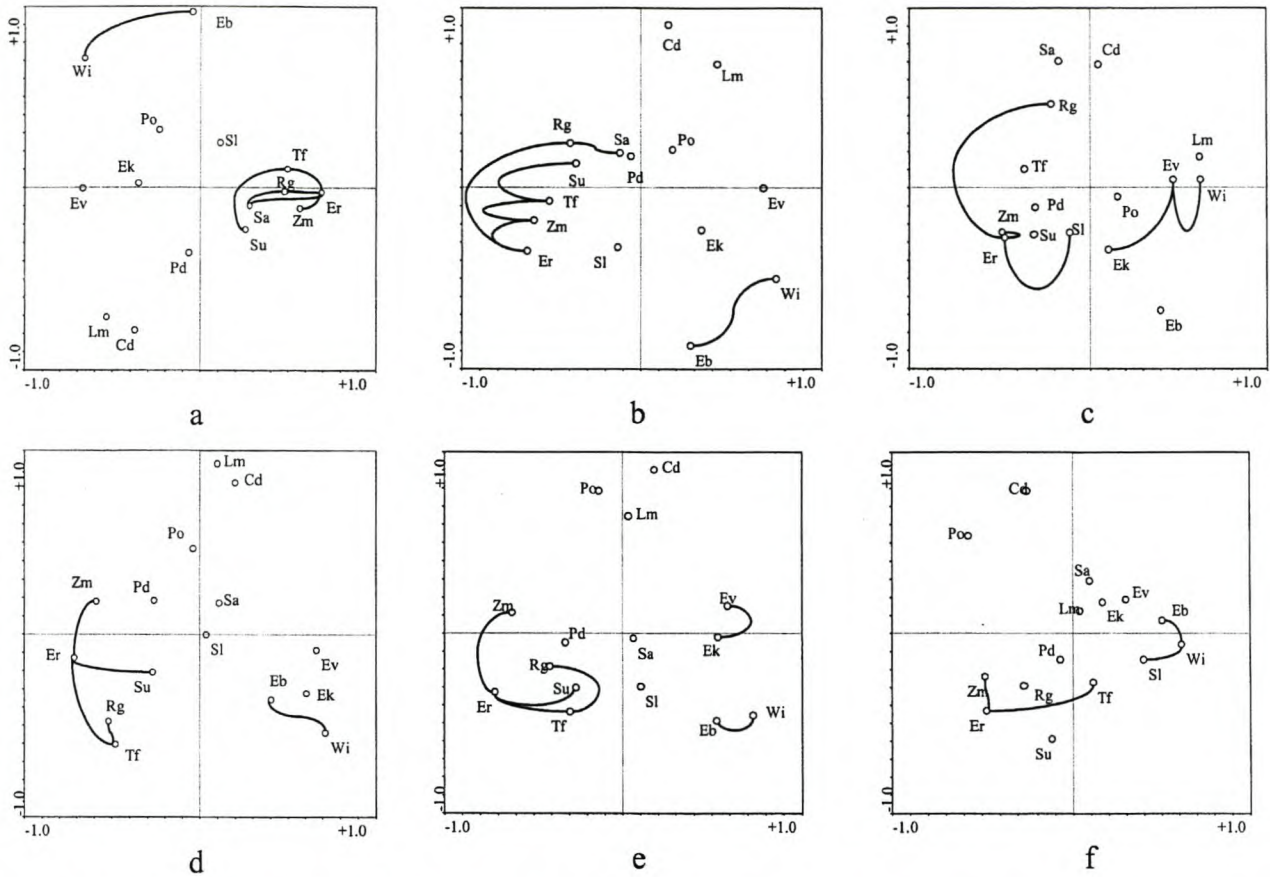


Figure 3.5. Biplots of the Jarccard Index for the MRV (a-individual, b-neighbour, c-neighbourhood) and the LRV (d-individual, e-neighbour, f-neighbourhood). Species that were significantly positive associated in the Chi² analysis are connected by solid lines.

3.4.3 Clump, Matrix and Gap Analysis

Both sites showed very small proportions of the transect as gap (MRV = 2%; LRV = 4%). The MRV had a slightly larger proportion of clumps (39%) than the LRV (35%), but both sites were composed mostly of matrix with 59% and 61% in the MRV and LRV respectively.

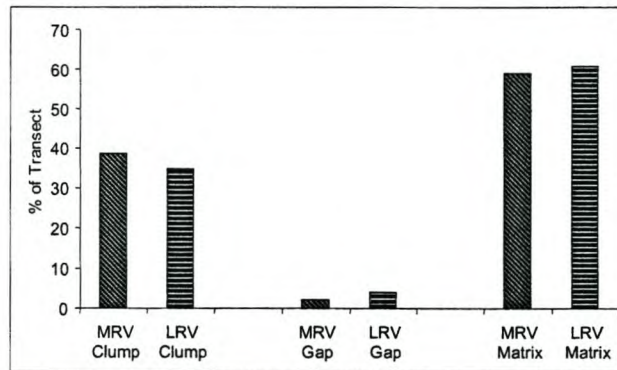


Figure 3.6. The proportion of each site that was occupied by Clump, Matrix or Gap for the MRV (Medium Rested Vegetation) and the LRV (Long Rested Vegetation).

Table 3.3 (a-f). Chi² scores for the 15 species with a frequency > than 10% at the individual, neighbour and neighbourhood scales in the Medium Rested Vegetation (MRV) and the Long Rested Vegetation (LRV) where ‘++’ shows significant positive; ‘+’ shows non-significant positive; ‘-’ shows non-significant vegetative; ‘--’ shows significant negative at the 5% confidence level of Chi² > 12.46. Division by a double line (▬) indicates clump associated species from matrix species, broken line (⊢) indicated the *Willdenowia* matrix association and the solid line (⊣) represents the *Pteronia onobromoides* matrix associations. Species codes: Cd- *Chaetobromus dregeanus*, Eb-*Euphorbia burmannii*, Ek- *Eriocephalus kingesii*, Er- *Euclea racemosa*, Ev- *Ehrharta villosa*, Lm- *Lebeckia multiflora*, Pd- *Pteronia divaricata*, Po- *Pteronia onobromoides*, Rg- *Rhus glauca*, Sa- *Senecio aloides*, Sl- *Salvia lanceolata*, Su- *Stoebria utilis*, Tf- *Tetragonia fruticosa*, Wi- *Willdenowia incurvata*, Zm- *Zygophyllum morgsana*.

| (a) MRV Individual | Tf | Rg | Zm | Su | Sa | Sl | Pd | Eb | Po | Ev | Cd | Ek | Lm | Wi | All > 10 % |
|--------------------|--------------|--------------|--------------|--------------|--------------|------------|------------|------------|------------|-------------|------------|-------------|------------|--------------|-------------|
| Er | ++ 12.576 | ++ 15.389 | ++ 32.922 | + 1.142 | ++ 13.383 | + 3.219 | - 0.003 | + 0.949 | - 4.081 | - 12.263 | - 2.645 | - 5.114 | - 6.924 | - 27.969 | -2.950 |
| Tf | | + 10.865 | + 12.262 | ++ 18.485 | -4.269 | + 0.323 | - 2.366 | + 2.162 | - 3.546 | - 11.734 | - 9.585 | - 6.321 | - 2.116 | - 16.753 | -1.315 |
| Rg | | | + 2.619 | + 0.229 | ++ 38.461 | + 0.137 | + 1.159 | + 0.949 | - 0.004 | - 4.030 | - 0.398 | - 10.485 | - 3.709 | - 12.925 | 0.044 |
| Zm | | | | -0.084 | + 12.169 | + 0.539 | + 2.771 | - 0.075 | - 2.101 | - 8.624 | - 2.035 | - 1.587 | + 7.450 | - 18.056 | -0.366 |
| Su | | | | | + 1.115 | + 1.786 | + 0.045 | + 0.061 | - 0.548 | - 8.414 | - 2.985 | - 1.480 | + 0.590 | - 17.770 | 0.001 |
| Sa | | | | | | + 0.909 | + 0.539 | - 1.627 | - 5.415 | - 5.477 | - 2.114 | - 1.590 | - 1.299 | - 8.282 | -0.050 |
| Sl | | | | | | | + 0.006 | + 7.048 | - 0.001 | - 6.640 | - 0.538 | - 0.169 | + 0.056 | - 1.846 | 0.807 |
| Pd | | | | | | | | + 0.006 | + 0.018 | - 0.904 | - 0.076 | - 0.054 | + 0.054 | - 4.684 | -0.008 |
| Eb | | | | | | | | | + 0.003 | - 2.800 | - 5.191 | - 0.426 | - 6.103 | ++ 14.044 | + 1.094 |
| Po | | | | | | | | | | - 7.790 | - 0.413 | - 3.414 | - 2.212 | + 0.085 | - 17.466 |
| Ev | | | | | | | | | | | - 0.424 | - 3.550 | - 8.429 | + 9.523 | - 15.821 |
| Cd | | | | | | | | | | | | + 0.209 | + 3.255 | - 9.985 | - 19.326 |
| Ek | | | | | | | | | | | | | - 6.604 | - 2.304 | - 10.490 |
| Lm | | | | | | | | | | | | | | + 0.010 | - -8.055 |
| Wi | | | | | | | | | | | | | | | - 48.991 |

| (b) MRV Neighbour | Er | Tf | Su | Sl | Rg | Sa | Pd | Eb | Po | Lm | Cd | Ek | Wi | Ev | All > 10 % |
|-------------------|--------------|--------------|--------------|------------|--------------|--------------|------------|------------|------------|------------|------------|-------------|-------------|--------------|-------------|
| Zm | ++ 38.605 | ++ 14.951 | + 2.927 | + 1.075 | + 1.299 | + 3.133 | + 1.191 | - 0.097 | - 4.412 | - 4.949 | - 1.325 | - 1.701 | - 25.868 | - 16.011 | +0.144 |
| Er | | + 7.225 | + 0.119 | + 6.095 | ++ 16.711 | + 10.527 | - 0.017 | + 4.971 | - 3.158 | - 9.815 | - 3.975 | - 5.461 | - 30.945 | - 16.852 | -0.086 |
| Tf | | | ++ 22.649 | + 4.431 | + 5.666 | - 6.073 | - 1.572 | - 0.204 | - 3.326 | - 0.400 | - 5.459 | - 9.130 | - 21.295 | - 19.824 | +0.812 |
| Su | | | | + 6.328 | + 0.052 | + 0.111 | + 0.322 | + 0.017 | - 0.101 | - 0.479 | - 1.236 | - 1.550 | - 25.644 | - 14.355 | +0.281 |
| Sl | | | | | - 0.003 | + 0.070 | + 0.177 | + 2.712 | - 0.078 | - 1.359 | - 0.620 | - 0.048 | - 0.309 | - 1.490 | +0.491 |
| Rg | | | | | | ++ 26.359 | + 0.992 | + 0.002 | - 0.490 | - 0.712 | - 0.007 | - 13.874 | - 15.096 | - 3.901 | +0.252 |
| Sa | | | | | | | + 1.651 | - 1.015 | - 1.250 | - 4.755 | - 0.002 | - 6.405 | - 4.409 | - 2.685 | +0.182 |
| Pd | | | | | | | | + 0.348 | - 0.124 | - 0.033 | - 0.038 | - 0.256 | - 8.374 | - 3.199 | +0.037 |
| Eb | | | | | | | | | + 0.428 | - 0.991 | - 5.017 | - 0.058 | - 21.945 | - 1.243 | +0.016 |
| Po | | | | | | | | | | - 4.519 | - 0.848 | - 1.774 | - 0.837 | - 1.279 | -4.858 |
| Lm | | | | | | | | | | | + 2.902 | - 5.463 | + 0.487 | + 9.451 | -6.002 |
| Cd | | | | | | | | | | | | - 0.140 | - 13.704 | - 1.211 | -4.651 |
| Ek | | | | | | | | | | | | | + 0.251 | + 6.914 | -2.175 |
| Wi | | | | | | | | | | | | | | ++ 23.447 | - 13.079 |
| Ev | | | | | | | | | | | | | | | -0.008 |

Table 3.3 continued.

| (c) MRV Neighbourhood | Zm | Sl | Rg | Tf | Su | Eb | Sa | Cd | Pd | Po | Ek | Ev | Lm | Wi | All > 10 % | |
|--------------------------|--------|--------|--------|-------|-------|-------|-------|-------|-------|-------|-------|--------|--------|--------|---------------|---|
| Er | 42.986 | 13.692 | 22.358 | 0.011 | 3.966 | 6.453 | 5.375 | 2.041 | 0.029 | 0.236 | 0.594 | 5.522 | 6.244 | 18.159 | * | |
| Zm | | 0.253 | 0.291 | 9.963 | 6.343 | 0.288 | 0.795 | 0.139 | 2.198 | 8.075 | 0.642 | 10.199 | 0.255 | 32.887 | * | |
| Sl | | | 0.048 | 1.652 | 1.626 | 1.264 | 0.868 | 0.452 | 1.171 | 1.842 | 8.411 | 0.244 | 4.853 | 0.031 | * | |
| Rg | | | | 5.411 | 0.050 | 6.945 | 8.561 | 4.366 | 0.021 | 0.205 | 5.736 | 0.091 | 0.042 | 4.855 | * | |
| Tf | | | | | 4.156 | 0.008 | 0.272 | 0.000 | 0.404 | 5.922 | 0.912 | -5.36 | 0.451 | 12.137 | * | |
| Su | | | | | | 2.469 | 0.007 | 1.210 | 0.001 | 0.008 | 2.412 | 5.623 | 0.145 | 44.248 | * | |
| Eb | | | | | | | | 3.389 | 1.566 | 2.994 | 4.586 | 0.757 | 0.268 | 2.902 | * | |
| Sa | | | | | | | | 1.272 | 1.272 | 0.394 | 5.981 | 0.365 | 1.914 | 5.586 | * | |
| Cd | | | | | | | | | | 0.009 | 8.299 | 4.17 | 0.045 | 1.639 | 3.346 | * |
| Pd | | | | | | | | | | 0.009 | 0.16 | 2.171 | 7.832 | 16.783 | * | |
| Po | | | | | | | | | | | 0.458 | 0.312 | 13.044 | 5.741 | * | |
| Ek | | | | | | | | | | | | 13.955 | 8.222 | +0.93 | * | |
| Lm | | | | | | | | | | | | | 5.823 | 9.755 | * | |
| Ev | | | | | | | | | | | | | | 26.443 | * | |
| Wi | | | | | | | | | | | | | | | * | |

| (d) LRV Individual | Tf | Zm | Su | Sl | Rg | Pd | Sa | Po | Eb | Lm | Cd | Wi | Ev | Ek | All > 10% |
|-----------------------|--------|--------|--------|--------|--------|-------|-------|-------|-------|-------|-------|--------|--------|--------|--------------|
| Er | 40.707 | 51.159 | 22.697 | 11.400 | 1.748 | 5.590 | 0.231 | 0.623 | 2.531 | 2.327 | 5.960 | 31.344 | 15.085 | 17.449 | 0.256 |
| Tf | | 4.676 | 2.736 | 10.196 | 54.607 | 0.000 | 2.725 | 3.383 | 1.010 | 1.118 | 3.140 | 4.076 | 15.318 | 1.167 | 0.874 |
| Zm | | | 0.028 | 0.905 | 10.535 | 3.724 | 0.167 | 1.566 | 0.908 | 0.279 | 3.394 | 13.918 | -8.899 | 21.386 | 0.256 |
| Su | | | | 1.763 | 0.045 | 2.757 | 0.168 | 3.587 | 0.019 | 1.156 | 3.909 | 1.935 | -0.346 | 3.808 | 0.087 |
| Sl | | | | | 4.612 | 0.949 | 3.128 | 5.093 | 0.67 | 1.812 | 0.515 | 0.162 | -0.780 | 0.513 | 1.301 |
| Rg | | | | | | 1.839 | 1.697 | 3.995 | 2.164 | 2.024 | 5.474 | 21.712 | 13.572 | 3.559 | 8.882 |
| Pd | | | | | | | | 1.265 | 0.050 | 2.577 | 0.342 | 5.787 | -2.788 | 5.168 | 7.394 |
| Sa | | | | | | | | 1.219 | 0.000 | 0.022 | 3.14 | 0.842 | -1.473 | 0.195 | 0.388 |
| Po | | | | | | | | | 5.756 | 1.979 | 0.710 | 20.049 | -1.951 | 15.849 | 59.839 |
| Eb | | | | | | | | | | 2.511 | 0.485 | 46.065 | 0.143 | 1.181 | 4.513 |
| Lm | | | | | | | | | | | 0.024 | 14.965 | 2.416 | -3.88 | 11.461 |
| Cd | | | | | | | | | | | | 8.896 | -4.018 | 0.006 | 28.941 |
| Wi | | | | | | | | | | | | | 5.776 | 2.148 | 9.802 |
| Ev | | | | | | | | | | | | | | 5.877 | 1.473 |
| Ek | | | | | | | | | | | | | | | 13.853 |

Table 3.3 continued.

| (e) LRV Neighbour | Tf | Zm | Su | Rg | Pd | Sl | Sa | Lm | Po | Cd | Eb | Ev | Ek | Wi | All > 10% |
|-------------------|--------|--------|--------|--------|-------|--------|-------|-------|--------|--------|--------|--------|--------|--------|-----------|
| Er | 57.162 | 74.786 | 27.181 | 3.952 | 8.864 | 10.251 | 0.779 | 4.023 | 0.108 | 12.045 | 0.806 | 7.669 | 13.566 | 37.109 | 0.803 |
| Tf | | 1.925 | 0.328 | 27.956 | 0.008 | 11.854 | 0.004 | 0.002 | 11.13 | 4.257 | 0.685 | 13.98 | 0.197 | 3.556 | 1.499 |
| Zm | | | 0.357 | 7.878 | 8.291 | 1.610 | 0.009 | 0.000 | 5.437 | 1.696 | 2.176 | 8.948 | 16.733 | 24.934 | 0.007 |
| Su | | | | 1.039 | 7.068 | 4.939 | 0.009 | 1.361 | 2.085 | 0.293 | 2.148 | 1.029 | 1.127 | 3.403 | 0.283 |
| Rg | | | | | 9.690 | 2.999 | 0.783 | 0.011 | 5.688 | 3.850 | 0.765 | 9.997 | 2.904 | 16.569 | 0.266 |
| Pd | | | | | | 1.290 | 0.034 | 5.441 | 4.286 | 0.624 | 0.022 | 10.895 | 5.140 | 2.518 | 0.007 |
| Sl | | | | | | | 6.441 | 0.973 | 10.253 | 0.135 | 0.155 | 2.546 | 0.004 | 3.185 | 0.136 |
| Sa | | | | | | | | 0.373 | 0.018 | 2.273 | 0.100 | 3.626 | -0.07 | 0.110 | 0.016 |
| Lm | | | | | | | | | 4.549 | 0.007 | 4.581 | 1.745 | 7.312 | 13.07 | 0.353 |
| Po | | | | | | | | | | 3.657 | 12.818 | 3.021 | 13.013 | 30.535 | 27.386 |
| Cd | | | | | | | | | | | 0.262 | 0.007 | 0.253 | 13.155 | 4.403 |
| Eb | | | | | | | | | | | | 1.612 | 0.283 | 80.524 | 0.409 |
| Ev | | | | | | | | | | | | | 12.497 | 5.023 | 0.481 |
| Ek | | | | | | | | | | | | | | 9.567 | 0.096 |
| Wi | | | | | | | | | | | | | | | 9.799 |

| (f) LRV Neighbourhood | Tf | Zm | Sl | Su | Pd | Rg | Eb | Lm | Sa | Cd | Ek | Ev | Po | Wi | All > 10% |
|-----------------------|--------|--------|-------|-------|-------|-------|-------|-------|-------|-------|-------|--------|--------|--------|-----------|
| Er | 15.568 | 47.138 | 1.502 | 8.705 | 8.656 | 3.32 | 0.014 | 1.681 | 0.068 | 0.494 | 3.469 | 3.811 | 0.332 | 15.914 | * |
| Tf | | 3.724 | 2.064 | 0.951 | 0.746 | 2.159 | 0.973 | 0.256 | 0.004 | 3.233 | 1.249 | 0.042 | 22.032 | 0.461 | * |
| Zm | | | 0.010 | 0.093 | 0.639 | 5.179 | 0.764 | 1.113 | 1.786 | 1.573 | 7.042 | 3.046 | 5.013 | 21.372 | * |
| Sl | | | | 6.286 | 0.001 | 8.620 | 3.771 | 0.002 | 1.806 | 2.028 | 2.731 | 0.455 | 30.251 | 19.775 | * |
| Su | | | | | 2.402 | 8.247 | 0.216 | 0.165 | 0.007 | 3.025 | 0.075 | 5.117 | 3.354 | 1.658 | * |
| Pd | | | | | | 2.412 | 0.021 | 0.009 | 0.206 | 2.266 | 0.066 | 13.297 | 6.324 | 0.005 | * |
| Rg | | | | | | | 2.387 | 0.224 | 1.634 | 0.785 | 0.019 | 2.477 | 2.393 | 6.483 | * |
| Eb | | | | | | | | 0.015 | 4.566 | 0.037 | 0.114 | 0.598 | 21.962 | 37.323 | * |
| Lm | | | | | | | | | 1.025 | 4.816 | 1.585 | 2.224 | 4.408 | 0.428 | * |
| Sa | | | | | | | | | | 1.089 | 0.269 | 1.473 | 0.005 | +0.13 | * |
| Cd | | | | | | | | | | | 0.349 | -2.54 | 10.709 | 28.22 | * |
| Ek | | | | | | | | | | | | 0.367 | 0.011 | 3.881 | * |
| Ev | | | | | | | | | | | | | 3.758 | 5.846 | * |
| Po | | | | | | | | | | | | | | - | * |
| Wi | | | | | | | | | | | | | | 50.577 | * |

3.5 Discussion

The general patterns that emerged from the analysis are interesting in that they lend weight to both the deterministic (Yeaton & Esler 1990) and stochastic models (Cowling et al. 1999) as well as the need to consider the possibility of additional processes. The presence of a clump-matrix structure confirmed that both of these models were valid for the vegetation. In considering the specific requirements of the vegetation models, it is useful to separate the expected outcomes between the overall vegetation level and the more refined patch-matrix level.

At the overall vegetation level, the requirements of the stochastic model were not met. Vegetation clumps and matrix were not randomly assembled, as they comprised specific species associations. In addition, the lack of overall positive associations between species at the individual and neighbour scale could indicate the presence of competitive interactions. The stochastic model does not seem applicable as a general model at the vegetation level. The deterministic nurse-plant model has greater explanatory power at this scale. A basic two-guild system of succulents and woody plants was present. In addition, all vegetation clumps had a close association with one particular species of succulent viz. *Stoeberia utilis*.

Two aspects of the vegetation are not explained by either model. First is the presence of the monodominant *Willdenowia incurvata* stands and its overall negative relationship with both woody and succulent shrubs which suggests that the nurse-plant model is not the only deterministic process in operation. Second are the lack of gaps in both sites for seedling recruitment. The second point receives discussion in Chapter 4 (Vegetation Demography).

At the individual clump level, the obvious, but profound observation was that clumps were composed of multi-species associations and that the relative abundance of these species in each clump was unequal. This would not be the case under purely determinist competition process as more competitive species would tend to dominate vegetation clumps in similar proportions. Thus one has to consider a basic element of stochasticity in the formation of the clumps.

Disregarding the *Willdenowia incurvata* stands, the vegetation cycle for the area could be proposed as follows:

The area is firstly occupied by ‘sun-loving’ woody and succulent shrubs (Yeaton & Esler 1990, Milton et al. 1999), which establish in open areas. Of particular interest is the presence of *Stoeberia utilis*, which is taller than the mean height of the vegetation and thus has the potential to act as bird dispersal sites for fleshy-fruited woody shrubs by providing elevated perches. These woody species are hypothesized to germinate when conditions are favourable to start the formation of a clump. The particular species present in a clump will be dependent largely on the feeding and flight patterns of the birds (thus a stochastic element). Growth of the clump is a process of net mutual interactions (Boucher 1982, Callaway & Walker 1997, Hacker & Gaines 1997, Jones et al. 1997, Eccles et al. 1999) but limited by water availability (Eccles et al. 2001). The clumps eventually senesce or succumb to drought, age or possibly infrequent fires, making way for the ‘sun-loving’ woody and succulent plants.

The placing of *W. incurvata* into the above process does not seem apt. Its overall negative association with both clump and matrix vegetation sets it aside as an outsider to the above process. In fact, the species is more affiliated to fynbos vegetation than the succulent karoo and thus it is possible that a specific secondary vegetation process is applicable to this association. The limits of this association seems to be tied to more acidic soils as where pH was generally lower (pH =5.5) it was more dominant (Chapter 1 & 2). Infrequent fire as a disturbance regimen may have been an important historical factor in maintaining these *Willdenowia* stands.

The lack of a difference in species richness between the two sites (Chapter 2) can largely be attributed to both sites having the same spatial structure and individual species associations. In other words there was no overall difference between the two sites. This is not the first time a ‘no-difference’ result has been recorded for fence-line contrasts in the region. Todd & Hoffman (1999) found no difference between commercially and community grazed areas in terms of species diversity and structure, though species cover and composition did change. However, one needs to consider that although the current structure and diversity is similar, differences may only be evident in the future. The reason is that changes in vegetation structure and diversity may take many years to become evident (Wiegand et al. 1995), as most woody species are considered good persisters and changes to community structure may only been seen after a dramatic event such as drought, above average rainfall years or a fire. For example the effects of the loss of seed production due to flower herbivory may take several more decades to emerge.

The wide geographical separation in study areas between Yeaton and Esler (1990) and Eccles (2000) allows for speculation as to why two such different process models (deterministic competitive vs. stochastic mutualistic) should occur within in structurally similar vegetation. Holmgren et al. (1997) discuss the physiological trade-off faced by seedlings establishing in shaded versus unshaded sites along moisture gradients. Their overall conclusion was that, as sites became more arid with higher transpiration demands, benefits to seedling establishment would increase under the canopy of established plants, thus accounting for the 'nurse plant' effect. The climatic conditions at the Tierberg Karoo Research Centre (TKRC), where Yeaton and Esler (1990) found the deterministic model to be applicable, could be described as extreme, with summer temperatures reaching 43°C. The benefits to seedlings under canopy shade would be significant. Thus, if species were confined to shading sites for establishment, they would need to be strong competitors for soil water and nutrients and should eventually out-compete the established plant. The climatic condition at the Groen River Research Area (GRRRA), where the stochastic model was developed (Cowling et al. 1999) could be described as milder, with summer temperatures only averaging 20°C. The excessive transpiration demands on seedlings in this area would be relatively reduced. As competition for soil water is high (Eccles et al. 2001) and the dependence on shade is reduced, seedlings should benefit establishing away from mature plants.

In addition, seed germination in many succulent Karoo species requires a specific temperature range of 10 – 20 °C (Esler 1999). At TKRC, this restricts germination to the autumn season, thus resulting in peak autumn recruitment events (Milton 1995). In contrast, at GRRRA mean summer temperature is 20 °C with a mean minimum in winter of 9 °C (Eccles 2000). Thus conditions are suitable for germination for much of the year. Not only does this allow for conditions suitable for continual recruitment, but seeds trapped in the deep shade under canopies should germinate to a lesser degree than seeds in the open due to the warmer temperatures. Due to these factors, and possibly to others, the dependence on 'nurse plant' dynamics is lessened as the climate becomes cooler. This allows for a greater number of interactions between species, with the overall effects of competition being reduced.

As Rocherpan geographically lies between these two research sites and displays characteristics of both the determinist and stochastic models, it is suggested that the relative importance of each model will be determined by the prevailing climatic regime, particularly

relative transpiration demands and extrinsic germination controls. However, this requires further investigation.

3.6 References

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CHAPTER 4: QUANTIFYING THE DIFFERENCE IN SHRUB DEMOGRAPHY BETWEEN MEDIUM RESTED AND LONG RESTED STRANDVELD SUCCULENT KAROO AND ITS IMPLICATIONS CONSERVATION MANAGEMENT

4.1 Abstract

Differences in size class frequency distributions for eight shrub species was compared across an historic fence line separating vegetation that had been rested from grazing for 34 years and vegetation that had been rested from grazing for 11 years in the Strandveld Succulent Karoo. In the area rested for 34 years succulent species had a greater mean size while woody matrix species had a smaller mean size. This trend resulted in a significant difference in size class frequencies recorded between the two sites. In both areas, seedling counts for all species were low. These results are discussed in terms of known community dynamics (recruitment and population turnover) and the consequences for biodiversity management.

4.2 Introduction

The vegetation of the Succulent Karoo is dominated by dwarf leaf succulent and non-succulent (woody) evergreen shrubs (Cowling et al. 1994, Milton et al. 1997, Cowling et al. 1999, Esler & Rundel 1999). Although these two life forms occur in multi-species clumps (Eccles et al. 1999, Eccles 2000), their life-history strategies are very different. Key elements of the life-history strategies of the leaf succulent shrubs (as characterised by the Mesembryanthemaceae) are short life spans, resulting in 'rapid' population turnover, coupled with peak autumn recruitment from weakly persistent seed banks (Esler 1993, Milton 1995, Esler 1999, Jürgens et al. 1999). Succulent seedlings can be hardy (Esler 1993, Esler & Phillips 1994, Carrick 2001), but availability of suitable 'open' sites and proximity to adult plants limit seedling survival (Milton 1995).

In contrast, non-succulent woody shrubs are relatively long lived and demonstrate 'slow' population turnover (Cowling et al. 1999, Milton et al. 1999). Establishment of new plants is episodic depending on favourable climatic conditions (Milton 1995), while modular vegetative growth from buds (roots and shoots) is important (Esler 1999). Woody seedlings are less hardy than succulents (Esler 1993, Esler & Phillips 1994, Carrick 2001) and require good follow-up rains for continued survival. Establishment sites seem to be limited to shaded

environments under plants canopies, but once established, woody shrubs out compete nurse plants (Yeaton & Esler 1990, Cowling et al. 1997).

These two contrasting life-histories result in profound differences in community dynamics depending on the relative dominance of woody or succulent shrubs. Where woody shrubs dominate, competitive based models apply (Yeaton & Esler 1990, Cowling et al. 1997), while where succulent shrubs dominate, mutualistic interactions prevail due to the high population turn over and random dispersion (Tilman 1994, Cowling et al. 1999, Eccles et al. 1999). However, with the introduction of small-scale disturbances, local system dynamics can be decoupled from biotic driven mechanisms towards abiotic events such as rainfall (Wiegand et al. 1998), while it is implied that the prevention of such disturbances would allow for a return to biotic driven mechanisms.

For conservation managers in the Succulent Karoo, these system dynamics have important implications for biodiversity management. As the Succulent Karoo's species richness lies primarily within the leaf succulents, conservation strategies should be inclined towards these species. At Rocherpan Nature Reserve, a management policy of vegetation resting (by removing disturbance by browsing, digging and fire) was employed for two previously grazed areas. These areas had been rested for 34 years (termed Long Rested Vegetation; LRV) and 11 years (termed Medium Rested Vegetation; MRV). This presented the opportunity to investigate the succulent and woody shrub demographic changes in differentially rested sites.

4.3 Materials and Methods

4.3.1 Study Area

Rocherpan Nature Reserve occurs on the west coast of South Africa within the Succulent Karoo Biome (32° 36'S, 18° 18'E) and within the Strandveld Succulent Karoo veld type (known as Strandveld) (Low and Rebelo 1996). The reserve is bounded by farmlands to the north, east and south and the Atlantic Ocean in the west. The present size of the reserve covers some 914 hectares. The area receives predominantly winter rainfall with an estimated average annual rainfall of 260 mm. Fog and dew are a regular occurrence and may contribute significantly to the total precipitation received (Desmet & Cowling 1999). Temperatures in area are moderated by the proximity of the Atlantic Ocean but maximum temperatures over

summer (November-February) can exceed 35°C (mean Max: January- February = 36.9°C). The coolest months are between June to August with mean minimum temperatures of 3.3°C being recorded. Frost occurs on average 10 day per year. Wind plays an important role in the climate of the area. Hot, easterly berg winds can occur throughout the year and have very high evaporative demands (Desmet & Cowling 1999) while rain bearing north westerly prevails during winter. Soils are aeolian deposited tertiary to residual sands (Wessels & Hanekom 1997) with a shallow A horizon and a deep (>2 m) B horizon.

The vegetation is dominated by scattered low to medium shrubs including the leaf succulent Mesembryanthemaceae (especially *Ruschia* spp. and *Stoebaria utilis*) and Euphorbiaceae. Sclerophyllous evergreen and deciduous shrubs including *Euclea* (Ebenaceae), *Rhus* (Anacardiaceae), *Chrysanthemoides*, *Pteronia*, *Eriocephalus*, *Othonna* (Asteraceae) and *Lebeckia* (Fabaceae) of subtropical affinities occur in distinct clumps. Geophytes are well represented and include *Albuca*, *Lachenalia*, (Hyacinthaceae) *Babiana* and *Gladiolus* (Iridaceae). Grasses occur in scattered patches and include *Stipagrostis*, *Cladoraphis* and *Odysea*. Restionaceae species (*Willdenowia*) become more dominant where Succulent Strandveld is associated with Sand Plain Fynbos.

4.3.2 Species Selection & Plot layout

Shrub species selected for investigation were chosen based on their type (succulent or woody), frequency, growth form (species that were very multi-stemmed where simple excavations could not reveal individual plants were excluded from analysis) and specific vegetation association (occurring in vegetation clumps or as part of the matrix). As such eight species were available for investigation (Table 4.1).

Two line transects, one in the medium rested vegetation (MRV) and one in the Long Rested Vegetation (LRV), covering a distance of 1 000 meters, were placed parallel to each other a distance of 100 meters apart. Each transect consisted of alternating 5 x 5 meter sub plots. For each subplot all individuals of the target species were sought and measured. For each species, a minimum of 150 to a maximum of 200 individuals were measured with the difference in number of individuals measured between sites did not exceeding 5. For each species, length, breath and height of the canopy was measured and canopy volume was considered the product of these three measurements. For each species as well as all species pooled, significant

difference in canopy volumes between sites was tested with a *t*-test. Canopy volumes for all plants were then placed into one of 14 size classes. The upper univariate canopy dimension (in centimetres) for each size class was as follows: 10; 25; 50; 75; 100; 125; 150; 175; 200; 225; 250; 275; 300 and 325 cm. Significant differences in cumulative class frequency for each species was tested with a Kolmogorov-Smirnov test.

Table 4.1 Characteristic Species selected for demographic investigation

| Species | Shrub Type | Vegetation Association | Dispersal Type |
|------------------------------|------------|------------------------|----------------|
| <i>Eriocephalus kingesii</i> | Woody | Matrix | Birds |
| <i>Lebeckia multiflora</i> | Woody | Matrix | Herbivore |
| <i>Pteronia divaricata</i> | Woody | Matrix | Wind |
| <i>Pteronia onobromoides</i> | Woody | Matrix | Wind |
| <i>Salvia lanceolata</i> | Woody | Clump | Herbivore |
| <i>Zygophyllum morgsana</i> | Woody | Clump | Wind |
| <i>Euphorbia burmannii</i> | Succulent | Matrix | Ants |
| <i>Stoeberia utilis</i> | Succulent | Clump | Water |

4.4. Results

For both sites, the majority of the shrub species measured were symmetrically shaped with a uni-dimension (the cube root of the plant volume) ranging between 75 – 150 cm with a mean 130 cm in the Long Rested Vegetation (LRV) and a mean of 139 cm in the Medium Rested Vegetation with the difference being significant (Figure 4.1, Table 4.2, $t = 3.030$; $p > 0.005$). Of the eight species selected, only *Eriocephalus kingesii* and *Stoeberia utilis* had canopy volumes that differed significantly between sites (Table 4.2), while *Eriocephalus kingesii*, *Euphorbia burmannii*, *Pteronia divaricata* and *Stoeberia utilis* had significantly different size class frequencies (Table 4.3).

Species responsible for the LRV having smaller mean canopy sizes can be grouped into two categories. The first are species that in the MRV had a greater percentage of medium sized individuals (100 – 150 cm diameter) than in the LRV. These included succulent species *Stoeberia utilis* and *Euphorbia burmannii* as well as the woody shrub *Pteronia divaricata*. In terms of the succulent species, the smaller proportion of medium size individuals in the LRV is due to a higher proportion of large individuals (diameter > 175 cm) (Figure 4.2), while for

the woody species, the smaller proportion of medium sized individuals is due to a larger portion of small individuals (diameter > 100 cm).

Table 4.2. Mean, SE and median results of shrub species univariate canopy volumes for Long Rested Vegetation (LRV) and Medium Rested Vegetation (MRV), with *t*-test scores.

| <i>Species</i> | Mean diameter Canopy Volume (cm) <i>median</i> | | <i>t</i> | <i>df</i> >300; <400 |
|-------------------------------|--|--------------------|----------|----------------------|
| | LRV (n >150; <200) | MRV (n >150; <200) | | |
| <i>Salvia lanceolata</i> | 124±60 (99) | 123±59 (103) | 0.045 | NS |
| <i>Zygophyllum morganiana</i> | 104±53 (84) | 102±53 (83) | 0.189 | NS |
| <i>Pteronia divaricata</i> | 133±69 (109) | 135±64 (121) | 0.237 | NS |
| <i>Lebeckia multiflora</i> | 164±76 (150) | 161±71 (149) | 0.538 | NS |
| <i>Euphorbia burmannii</i> | 107±55 (76) | 97±49 (80) | 1.585 | NS |
| <i>Pteronia onobromoides</i> | 111±53 (96) | 123±59 (111) | 1.919 | NS |
| <i>Erioccephalus kingesii</i> | 99±49 (82) | 112±55 (96) | 2.063 | 0.05 |
| <i>Stoeberia utilis</i> | 202±88 (196) | 154±69 (139) | 5.813 | 0.001 |
| <i>All spp. Pooled</i> | 130±45 (103) | 139±53 (108) | 3.030 | 0.005 |

Table 4.3. Results of a Kolmogorov-Smirnov test for cumulative frequencies of canopy volumes for species in Long Rested Vegetation (LRV) and Medium Rested Vegetation (MRV)

| <i>Species</i> | <i>D</i> | <i>n</i> | <i>p</i> |
|-------------------------------|----------|----------|----------|
| <i>Zygophyllum morganiana</i> | 0.0333 | > 150 | NS |
| <i>Salvia lanceolata</i> | 0.0435 | > 160 | NS |
| <i>Pteronia onobromoides</i> | 0.0879 | > 150 | NS |
| <i>Lebeckia multiflora</i> | 0.0889 | > 150 | NS |
| <i>Erioccephalus kingesii</i> | 0.1087 | > 160 | 0.05 |
| <i>Euphorbia burmannii</i> | 0.1136 | > 160 | 0.05 |
| <i>Pteronia divaricata</i> | 0.1333 | > 150 | 0.01 |
| <i>Stoeberia utilis</i> | 0.4222 | 200 | 0.001 |

The second category is species that had a greater proportion of small individuals (diameters < 100 cm) in the LRV when compared to the MRV. This category comprises *Erioccephalus kingesii*, *Pteronia onobromoides* and *Lebeckia multiflora*, all woody matrix shrubs. Only *Erioccephalus kingesii* showed significant differences in size class frequency. Clump associated species, *Zygophyllum morganiana* and *Salvia lanceolata*, showed no difference in size frequency distribution. For all species recorded, there was a lack of seedlings (diameter > 10 cm) present.

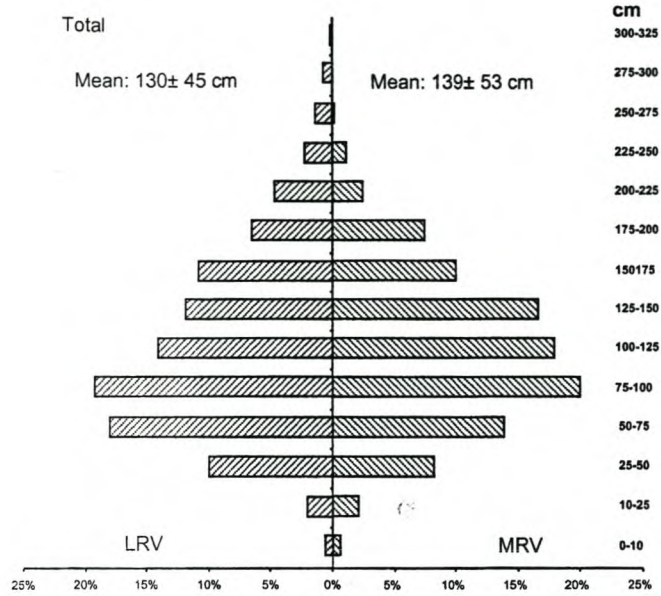


Figure 4.1 Size frequency profiles for all species pooled for Long Rested Vegetation (LRV) and Medium Rested Vegetation (MRV) showing that the LRV had on average smaller plants (mean LRV: 130 cm; MRV: 139 cm, units are univariate dimensions, i.e. the cube root of plant volume).

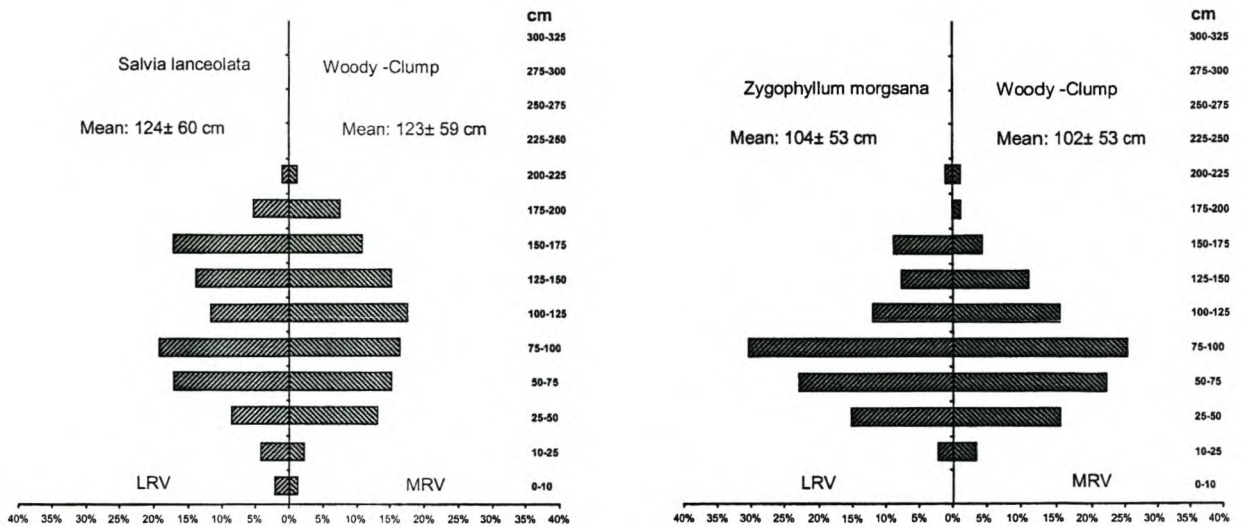


Figure 4.2 Size frequency profiles for individual species for Long Rested Vegetation (LRV) and Medium Rested Vegetation (MRV) showing mean \pm SE (units are univariate dimensions, i.e. the cube root of plant volume).

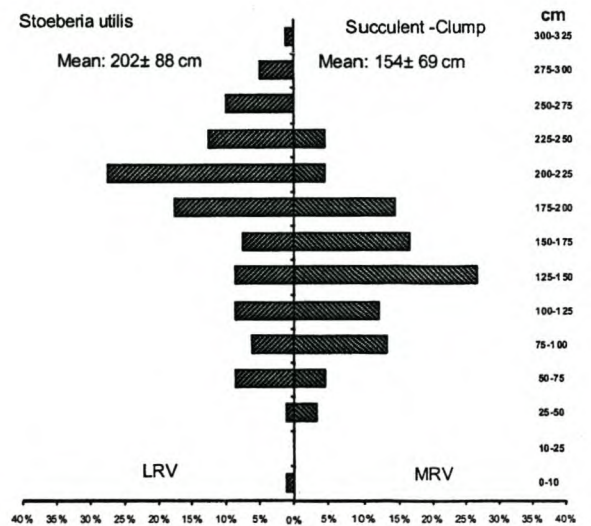
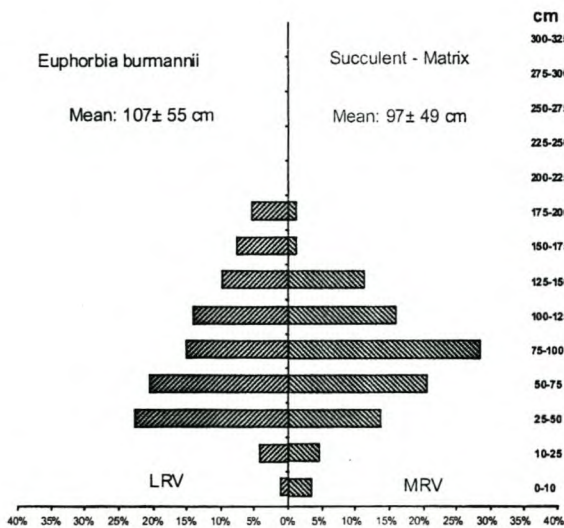
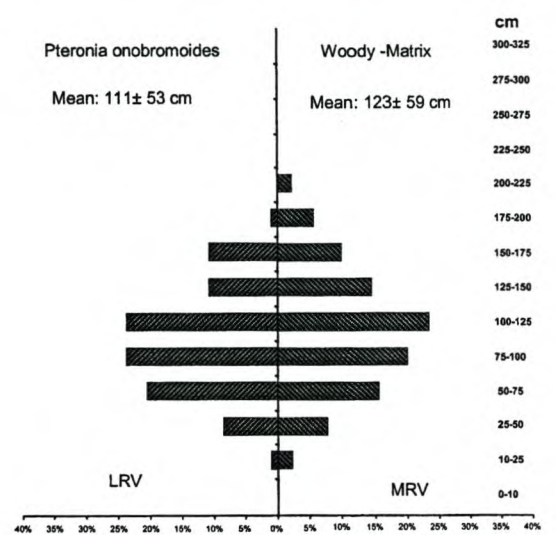
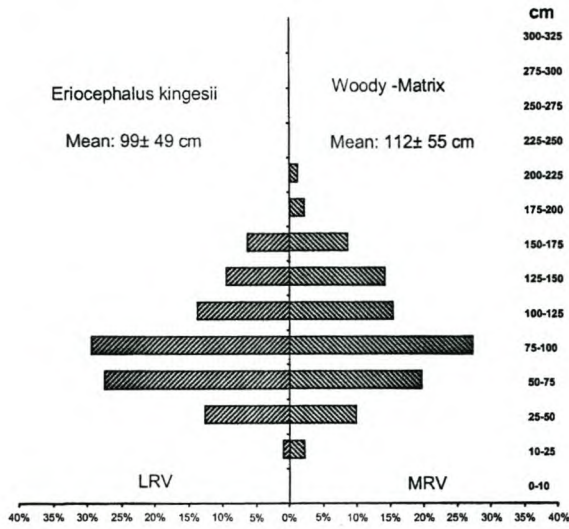
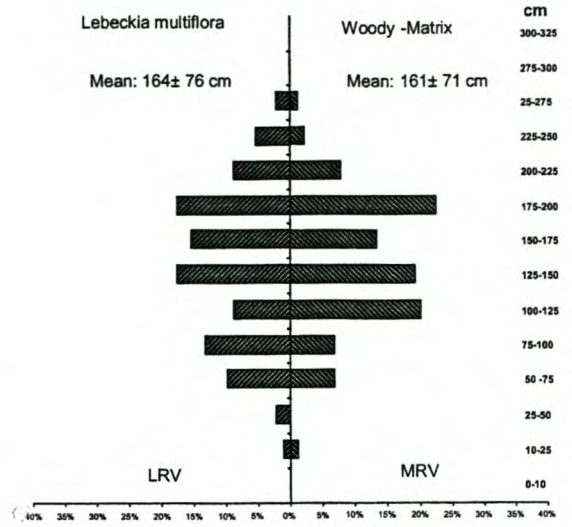
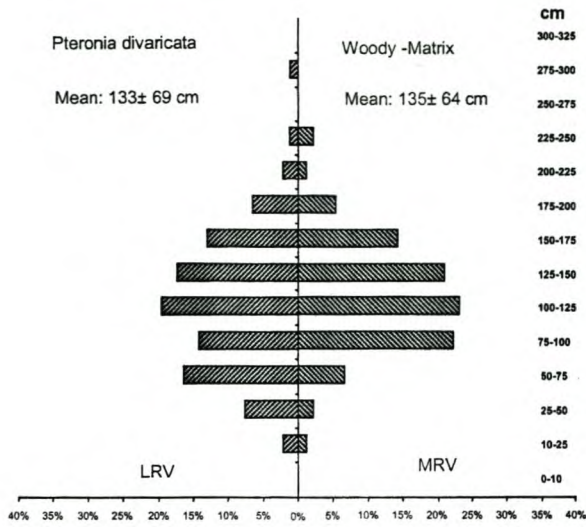


Figure 4.2 Continued.

4.5 Discussion

A number of short-term plant demographic studies in the Succulent Karoo rangelands assume a positive relationship between plant canopy volumes and plant age (e.g. Todd & Hoffman 1999, Wiegand et al. 2000, Carrick 2001, Riginos & Hoffman 2003) with the premise that negative changes in canopy cover can be attributed to a difference in grazing intensity or shrub growth. However, long-term studies from Australian shrublands (Watson et al. 1997) found that there was no consistent incremental growth between years and that shrub canopy volumes could decrease over time in the absence of grazing. Thus in terms of this study, a precautionary approach is taken with no assumption of a relationship between canopy volumes and plant age. Instead, species demography is referred to in terms of size frequency distributions.

Based on the size class distributions, the trends with increased vegetation resting can summarised by 1) woody species associated with vegetation clumps showed no difference in size distribution, 2) succulent species showed a greater proportion of larger individuals, 3) woody matrix species showed increasing proportion of small individuals and 4) recruitment at both sites for all species was limited. Speculations on the mechanisms responsible for these trends are presented as follows.

For woody species in vegetation clumps, clump association comprises random membership primarily due to random dispersion and mutualistic interactions, coupled with low but continuous recruitment and turnover (Cowling et al. 1999, Eccles et al. 1999, Eccles 2000). Thus as recruitment into clumps is stochastic at both sites, this could account for the lack of difference for woody shrubs and the relative effect of vegetation resting on vegetation clumps could be minimal.

The size frequency distributions of the clump succulent, *Stoebaria utilis*, showed clear differences between the sites with the LRV having on average larger individuals. For many leaf succulents in the Mesembryanthemaceae, a key element for regeneration is the availability of open, sunny sites that are often linked to disturbance (Esler 1993, Milton 1995, Carrick 2001). The low occurrence of succulent seedlings of these species could indicate that there is a lack of suitable germination sites (i.e. recruitment sites are saturated in the vegetation) at both sites due to lack of disturbance. This apparent lack of suitable sites for

germination of succulent species requiring open or disturbed sites is of importance as many of these species have the weakly persistent soil seed banks associated with succulent species (Esler 1993) are therefore at high risk of becoming locally extinct.

For the woody species in the matrix vegetation, the population of the LRV comprises a greater proportion of smaller size classes when compared to the MRV, which has a more uniform size class distribution of medium sized individuals, but lacks large individuals. Although the occurrence of even size classes has been put forward as evidence for continual recruitment (Watson et al. 1997, Wiegand et al. 2000), even sized cohorts could also be an artefact of long term grazing pressure. Before resting was initiated at Rocherpan, the area had been used for livestock grazing since *circa* 1840 (Wessels & Hanekom 1997) and this could have created a uniform sized class in the matrix of medium sized shrubs. With the release of grazing pressure in the LRV, some individual plants have become bigger at the expense of others, creating gaps for recruitment. As the MRV has not been rested as long as the LRV (11 and 34 years respectively), it still comprises the even sized cohorts. It is predicted that given more resting time, these even sized cohorts will under go maturation thinning with the result of a greater range in size classes. The lack of recruitment of woody species into the matrix vegetation could be due to competition and lack of available space (Milton 1995).

Due to the apparent lack of germination sites for sun establishing succulents and the strong competitive interaction from woody species, sun establishing succulents could be poised to become locally extinct. If biodiversity management is the key management objective for the area, then this should be of concern to conservation management, as the replacing woody species are from sub tropical affinities are less species rich than the succulent flora. Thus if disturbance is withheld for very long periods of time, overall species diversity should decrease as woody species begin to dominate. It is probable that in the past, grazing and browsing animals such as rhino and elephant played an important role in inducing small-scale disturbances (Skead 1980). These disturbances would have created opportunity for opening up of the matrix and thicket for succulent recruitment. Conservation management need to consider ways of reintroducing small-scale disturbance regimes to the area if the succulents requiring open and disturbed sites are to be maintained.

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CHAPTER 5: GENERAL CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS

The Succulent Karoo occupies an area of some 82 500 km² and less than 3% of the area is formally conserved (Low & Rebelo 1996). Within this area, an estimated 2 750 vascular plants occur, including approximately 10% of the world's succulent species (Cowling et al. 1999). The need to correctly manage areas under formal conservation is paramount. Current understanding of management principles stem from two community models. The first model emphasises deterministic competitive interactions, where short lived, disturbance adapted, succulent shrubs are replaced by woody shrubs (Yeaton and Esler 1990). The second model is based on stochastic mutualistic interactions, where continuous population turnover creates regular gap formation, which results in multi-species vegetation clumps (Cowling et al. 1999, Esler et al. 1999).

Key to both models is the need for small-scale gap creation, either through disturbance by animal activity or population turnover. With vegetation resting at Rocherpan Nature Reserve, the effects of disturbance removal for a medium period (11 years) and a long period (34 years) was investigated. This thesis focused on two themes. The first was the effects of resting on biodiversity and the second was the effect of resting on community dynamics, especially the specific changes to the succulent component of the vegetation.

Findings from chapter 2 show that plant species richness was not affected by vegetation resting. However this does not mean that two sites were the same. In the medium rested vegetation, drivers of diversity were the woody and succulent shrubs, while in the long rested vegetation, diversity was driven by woody shrubs and annuals. These results are consistent with a number of other studies where a loss in succulent cover due to grazing was compensated by an increase in annuals (Todd & Hoffman 1999, Carrick 2001, Riginos & Hoffman 2003) thus species richness *per se* did not change. However, conservation managers need to be aware of the relative importance and suitability of cosmopolitan annuals driving diversity as opposed to endemic succulents.

In chapters 3 and 4, definite changes in the succulent component of the community were identified. Here, a longer resting period resulted in succulent populations 'ageing' with little recruitment. This should be of concern to conservation managers, as some succulent species

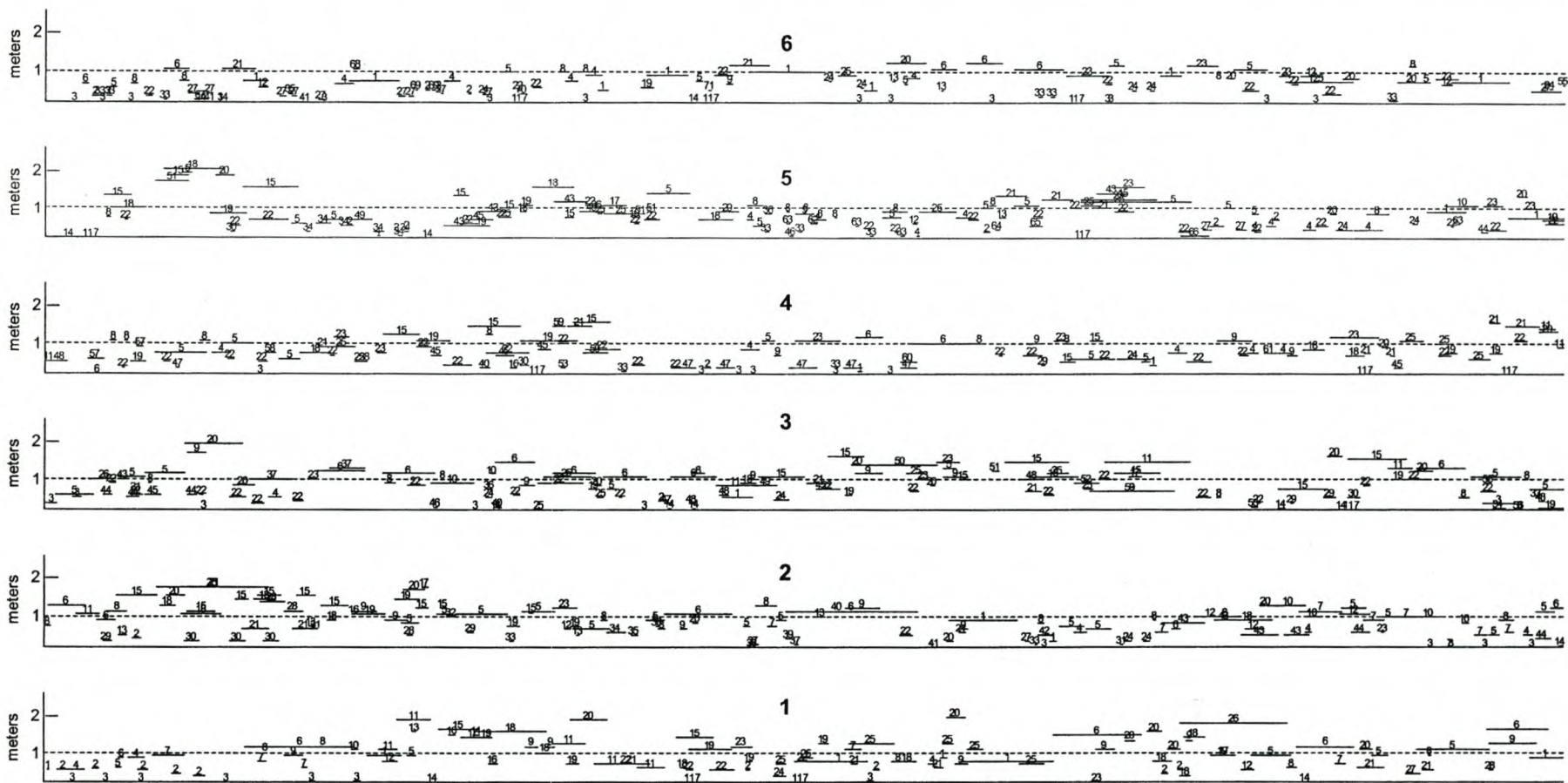
(e.g. Mesembryanthemaceae) have weakly persistent seed banks, do not disperse great distances and do not undergo modular growth. Several authors (e.g. Esler 1993, Milton 1995) attribute disturbance (the creation of open sites) as a requirement for these succulents to recruit. If vegetation resting continues and small-scale disturbances are withheld, it is possible that succulents associated with disturbance will be lost from the community. These results are consistent with studies from coastal fynbos where species rich fynbos was replaced by woody thicket when disturbance (being fire) was withheld (Cowling et al. 1997).

A clear insight gained from this thesis, also reported by Carrick (2001), is that known community dynamics for the Succulent Karoo differ widely between sites. In the south eastern region, deterministic competitive interactions prevail (Yeaton & Esler 1990), while in the north western region, stochastic mutualistic associations dominate (Cowling et al. 1999). I believe that climatic conditions govern this relationship, particularly around germination and growth temperature ranges for woody seedlings. It is speculated that as temperatures become warmer (while precipitation is kept constant), seedling water stress should increase. This could result in observed germination strategies where in hot areas, germination is confined to cooler autumn months and in shaded environments, while in milder areas, germination is continuous and may be limited to sunny environments. This is supported to some degree by Esler & Rundel (1999) who attribute a small difference in minimum winter temperatures for the stark difference in growth forms between the Succulent Karoo and the Mojave Desert. A possible area for further research could be to decouple the effect of climate on the known community dynamics models governing the Succulent Karoo. For example, a key question could be: as seeds are a key regeneration strategy for many Succulent Karoo species, why are seed banks not persistent? The answer could be climate based and different climatic conditions should result in different seed strategies. This area of research would become increasingly important in understanding Succulent Karoo vegetation changes under changing global climates.

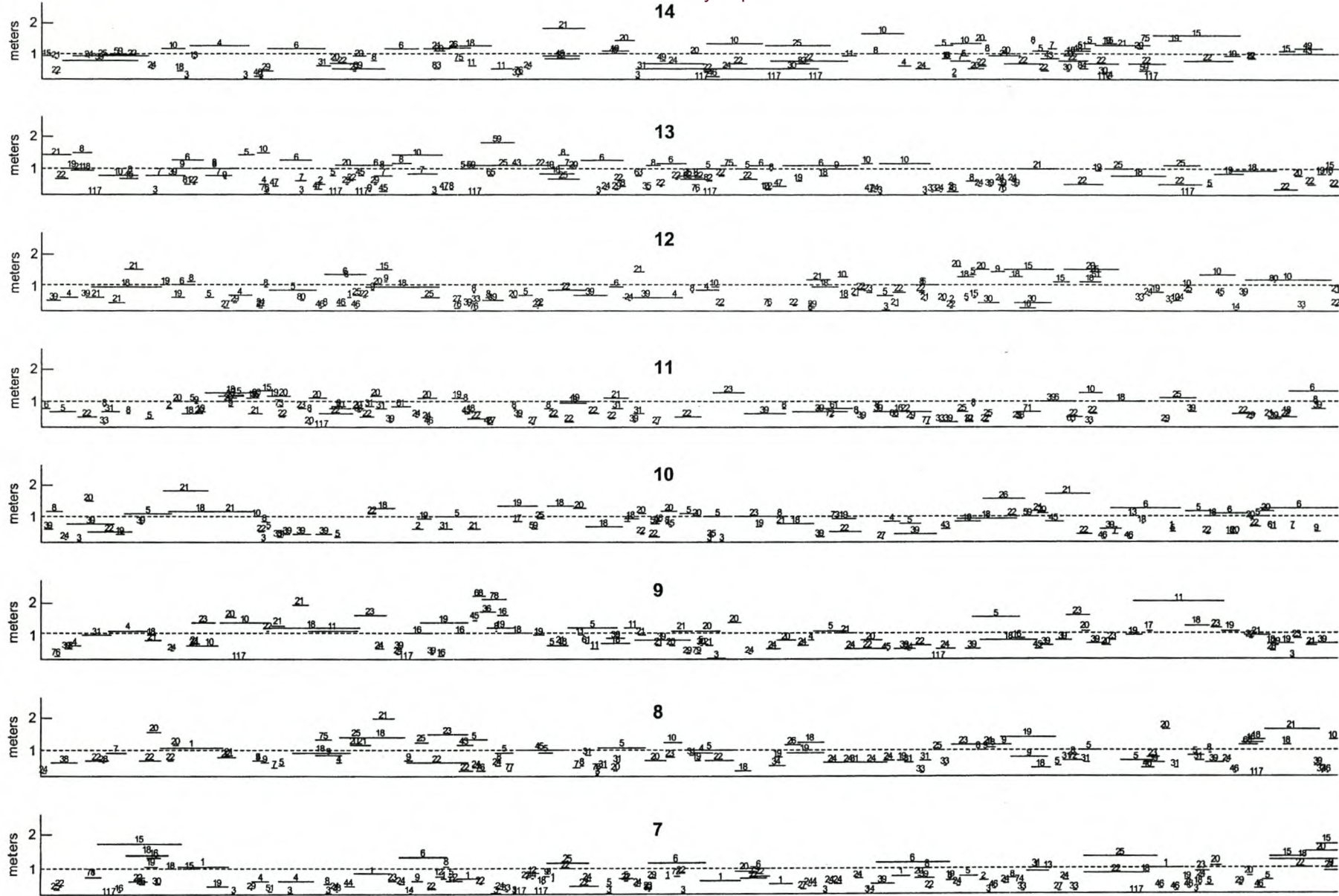
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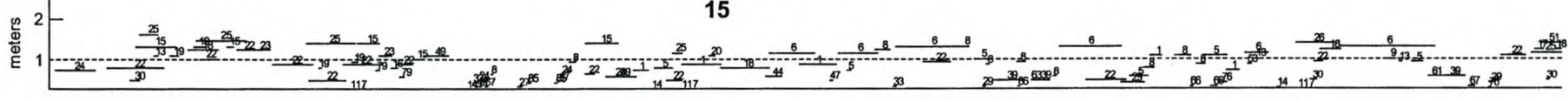
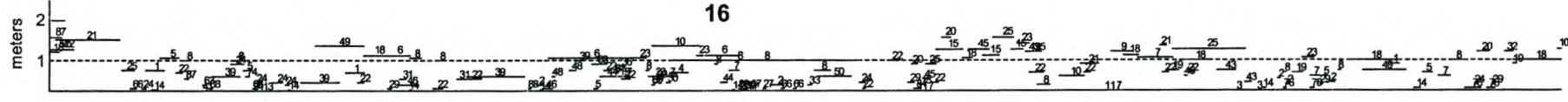
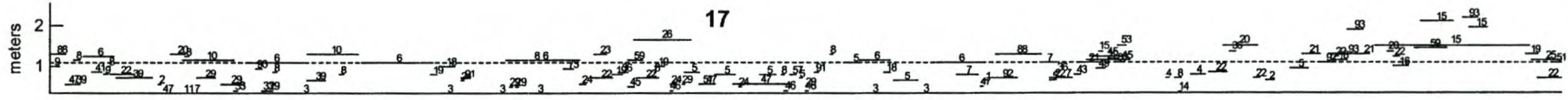
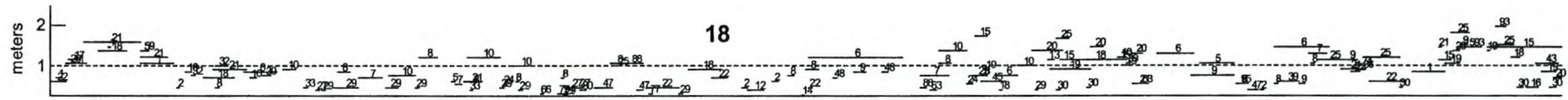
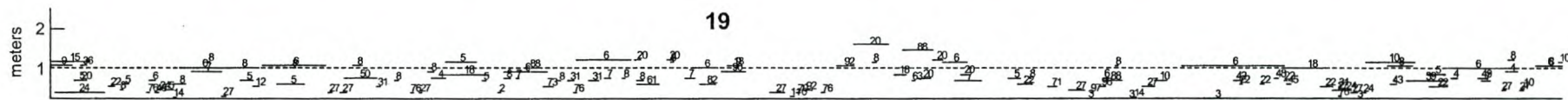
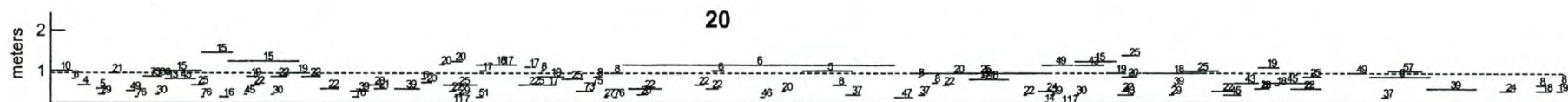
Appendix 1 – Graphical representation of Medium Rested and Long Rested sites sub-transects. Species Codes as per Appendix 2.



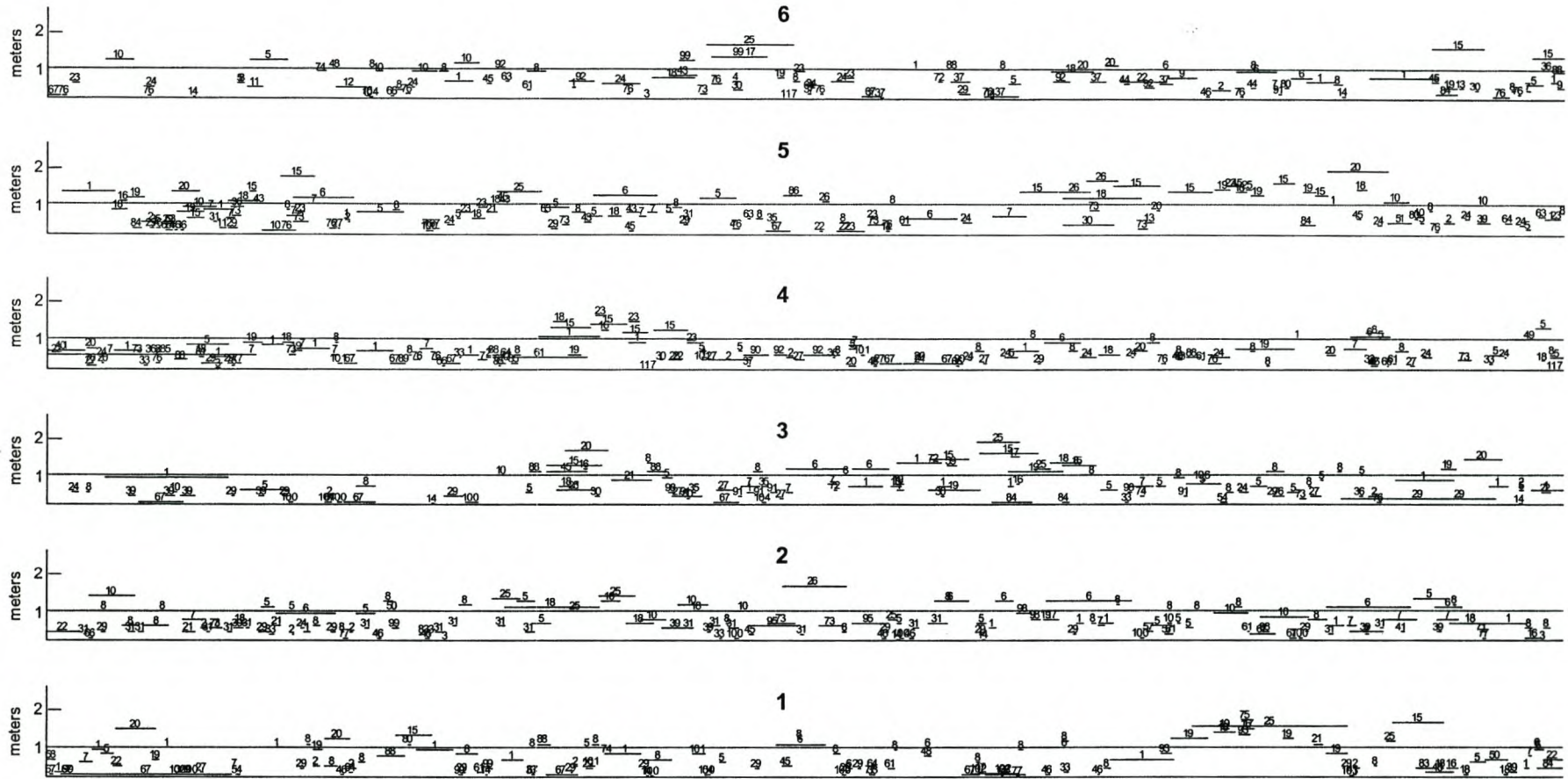
Medium Rested Vegetation – Sub Transects 1 – 6. Horizontal axis is 50 meters; broken line depicts the 1 meter height level.



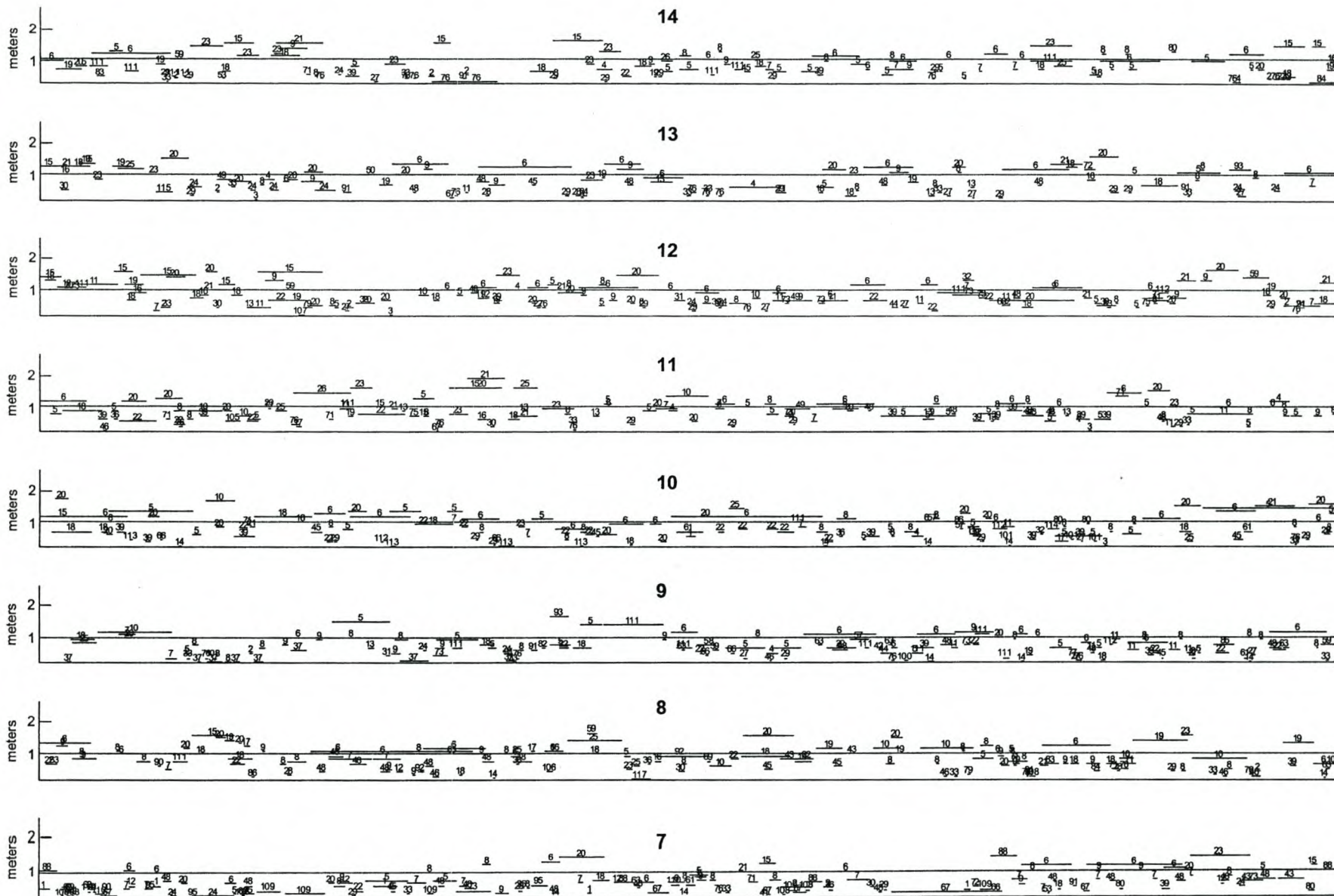
Medium Rested Vegetation – Sub Transects 7 - 14



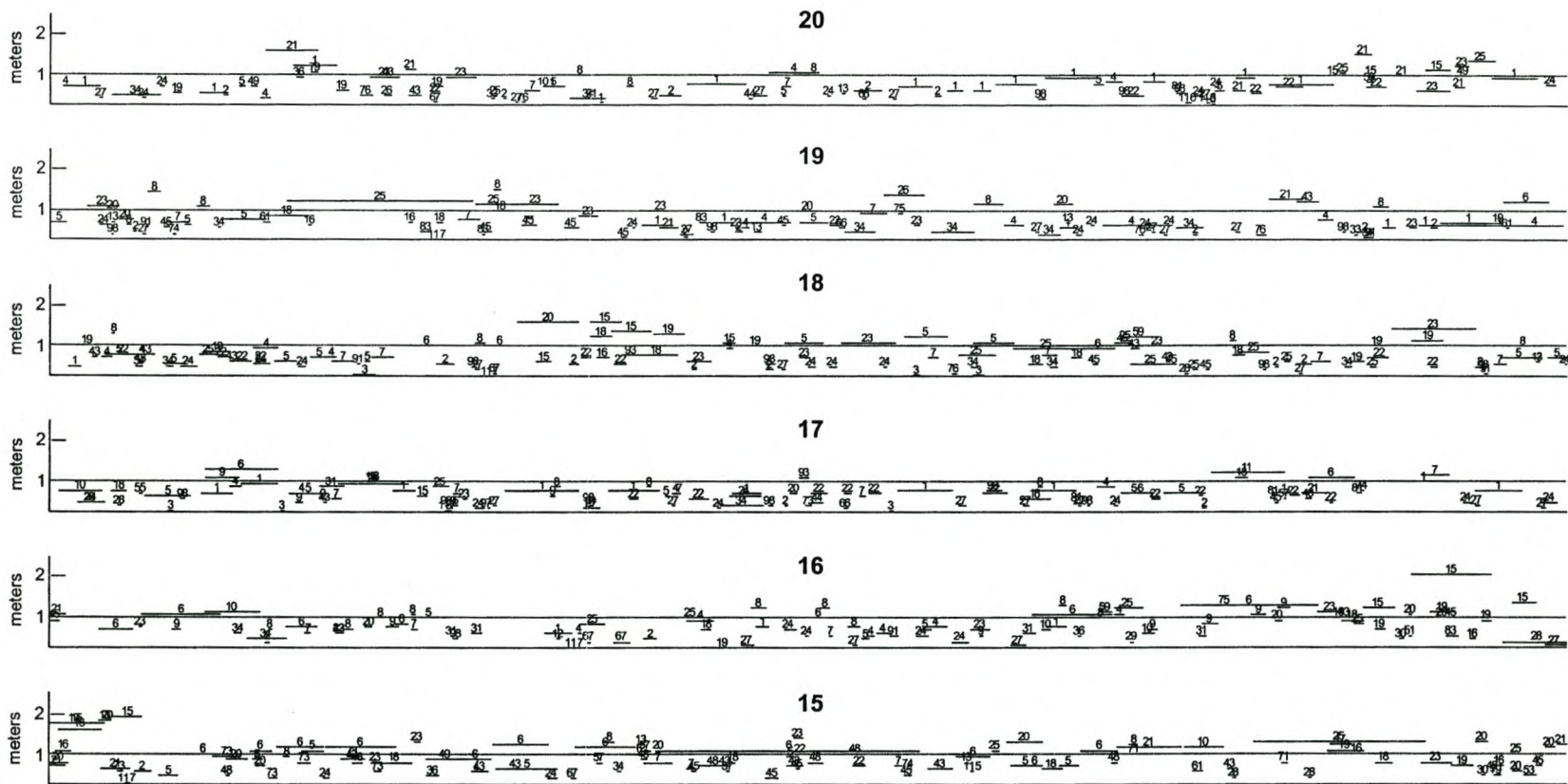
Medium Rested Vegetation – Sub Transects 15 - 20



Long Rested Vegetation – Sub Transects 1 - 6



Long Rested Vegetation – Sub Transects 7 - 14



Long Rested Vegetation – Sub Transects 15 - 20

Appendix 2: Plant species list for Medium Rested Vegetation (MRV) and Long Rested Vegetation (LRV) with the total cover measured on each transect and growth form used in analysis. Species codes correspond to Appendix 1. Nomenclature as per Germishuizen and Meyer 2003.

| Family | Genus | Species | Growth Form | MRV Cover (cm) | LRV Cover (cm) | Species Code |
|----------------|-------------------------|---------------------|-------------|----------------|----------------|--------------|
| Aizoaceae | <i>Adenogramma</i> | <i>glomerata</i> | ANN | 20 | 0 | 94 |
| | <i>Limeum</i> | <i>africanum</i> | ANN | 40 | 60 | 54 |
| | <i>Pharnaceum</i> | <i>albens</i> | ANN | 40 | 90 | 74 |
| | <i>Pharnaceum</i> | <i>exiguum</i> | ANN | 80 | 2615 | 67 |
| | <i>Tetragonia</i> | <i>fruticosa</i> | NDLS | 10090 | 6170 | 18 |
| Anacardiaceae | <i>Rhus</i> | <i>glauca</i> | NSS | 7060 | 5400 | 25 |
| | <i>Rhus</i> | <i>laevigata</i> | NSS | 1130 | 830 | 26 |
| Apiaceae | <i>Capnophyllum</i> | <i>leiocarpon</i> | GEO | 380 | 610 | 37 |
| Asclepiadaceae | <i>Microloma</i> | <i>sagittatum</i> | NSP | 270 | 225 | 36 |
| Asparagaceae | <i>Asparagus</i> | <i>capensis</i> | NSS | 70 | 100 | 40 |
| | <i>Asparagus</i> | <i>declinatus</i> | NSP | 240 | 1360 | 73 |
| | <i>Asparagus</i> | <i>kraussianus</i> | NSP | 80 | 30 | 42 |
| | <i>Asparagus</i> | <i>retrofractus</i> | NSS | 760 | 510 | 59 |
| | <i>Asparagus</i> | <i>rubicundus</i> | NSS | 80 | 0 | 96 |
| | <i>Asparagus</i> | <i>undulatus</i> | NSP | 830 | 660 | 16 |
| Asphodelaceae | <i>Trachyandra</i> | <i>divaricata</i> | GEO | 1110 | 620 | 31 |
| | <i>Trachyandra</i> | <i>falcata</i> | GEO | 380 | 665 | 61 |
| Asteraceae | <i>Chrysanthemoides</i> | <i>incana</i> | NSS | 1975 | 1250 | 11 |
| | <i>Eriocephalus</i> | <i>kingesii</i> | NSS | 8760 | 9920 | 5 |
| | <i>Felicia</i> | <i>hyssoifolia</i> | ANN | 20 | 40 | 81 |
| | <i>Felicia</i> | <i>sp1</i> | ANN | 20 | 340 | 98 |
| | <i>Helichrysum</i> | <i>bachmannii</i> | NSS | 0 | 1120 | 111 |
| | <i>Helichrysum</i> | <i>hebelepis</i> | ANN | 40 | 390 | 95 |
| | <i>Helichrysum</i> | <i>sp1</i> | NSS | 1810 | 1610 | 43 |
| | <i>Leysera</i> | <i>gnaphalodes</i> | ANN | 40 | 355 | 91 |
| | <i>Nestlera</i> | <i>biennis</i> | NSS | 20 | 25 | 85 |
| | <i>Othanna</i> | <i>cylindrica</i> | NDLS | 2445 | 3515 | 7 |
| | <i>Pteronia</i> | <i>divaricata</i> | NSS | 2930 | 3750 | 23 |
| | <i>Pteronia</i> | <i>onobromoides</i> | NSS | 4495 | 8630 | 1 |
| | <i>Senecio</i> | <i>aloides</i> | NDLS | 12299 | 2960 | 22 |
| | <i>Senecio</i> | <i>corymbiferus</i> | NDLS | 60 | 30 | 58 |
| | <i>Senecio</i> | <i>vulgaris</i> | ANN | 20 | 0 | 70 |
| | <i>Senecio</i> | <i>sp1</i> | NDLS | 640 | 230 | 12 |
| | <i>Tripteris</i> | <i>clandestina</i> | ANN | 20 | 0 | 62 |
| | <i>Ursinia</i> | <i>anthemoides</i> | ANN | 20 | 110 | 90 |
| | <i>Unident</i> | <i>sp1</i> | ANN | 910 | 1370 | 29 |
| | <i>Unident</i> | <i>sp3</i> | ANN | 50 | 0 | 60 |
| <i>Unident</i> | <i>sp10</i> | ANN | 0 | 125 | 112 | |

| Family | Genus | Species | Growth Form | MRV Cover (cm) | LRV Cover (cm) | Species Code |
|----------------|---------------------|----------------------|-------------|----------------|----------------|--------------|
| Brassicaceae | <i>Heliophila</i> | <i>arenaria</i> | ANN | 210 | 190 | 57 |
| Campanulaceae | <i>Cyphia</i> | <i>sp1</i> | NSP | 220 | 360 | 13 |
| | <i>Wahlenbergia</i> | <i>capensis</i> | ANN | 365 | 280 | 33 |
| | <i>Wahlenbergia</i> | <i>sp 1</i> | ANN | 15 | 15 | 89 |
| | <i>Wahlenbergia</i> | <i>sp2</i> | ANN | 10 | 0 | 97 |
| Celastraceae | <i>Maytenus</i> | <i>heterophylla</i> | NSS | 300 | 300 | 93 |
| | <i>Putterlickia</i> | <i>pyracantha</i> | NSS | 90 | 0 | 78 |
| Chenopodiaceae | <i>Exomis</i> | <i>microphylla</i> | ANN | 0 | 30 | 106 |
| Crassulaceae | <i>Cotyledon</i> | <i>orbiculata</i> | NDLS | 0 | 340 | 99 |
| | <i>Crassula</i> | <i>capitella</i> | ANN | 0 | 70 | 115 |
| | <i>Crassula</i> | <i>glomerata</i> | ANN | 0 | 10 | 103 |
| | <i>Crassula</i> | <i>muscosa</i> | DLS | 65 | 0 | 65 |
| | <i>Crassula</i> | <i>oblanceolata</i> | ANN | 55 | 25 | 41 |
| | <i>Crassula</i> | <i>thunbergiana</i> | ANN | 0 | 30 | 104 |
| Cucurbitaceae | <i>Kedrostis</i> | <i>psammophila</i> | GEO | 1495 | 265 | 3 |
| Cyperaeae | <i>Isolepis</i> | <i>antarctica</i> | GR | 0 | 65 | 108 |
| Ebenaceae | <i>Euclea</i> | <i>racemosa</i> | NSS | 6830 | 5670 | 15 |
| | <i>Euclea</i> | <i>tomentosa</i> | NSS | 100 | 70 | 32 |
| Euphorbiaceae | <i>Euphorbia</i> | <i>burmannii</i> | SS | 2735 | 2680 | 9 |
| | <i>Euphorbia</i> | <i>caput-medusae</i> | SS | 400 | 130 | 44 |
| | <i>Euphorbia</i> | <i>mauritanica</i> | SS | 50 | 0 | 87 |
| Fabaceae | <i>Crotalaria</i> | <i>excise</i> | NSP | 250 | 1350 | 48 |
| | <i>Lebeckia</i> | <i>multiflora</i> | NSS | 4225 | 3330 | 10 |
| | <i>Lotononis</i> | <i>sp1</i> | NSP | 465 | 185 | 46 |
| | <i>Wiborgia</i> | <i>obcordata</i> | NSS | 510 | 750 | 88 |
| Fumariaceae | <i>Cysticapnos</i> | <i>vesicarius</i> | ANN | 160 | 380 | 71 |
| Geraniaceae | <i>Pelagonium</i> | <i>fulgidum</i> | NSS | 160 | 55 | 51 |
| | <i>Pelagonium</i> | <i>gibbosum</i> | NSS | 370 | 10 | 53 |
| Hyacinthaceae | <i>Albuca</i> | <i>flaccida</i> | GEO | 170 | 90 | 75 |
| | <i>Lacinalia</i> | <i>sp1</i> | GEO | 105 | 0 | 38 |
| | <i>Unident</i> | <i>sp8</i> | GEO | 165 | 195 | 63 |

| Family | Genus | Species | Growth Form | MRV Cover (cm) | LRV Cover (cm) | Species Code |
|---------------------|----------------------|-----------------------|-------------|----------------|----------------|--------------|
| Iridaceae | <i>Babiana</i> | <i>ringens</i> | GEO | 60 | 70 | 35 |
| | <i>Babiana</i> | <i>sp1</i> | GEO | 185 | 180 | 66 |
| | <i>Ferraria</i> | <i>divaricata</i> | GEO | 15 | 10 | 55 |
| | <i>Gladiolus</i> | <i>speciosus</i> | GEO | 5 | 10 | 86 |
| | <i>Labeirousia</i> | <i>anceps</i> | GEO | 10 | 70 | 110 |
| | <i>Melasphaerula</i> | <i>ramosa</i> | GEO | 680 | 340 | 30 |
| | <i>Moraea</i> | <i>sp 1</i> | GEO | 45 | 100 | 80 |
| Lamiaceae | <i>Ballota</i> | <i>africana</i> | NSP | 70 | 240 | 83 |
| | <i>Salvia</i> | <i>lanceolata</i> | NSS | 5190 | 5674 | 20 |
| Melanthaceae | <i>Melianthus</i> | <i>minor</i> | NSS | 900 | 470 | 49 |
| Menispermaceae | <i>Cissampelos</i> | <i>capensis</i> | NSP | 1745 | 925 | 45 |
| Mesembryanthemaceae | <i>Apatesia</i> | <i>helianthoides</i> | DLS | 1050 | 20 | 47 |
| | <i>Dorotheanthus</i> | <i>sp1</i> | DLS | 0 | 190 | 100 |
| | <i>Lampranthus</i> | <i>amoenus</i> | NDLS | 80 | 0 | 52 |
| | <i>Rushia</i> | <i>brevibracteata</i> | NDLS | 2640 | 2035 | 4 |
| | <i>Stoeberia</i> | <i>utilis</i> | NDLS | 5865 | 2700 | 21 |
| | <i>Unident</i> | <i>sp6</i> | DLS | 230 | 660 | 92 |
| | <i>Unident</i> | <i>sp7</i> | DLS | 0 | 90 | 113 |
| Orchidaceae | <i>Satyrium</i> | <i>sp1</i> | GEO | 0 | 130 | 107 |
| Oxalidaceae | <i>Oxalis</i> | <i>sp1</i> | GEO | 305 | 145 | 14 |
| Poaceae | <i>Chaetobromus</i> | <i>dregeanus</i> | GR | 2800 | 2090 | 24 |
| | <i>Ehrharta</i> | <i>delicatula</i> | GR | 820 | 1745 | 2 |
| | <i>Ehrharta</i> | <i>villosa</i> | GR | 4465 | 5170 | 8 |
| | <i>Pentaschistis</i> | <i>pusilla</i> | GR | 0 | 330 | 109 |
| Polygonaceae | <i>Rumex</i> | <i>sp1</i> | NSP | 0 | 125 | 101 |
| Restionaceae | <i>Willdenowia</i> | <i>incurvata</i> | GR | 13710 | 18980 | 6 |
| Rubiaceae | <i>Galium</i> | <i>tomentosum</i> | NSP | 40 | 100 | 79 |
| Scrophulariaceae | <i>Dischisma</i> | <i>sp1</i> | ANN | 40 | 55 | 77 |
| | <i>Hebenstreitia</i> | <i>sp1</i> | ANN | 0 | 160 | 102 |
| | <i>Lyperia</i> | <i>tristis</i> | ANN | 15 | 30 | 69 |
| | <i>Nemesia</i> | <i>sp1</i> | ANN | 10 | 75 | 64 |
| | <i>Phyllopodium</i> | <i>capillare</i> | ANN | 400 | 1085 | 76 |
| | <i>Phyllopodium</i> | <i>cephalophorum</i> | ANN | 840 | 950 | 27 |

| Family | Genus | Species | Growth Form | MRV Cover (cm) | LRV Cover (cm) | Species Code |
|----------------|--------------------|---------------------|-------------|----------------|----------------|--------------|
| Solanaceae | <i>Cestrum</i> | <i>sp1</i> | NSS | 0 | 50 | 105 |
| | <i>Lycium</i> | <i>ferocissimum</i> | NSS | 160 | 0 | 68 |
| | <i>Solanum</i> | <i>nigrum</i> | NSS | 195 | 800 | 28 |
| Sterculiaceae | <i>Hermannia</i> | <i>longifolia</i> | NSP | 260 | 1120 | 34 |
| | <i>Hermannia</i> | <i>sp1</i> | NSP | 5115 | 1420 | 39 |
| | <i>Hermannia</i> | <i>trifurca</i> | NSS | 460 | 350 | 50 |
| Urticaceae | <i>Droguetia</i> | <i>iners</i> | ANN | 50 | 500 | 84 |
| Viscaceae | <i>Viscum</i> | <i>capense</i> | NSP | 465 | 270 | 17 |
| Zygophyllaceae | <i>Zygophyllum</i> | <i>morgsana</i> | NDLS | 4960 | 3750 | 19 |
| Unknown | <i>Unident</i> | <i>sp2</i> | ANN | 5 | 0 | 56 |
| | <i>Unident</i> | <i>sp4</i> | ANN | 90 | 100 | 72 |
| | <i>Unident</i> | <i>sp5</i> | ANN | 130 | 20 | 82 |
| | <i>Unident</i> | <i>sp6</i> | ANN | 1480 | 280 | 117 |
| | <i>Unident</i> | <i>sp7</i> | ANN | 0 | 40 | 114 |
| | <i>Unident</i> | <i>sp8</i> | ANN | 0 | 30 | 116 |

Reference

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Strelitzia 14.