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**Spatio-temporal distribution of grass and shrubs at the ecotone
between an arid grassland and succulent shrubland: ecological
interactions and the influence of soils**

NDAFUDA NANGULA SHIPONENI

**Thesis Presented for the Degree of
DOCTOR OF PHILOSOPHY
in the Department of Botany, Faculty of Science
UNIVERSITY OF CAPE TOWN**

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UT 580 SHIP

823588

University of Cape Town

Declaration

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

Signature

Date

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Dedication

To the arid zone ecology under the current challenge of environmental change.

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Abstract

This thesis presents ecological investigations of vegetation at an ecotone between the Namaqualand shrublands and Bushmanland arid grassland at the climatic transition between the predominantly winter rainfall Succulent Karoo and the predominantly summer rainfall Nama-Karoo biomes. The work focused on the determinants of grass and succulent shrub vegetation characterising the ecotone, and on determining the current and past distribution of this vegetation. A combination of detailed community level investigations (both observational and experimental), and a variety of remotely sensed data and techniques were applied to capture processes and patterns at different scales. In the first set of investigations, I have investigated the role of soil and competition on vegetation patterns. Secondly, field data were combined with remote sensing technology to establish the current distribution of grasses and shrubs along the ecotone, and to determine how this vegetation has changed over the past 20 years.

Along the gradients of grass and succulent shrub communities, multivariate ordination and statistical techniques have revealed that variation in the underlying physical and chemical soil properties explained less than 15% of the variation in vegetation patterns and thus contributes little to the observed vegetation patterns at the ecotone. Similarly, a reciprocal seedling transplant experiment in these communities did not result in significant influence of soil on the establishment of seedlings, especially for a leaf succulent shrub *Ruschia robusta* which could be monitored for the duration of the experiment. The same experiment has revealed the importance of root competition from the established grass vegetation in preventing the establishment of *R. robusta* seedlings in grass community. Evidences of competitive relationships were also found between the grass *Stipagrostis brevifolia* and the shrub *R. robusta*, the two abundant species in communities where the two growth forms co-occur, as inferred from the nearest-neighbour analysis technique. The pattern from these studies is that the vegetation pattern at the ecotone is not due to soil preferences, but plant interactions play a significant role in these communities. Furthermore, *S. brevifolia* had stronger competitive effects on *R. robusta* than vice versa, as inferred from the nearest-neighbour analysis in communities where they co-occurred. Root excavations of the rooting systems of the respective species have revealed that grass has deeper root system in relation to shallow root system characterising the leaf succulent shrub species. This differentiation was used to explain the co-existence between the two growth forms, but the partial overlap in the root systems between *S. brevifolia* and *R. robusta* allowed for the observed competitive relationships.

With the use of field data and the recent ASTER satellite data, a detailed vegetation map depicting the spatial distribution of grass and shrubs at the ecotone was produced. The strength in the map lies in the mapping of grass vegetation patches embedded in the matrix of Namaqualand shrublands in the western part of the study area, which have not been mapped before, and the high classification accuracy at which the map was produced. The established spectral characteristics of grass and shrub vegetation were used in an image differencing change-detection technique, using multi-temporal Landsat data, to derive spectral changes reflecting vegetation shifts over the past 20 years. A change-detection method was also applied on the same multi-temporal Landsat data to derive spectral changes reflecting changes in vegetation cover. According to the analysis, most of the detected areas of change were characterised by fluctuations in the direction of vegetation change, indicating that the vegetation has been relatively stable over the period of 20 years, and only a small area showed signs of directional vegetation change. Where directional change was detected, it was related either to a decrease in general vegetation cover or to an increase in grass cover.

Evidence of increasing grassiness, together with the observed strong competitive effects on the succulent shrubs by the grass is of significance to ecotone dynamics, and may be related to the perceived decrease in winter rainfall to which the succulent shrubs in the area are well adapted.

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1. Introduction

1.1 Problem statement

This research project was prompted by a number of interrelated lines of concern encompassing both physical and ecological components; the patchiness and dynamics of Karoo vegetation, the perceived and predicted climate change in the area, the perception that livestock grazing (the main land use type in the area) causes vegetation change, and the perceived sensitive nature of ecotones to change. Ecotones or transition zones between biotypes are perceived to be highly sensitive to environmental changes. Roux and Theron (1987) have long referred to the existence of several ecotones in the Karoo where change is thought to be taking place faster than elsewhere in the area. They have then pointed out that monitoring vegetation change of Bushmanland (a desert grassland) and its transition with the winter rainfall Succulent Karoo, should be regarded as a high priority. The area along the border between Namaqualand and Bushmanland lies within the zone separating the predominantly winter rainfall Succulent Karoo and predominantly summer rainfall Nama-Karoo biomes. Climate change scenarios suggest that winter rainfall in the region will decrease and that species characteristic of the Succulent Karoo will go extinct with this climate shift (Rutherford, Powrie and Schulze 1999; Hannah, Midgley and Millar 2002). A more recent analysis of the rainfall in the Namaqualand region over the past 50 years has also shown a trend of decreasing winter rainfall and an increase in summer rainfall (MacKellar, Hewitson and Tadross 2007).

The ecotonal vegetation is characterised by communities of Bushmanland arid grasslands and Namaqualand succulent shrublands adjacent to each other, and communities where grass and shrubs intermingle to form mixed communities. This vegetation pattern and the potential link between ecotones and climate have raised questions such as what factors or what are the key processes that control vegetation distribution, and how these processes affect vegetation responses to predicted change in climate. Drivers of the vegetation at the ecotone are not well understood and it is not known how the vegetation is likely to respond to predicted shifts in climate. Furthermore, it is also not clear how or if the vegetation has changed in recent years. A clear understanding of ecological interactions among grass and shrub vegetation characterising the ecotone is lacking. A detailed analysis of current and past patterns in vegetation distribution is also required. These are important information that will provide an improved understanding of the vegetation functioning and dynamics at the ecotone, and thus guide future scenario development.

1.2 Background and context

1.2.1 Properties of ecotones

In the literature, the term ecotone dates back to early 1900s to denote the junction zone between two vegetation communities (Clements 1905). There has been an expansion in this definition, to the concept that is of many spatial and temporal scales (Holland 1988). Literature on ecotones however is notable for the speculations that have been made about them rather than for the hard data (Lloyd et al. 2000). Among the commonly mentioned generalisations about ecotones in the literature are probably that these areas hold high species and community diversity comparing to the biomes that separate them, and that these areas represent regions of high sensitivity to directional environmental changes (Shmida and Wilson 1985; Delcourt and Delcourt 1988; Holland 1988; Hansen and di Castri 1992; Gosz 1993; Neilson 1993; Risser 1995; Lloyd et al. 2000; Hochstrasser et al. 2002). Such hypotheses have rarely been tested, but available evidence indicate that characteristics are not intrinsic properties of ecotones, but depends on particular ecological conditions and the ecology of the species present (Delcourt and Delcourt 1988; Hansen and di Castri 1992; Noble 1993; Lloyd et al. 2000; Walker et al. 2003; Prous, Ferreira and Martins 2004).

At the ecotone, certain species from adjacent vegetation types are expected to overlap and co-exist as they reach the edge of their geographical distribution, and together with the new species specific to the ecotone itself create an area of high level of biological diversity (Shmida and Wilson 1985; Delcourt and Delcourt 1988; Hansen, di Castri and Naiman 1988; Holland 1988; Gosz 1993; Neilson 1993; Risser 1995). The literature did not show consistency in results regarding higher species richness in ecotones however, but Hansen et al. (1988) have suggested that an increase in diversity is only one possibility for ecotones, and diversity can be greater, intermediate or lower than that of the neighbouring areas, as supported by recent evidences comparing a number of different ecotones (Lloyd et al. 2000; Walker et al. 2003). For example, Walker et al. (2003) have indicated that only one out of four ecotones analysed has higher species richness than the adjacent communities, whereas the others have intermediate species richness.

At ecotones, species occurrences are expected to be more sensitive to environmental heterogeneity as conditions for many species become marginal (Shmida and Wilson 1985; Solomon 1986; Gosz 1993; Neilson 1993; Hochstrasser et al. 2002). High sensitivity to directional changes in climate at ecotonal areas is based on the argument that the species range limits at ecotones particularly at biome levels are often directly controlled by climate (Shmida and Wilson 1985; Holland 1988; Gosz 1992; Neilson 1993; Noble 1993; Risser 1993).

Conversely, one may also argue that ecotonal species are least responsive to environmental change as the species are adapted to the ecotonal environment. Empirical support of ecotonal species in the sense of species mainly restricted to the ecotone or species that occurred more frequently within ecotones than in the adjacent vegetation has been recently offered from an investigation of different ecotones in south western New Zealand (Lloyd et al. 2000).

Several boundaries have been proposed within the broader Karoo region, where vegetation change is thought to be taking place. The most documented is probably the replacement of sweet grassveld by an open karroid shrubland in the eastern Karoo around which Acocks' (1975) expanding Karoo theory¹ is centred. Subsequent research however, has challenged this theory indicating that fluctuations between grass and Karoo shrubs may be an important characteristic of the eastern Karoo shrublands (Hoffman, Barr and Cowling 1990; Hoffman and Cowling 1990; Bousman and Scott 1994; O'Connor and Roux 1995). Furthermore, insights into the causes of vegetation change indicated that grazing alone is not responsible for the dynamics of this vegetation, but variations in rainfall patterns have profound effects on the response of the vegetation.

The current project focuses on the ecotone along a climatic transition between the predominantly winter rainfall Namaqualand vegetation (Succulent Karoo biome) and the predominantly summer rainfall Bushmanland vegetation (Nama-Karoo biome). Rainfall seasonality becomes less defined as one grades into this zone of overlap between the two biomes and rainfall can occur any time of the year (Cannon 1924; Desmet and Cowling 1999). Rainfall patterns at different sites along the ecotone are presented in the next chapter. Acocks (1975) has proposed that there is an invasion of Succulent Karoo elements into the Arid Karoo (a part of Nama-Karoo), marked by the replacement of the non-succulent palatable shrubs by the unpalatable succulents in an eastward direction. Acocks (1975) however, further argued that this movement was relatively small because the Succulent Karoo is generally confined to the winter rainfall region and is not that well adapted to the summer rainfall area that it is invading. With the predicted decrease in winter rainfall mentioned earlier in this chapter, this might have an important implication on the type and direction of changes.

Lack of ecological investigations along vegetation boundaries in general and within the Karoo has led to poor understanding of these regions. In this thesis, I do not intent to test the generalisations that are made about ecotones, but from a variety of empirical studies introduced

¹ John Acocks, one of South Africa's prominent botanist proposed that various Karoo veld types were expanding eastwards into areas that would otherwise be grassland, as a direct result of mismanagement of the rangelands.

in this chapter and undertaken as part of this project, inferences will be made to describe the ecotone regarding some of the hypotheses. The focus of this research project is on the functional diversity of the ecotone, and thus in gathering information contributing to the understanding of the dynamics and functioning of the ecotone.

1.2.2 The influence of climate, land use and soils on vegetation distribution

Understanding the determinants of vegetation distribution is one of the most important questions in community ecology as it contributes to understanding patterns and behaviour (dynamics) of communities. Lechmere-Oertel and Cowling (2001) emphasise on increasing interest in the determinants of vegetation boundaries, as an attempt to explain and predict possible responses of vegetation with anticipated climate changes. The Succulent Karoo and the Nama-Karoo biomes are climatically differentiated based on the main season of rainfall and the Summer Aridity Index (Rutherford 1997). A combination of climate variables such as the variability and the seasonality of rainfall, together with temperature maxima and minima in the Karoo, is thought to contribute significantly to the evolution of the Karoo vegetation, contributing to a distinct vegetation between the Succulent Karoo and the Nama-Karoo biomes (Hoffman and Cowling 1987; Milton et al. 1997; Rutherford 1997).

Climatic variables are likely to be the main control of species or life forms characterising the biome (Neilson 1991), but site-specific characteristics such as soil discontinuities, microclimate and competition become more important at smaller scales (hundreds of meters) where climate appears constant (Gosz and Sharpe 1989; Gosz 1993; Milton et al. 1997; Rutherford 1997). Abrupt boundaries between plant communities along edaphic discontinuities have been demonstrated in the broader Karoo region; such as the confinement of dwarf succulent shrubs to the shallow saline soils of the slope whereas non-succulent shrub communities were related to deeper soils in the southern Succulent Karoo (Milton et al. 1997). Similarly, plant communities in Vaalputs in Bushmanland vary from low, dwarf semi-open shrublands, with a higher degree of succulence and spinescence over calcrete and saline soils, to low, short open grassy shrublands in areas of soil mixed with aeolian sand, to low, open grasslands in areas of deeper, strongly acid aeolian sand (Lloyd 1989). Abiotic factors such as soil properties, have been indicated to have significant influence on the distribution of Fynbos species at the biome ecotone between the Fynbos and Succulent Karoo biomes (Lechmere-Oertel and Cowling 2001; Agenbag et al. 2004). The Succulent Karoo species on the other hand at the Fynbos/Succulent Karoo boundary are not influenced by abiotic factors and are suggested to be limited by plant interactions and fire. In this project, the influence of edaphic factors on the ecotonal vegetation

pattern is investigated both inferentially (Chapter 3) and experimentally (Chapter 4) as a contribution towards determining factors influencing the distribution of ecotone vegetation.

In addition to climate and soils, land use especially grazing, is a biotic factor of concern in rangelands, especially in arid and semi-arid areas, which are influenced by inter-annual rainfall variability (O'Connor 1996). Livestock grazing is reported as the most extensive form of land use in Southern Africa, especially in arid areas where conditions do not favour efficient crop production (Oba, Stenseth and Lusigi 2000; Darkoh 2003; Jonas 2004). Vegetation changes associated with heavy grazing are documented in the Karoo, marked by changes in species composition characterised by a decrease in certain, usually palatable species and an increase in annuals or unpalatable species (Hoffman et al. 1999; Milton, Davies and Kerley 1999; Todd and Hoffman 1999; Riginos and Hoffman 2003; Anderson and Hoffman 2007). Recent evidence, however, from many studies spanning a range of arid ecosystems have revealed that vegetation changes which have been attributed to land use impacts such as heavy grazing were in most cases confounded by the effects of year to year variations in rainfall, and could not be attributed to herbivore impacts alone (Bousman and Scott 1994; Meadows and Watkeys 1999; Dahlberg 2000). Very few studies have attempted, or managed to effectively separate the impacts of grazing and climatic factors (Dean and Macdonald 1994; Dodd 1994; Seymour and Dean 1999; Archer 2004), since the extreme annual climatic fluctuations in arid and semi-arid environments make it difficult to distinguish between the two effects (Hoffman and Cowling 1987). Conclusions from such studies indicate that climate plays a role in influencing the vegetation, but its effects differ in magnitude and type depending on land use management status and underlying soil types (see Milton and Hoffman 1994; O'Connor and Roux 1995; Dahlberg 2000; Teague, Dowhower and Waggoner 2004). This conforms to recent conceptual models detailing the interactions between climate, plants and herbivory in arid zones which have been proposed to better explain the behaviour of vegetation than grazing or rainfall alone (Oba et al. 2000; Vetter 2005). Accordingly, climate and land use act synergistically to influence vegetation patterns (Milton et al. 1999; Hutchinson, Unruh and Bahre 2000; Richardson, Hahn and Hoffman 2005). A focused investigation on the influence of land use on the vegetation is not undertaken in this project, but inferences are made from the remote sensing analysis of multi-temporal satellite imagery. Similarly, rainfall patterns are compared to vegetation change maps generated from multi-temporal remote sensing data (Chapter 7).

1.2.3 Plant interactions

It is widely accepted that measurements of edaphic and climatic tolerances of plant populations and species are imperfect predictors of their distributions (Dunnett and Grime 1999). The distribution of plants may reflect underlying patterns in edaphic conditions, but direct interference between neighbouring plants may also impose patterns on the vegetation. Competitive interactions between individuals and species has drawn much attention in community and population ecology, as one of the important factors that determine the distribution and the dynamics of natural plant communities (Yeaton and Cody 1976; Grime 1977; Grime 1979; Fonteyn and Mahall 1981; Tilman 1982; Walter 1985; Fowler 1986; Keddy 1989; Grace and Tilman 1990; Yeaton and Esler 1990; Goldberg and Barton 1992; Damgaard 1998; Dunnett and Grime 1999; Weigelt and Jolliffe 2003; Damgaard 2004). Interactions between plants are experienced locally between neighbour plants, but the results of these interactions ramify to affect population, community and ecosystem level processes (Lauenroth and Aguilera 1998).

A number of competitive co-existence theories and models have been proposed and tested in community ecology to explain non-random distribution of species and co-existence between species. At the basis of these models is the competitive exclusion principle (Hardin 1960), which has served as the conceptual basis for legacy of investigations of ecological co-existence (Gordon 2000). The competitive exclusion principle assumes complete exclusion of other species by the dominant ones, but when competition is not strong enough to cause high mortality or complete exclusion, plants co-exist (Scholes and Archer 1997). Many existing models to explain co-existence between species are based on the classical niche differentiation through resource partitioning in space and time as the main mechanism (Yeaton, Travis and Gilinsky 1977; Walker and Noy-Meir 1982; Knoop and Walker 1985; Cody 1986; Sala et al. 1989). Niche differentiation is the basis around which Walter's (1971) two-layer hypothesis to explain co-existence between grass and shrubs in the savanna systems is centred. This hypothesis has however not been supported in certain savanna ecosystems particularly in humid savannas (Le Roux, Bariac and Mariotti 1995; Mordelet, Menaut and Mariotti 1997) but also in an arid savanna ecosystem (Hipondoka et al. 2003).

In the Succulent Karoo, perennial species are reported to co-exist through spatial and temporal partitioning of resources (Van der Heyden 1992) and microsites (Milton 1990; Esler and Cowling 1993). Carrick (2003) has reported evidences of competition between the two leaf succulent shrubs *Leipoldtia schultzei* and *Ruschia robusta* (Aizoaceae), and the absence of competition between these succulents and a non-succulent Asteraceae shrub *Hirpicium*

alienatum. Carrick (2003) ascribed these results to vertical separation in the rooting morphologies. Few studies have investigated the root systems of perennial grasses in the broader Karoo region and it is not clear how species within this growth form interact or co-exist with other growth forms such as succulent shrubs. Midgley and van der Heyden (1999) have proposed that grasses and succulent shrubs may be competing for water in the same horizontal plane. Focused studies on competitive interactions between grasses and shrubs in the Karoo are also lacking. In the eastern Karoo, it is proposed that the abundance of grasses regulates the abundance of dwarf shrubs through competition (Hoffman et al. 1990), but current debate on the co-existence of the two growth forms is centred around the importance of seasonal distribution of rainfall in regulating the vegetation (Roux and Vorster 1983; Hoffman et al. 1990; O'Connor and Roux 1995). O'Connor and Roux (1995) who have provided a more recent analysis of the vegetation in the eastern Karoo have confirmed a general positive effect of summer rainfall on grasses and of autumn to winter rainfall on shrubs.

Both experimental (Chapter 4) and inferential (Chapters 5) studies were conducted in this project to investigate competitive interactions between grasses and succulent shrubs. Rooting depths and morphologies were also compared to explain the emerging competitive relationships (Chapter 5).

1.2.4 Scale-dependence

The significance of scale-dependent investigations has been emphasised in ecological literature, and it is recognised that ecological processes and the environmental variables that constrain them vary as a function of both spatial and temporal scales (Delcourt and Delcourt 1988; Gosz and Sharpe 1989; Gosz 1991). As a basic strategy to understand these cross-scale ecological phenomena, studies must be undertaken at different scales where different constraints operate (Gosz 1991, 1993). Gosz and Sharpe (1989) further suggest that the identification of constraining variables at every scale holds excellent promise for both monitoring and predicting ecological response to change. Thus by studying a range of scales we may reach a better understanding of how processes operating over gradients can be used to explain and predict long-term changes (Kerr and Ostrovsky 2003).

As zones of transition between adjacent ecological systems, ecotones occur over a broad spectrum of space and time scales, resulting in an increased heterogeneity (Gosz 1993). Many ecological investigations introduced in the preceding sections were aimed at capturing ecological patterns and processes at a relatively fine spectrum of spatial scale, and in a short time scale. However, processes operating at a broad spectrum of landscape scale and over large temporal

scales are better captured with different set of technology such as that offered by remote sensing. A combination of remote sensing and ecological field measurements was thus employed in this project, to capture processes at different scales. Field-based investigations provide detailed measurements over small areas, whereas the most commonly used remote sensing data provide synchronous measurements but with reduced potential for local detail (Kerr and Ostrovsky 2003). Reliable field data are required to support interpretations from remotely sensed datasets (Gosz and Sharpe 1989).

1.2.5 Remote sensing in vegetation ecology

A variety of ecological studies require data through time and from broad spatial areas. However, such data can be expensive or impractical to collect directly using field-based methods. Remote sensing technology provides such data, and serves as a valuable tool for evaluating dynamics at broad scales. Recent advances in spatial and spectral resolutions, the availability of remotely sensed data, and improved computation power, have greatly improved the utility of remote sensing in ecological research, and it has become an important tool in vegetation assessments and monitoring (e.g Wallace, Watts and Yool 2000; Langley, Cheshire and Humes 2001; Kerr and Ostrovsky 2003; Turner et al. 2003; Fassnacht, Cohen and Spies 2006). Vegetation or land cover mapping, and vegetation change detection are the most common applications of remote sensing in ecological investigations (Song et al. 2001; Kerr and Ostrovsky 2003; Turner et al. 2003).

Satellite imagery are processed into thematic vegetation maps, during a computer-assisted classification process which involves grouping the contents of an image into classes depicting the same vegetation type (Foody 2002). Classification processes can be unsupervised or supervised. In unsupervised classification, there is no thematic ground reference information upon which to train the assignment of classes (Jensen 2000). The pixels in an image are aggregated into a defined number of classes containing the same spectral range, resulting in classes that are purely spectral (Lillesand, Kiefer and Chipman 2004). Supervised classification processes on the other hand require a set of user defined sampling areas known as training areas (that have been characterised by ground reference data), to be collected for each vegetation type of interest to be mapped. Image pixels are then partitioned on the basis of their similarity to such training areas, following a confined statistical algorithm (Jensen 2000; Foody 2002), or an appropriate nonparametric supervised classification algorithms (Chapter 6). Lack of detailed information on the historical vegetation status including repeated vegetation classifications has

been pointed out as one of the main challenges in vegetation change analysis (Turner et al. 2003).

The repetitive coverage of large areas gives remote sensing an advantage for application in vegetation monitoring (Fung 1990; Mas 1999). Remotely sensed change detection techniques are based on the fact that natural or induced disturbances in land cover produce detectable variations in the spectral response of ground targets (Singh 1989; Fung 1990; Mas 1999; Almeida-Filho and Shimabukuro 2002). As a result, many different change detection techniques have been developed and used for a variety of different purposes (Singh 1989; Mouat, Mahin and Lancaster 1993; Kaufmann and Seto 2001; Rogan, Franklin and Roberts 2002; Kerr and Ostrovsky 2003; Cakir, Khorram and Nelson 2006). Efforts to monitor vegetation change with remotely sensed spectral data have been limited to detecting abrupt land cover changes which present little challenge, such as changes associated with the clearing of natural vegetation, increased cultivation, post-fire vegetation regeneration and heavy grazing (Price, Pyke and Mendes 1992; Cakir et al. 2006). Nonetheless, environmental impacts that result in a gradual change of vegetation type allow one to test the sensitivity and utility of remotely sensed data to monitor subtle changes such as changes in plant composition that are more challenging than the standard land cover analysis (Price et al. 1992; Frank and Menz 2003). The application of remote sensing data and technology is investigated in this project, to determine the spatial and the temporal distribution of the ecotonal vegetation (grasslands and shrublands) (Chapters 6 and 7).

1.3 Objectives of the study

This study focuses on the distribution of vegetation along an ecotone, and the associated abiotic and biotic determining factors, as well as on the spatial and temporal distribution of the vegetation. The main objectives are:

1) to investigate the abiotic and biotic factors influencing the distribution of the vegetation along an ecotone between the Succulent Karoo and Nama-Karoo biomes, and
2) to determine the spatial and the temporal distribution patterns of this vegetation, particularly grasses and succulent shrubs which characterise the ecotone. To achieve these objectives, the following specific objectives are addressed:

- Determining the influence of soils on the distribution of grass and succulent shrubs characterising the ecotone.
- Examining the competitive interactions between selected species of perennial grass and succulent shrubs along the ecotone.

- Establishing the detailed spatial distribution of grasslands and shrublands along the ecotone.
- Determining how the spatial distribution of grass and shrub vegetation has changed over time.

1.4 General approach and research design

In this project, I have made use of detailed community level ecological investigations, and a variety of remotely sensed data and techniques to address the set objectives. Plant interactions and soil factors were investigated at community level, but vegetation distribution (both spatial and temporal patterns as determined from remote sensing) were investigated at relatively larger temporal and spatial extent, capturing large scale processes such as land use and climatic patterns. A combination of field sampling, analysis of soil samples, field experimental and observational studies, as well as archival rainfall data collection was thus employed to collect the necessary data and information. The aforementioned data contributed significantly to guiding and verifying the remote sensing analyses.

1.5 Thesis outline

Chapter 1 introduces the project with the problem statement. In the background and context section, I review the literature and provide a theoretical underpinning on related topics: properties of ecotones; relative influence of climate, land use and soils in plant distribution; plant interactions; the concept of scale-dependent investigations, which is inherent to this study; and the use of remote sensing in ecological investigations. Chapter 2 provides a detailed description of the biophysical properties of the ecotonal study area, based on available vegetation descriptions, climate, land use and soil properties. Chapters 3 to 7 are grouped into two sections and are the main data chapters addressing the different objectives of the project. The first section (Chapters 3 to 5) comprises the field-based ecological analyses of the vegetation, investigating the role of soils and biotic interactions in influencing grassland and succulent shrubland communities along the ecotone. The analysis of soil properties across community gradients of grasslands and succulent shrublands is presented in Chapter 3. Chapter 4 deals with the effects of root competition from established adults, and soils on cross-transplanted seedlings in a reciprocal field experimental study. In Chapter 5, the nature of competitive interactions between the dominant species, as inferred from the nearest-neighbour analysis as well as results of root excavation, is presented. The second section (Chapters 6 and 7) is based on remote sensing analyses. In particular, Chapter 6 investigates the spatial distribution of the vegetation while

Chapter 7 measures the change in vegetation over time. Each of the data chapters is presented in a publishable article format, and consists of an abstract, a specific subject introduction to the study undertaken, building on the literature review in the main introductory chapter, the methods used, results and discussion. Where possible, repetition between chapters is avoided. In the last chapter (Chapter 8), I provide a general discussion of the findings and conclude with a synthesis, pointing out several applications of the study, and suggest possible future research directions.

University of Cape Town

2. Biophysical description of the ecotonal study area

2.1 Introduction

The aim of this chapter is to present a description of the study area (the ecotone) in terms of geographic location, topography, soils, climate, land use, and vegetation. To place the study area in its wider picture, the chapter starts with the introduction to the Succulent Karoo and the Nama-Karoo biomes that encompass the ecotone.

2.2 Succulent Karoo and Nama-Karoo biomes

The Succulent and the Nama-Karoo biomes together form the largest part of the arid south-western zone of Africa, which also comprises the Namib Desert and the arid Savanna of the Kalahari in the north. The two Karoo biomes are bounded by the Atlantic coastline to the west, the winter rainfall Fynbos to the south, the arid Savanna to the north and north east and by the Grassland biome to the east (Figure 2.1). A zone extending north-westerly separates the Succulent Karoo to the west and south (with rains mainly in winter, April-September) from the Nama-Karoo to the east (with rains mainly in summer, October-March) (Desmet and Cowling 1999). Rainfall seasonality becomes less defined in this zone of overlap between the two biomes, and precipitation may become dominated by one or the other season or may also occur anytime of the year or most of the year (Cannon 1924; Desmet and Cowling 1999) (section 2.6 below). In addition to variations in rainfall seasonality, Desmet and Cowling (1999) recognised a number of distinct patterns in rainfall regimes across the Karoo at finer scales particularly in terms of the degree of intensity of the rain season and the dry season, the duration of rainfall occurrence and differences in reliability and intensity of rainfall events.

The Succulent Karoo biome is characterised by low (20 – 290 mm/yr) but fairly reliable (coefficient of variation < 50%) annual rainfall, and by relatively high summer aridity (Hilton-Taylor 1987; Cowling and Hilton-Taylor 1997; Schulze 1997). The Succulent Karoo is also associated with higher minimum temperatures during the winter months and lower maximum summer temperatures than the Nama-Karoo (Rutherford and Westfall 1986; Milton et al. 1997; Palmer and Hoffman 1997). Mean annual rainfall in the Nama-Karoo varies from 60 mm in the west where it borders with the Succulent Karoo to 400 mm in the east where it borders with a more mesic Grassland biome (Palmer and Hoffman 1997). Rainfall variability is generally higher in the Nama-Karoo biome (43% - 75%) than in the Succulent Karoo biome (Rutherford and Westfall 1986; Palmer and Hoffman 1997; Desmet and Cowling 1999).

Rainfall seasonality and variability, together with temperature maxima and minima in the Karoo, are thought to have been powerful forces in the evolution of the Karoo vegetation (Hoffman and Cowling 1987; Milton et al. 1997), contributing to a distinct florae in the Succulent Karoo and the Nama-Karoo biomes (Rutherford 1997). In the Succulent Karoo biome, predictable, light winter rainfall and hot arid summers have favoured leaf succulence with CAM (Crassulacean Acid Metabolism) photosynthesis and shallow roots (Milton et al. 1997), whereas Nama-Karoo's more variable rainfall enables a greater variety of structural forms to co-exist (Rutherford and Westfall 1986; Cowling et al. 1994; Palmer and Hoffman 1997; Mucina et al. 2006). Succulents are thus well represented in the Succulent Karoo floras and are associated with many of the larger families (Aizoaceae, Asteraceae, Liliaceae *sensu lato*, Crassulaceae, Geraniaceae, Euphorbiaceae and Asclepiadaceae) (Hilton-Taylor 1996; Cowling and Hilton-Taylor 1999; Mucina et al. 2006). Nama-Karoo flora is characterised as a dwarf open shrubland or open dwarf-shrub steppe, dominated by the Asteraceae, Fabaceae and Poaceae (Mucina et al. 2006).

There is an overall increase in grass cover from west to east within the Karoo region, and the Nama-Karoo biome has a higher dominance of grass compared to a relatively lower occurrence of grass in the Succulent Karoo (Rutherford and Westfall 1986). On the other hand, leaf succulents decrease in abundance eastwards as summer rainfall increases (Milton et al. 1997). This directional change in growth forms is related to an overall increase in rainfall eastward and a declining proportion of winter rain (Acocks 1953; Werger 1978; Rutherford and Westfall 1986; Werger 1986). It has, however, also been proposed that both grazing and aridity lead to a reduction in grassiness and an increase in the proportion of succulents in Karoo shrublands (Acocks 1953; Roux and Vorster 1983; Milton 1990). Both grasses and succulent shrubs form an important component of vegetation at the Namaqualand Bushmanland ecotone described in the remainder of this chapter, and they are the main subject of this thesis.

2.3 Location and general description of the study area

The study area lies along the border between Namaqualand and Bushmanland, which forms part of a zone separating the Succulent Karoo and the Nama-Karoo biomes in the northern Cape Province of South Africa. The area includes the region north of the farm Burdensputs (30° 24'S; 18° 34'E) near Kliprand in the southeast, up to Goegap Nature Reserve (29° 42'S; 17° 59'E) near Springbok to the northwest, covering the western edge of the Bushmanland plateau, and continues into the eastern end of the Leliefontein communal area, east of the Kamiesberg

mountain range (Figure 2.2). The area is transverscd by the Springbok-Kliprand road, and covers the total area of about 4 000 km².



Figure 2.1 The section of south western Africa highlighting the two Karoo biomes and the location of the study area (ring) (Rutherford and Westfall 1986).

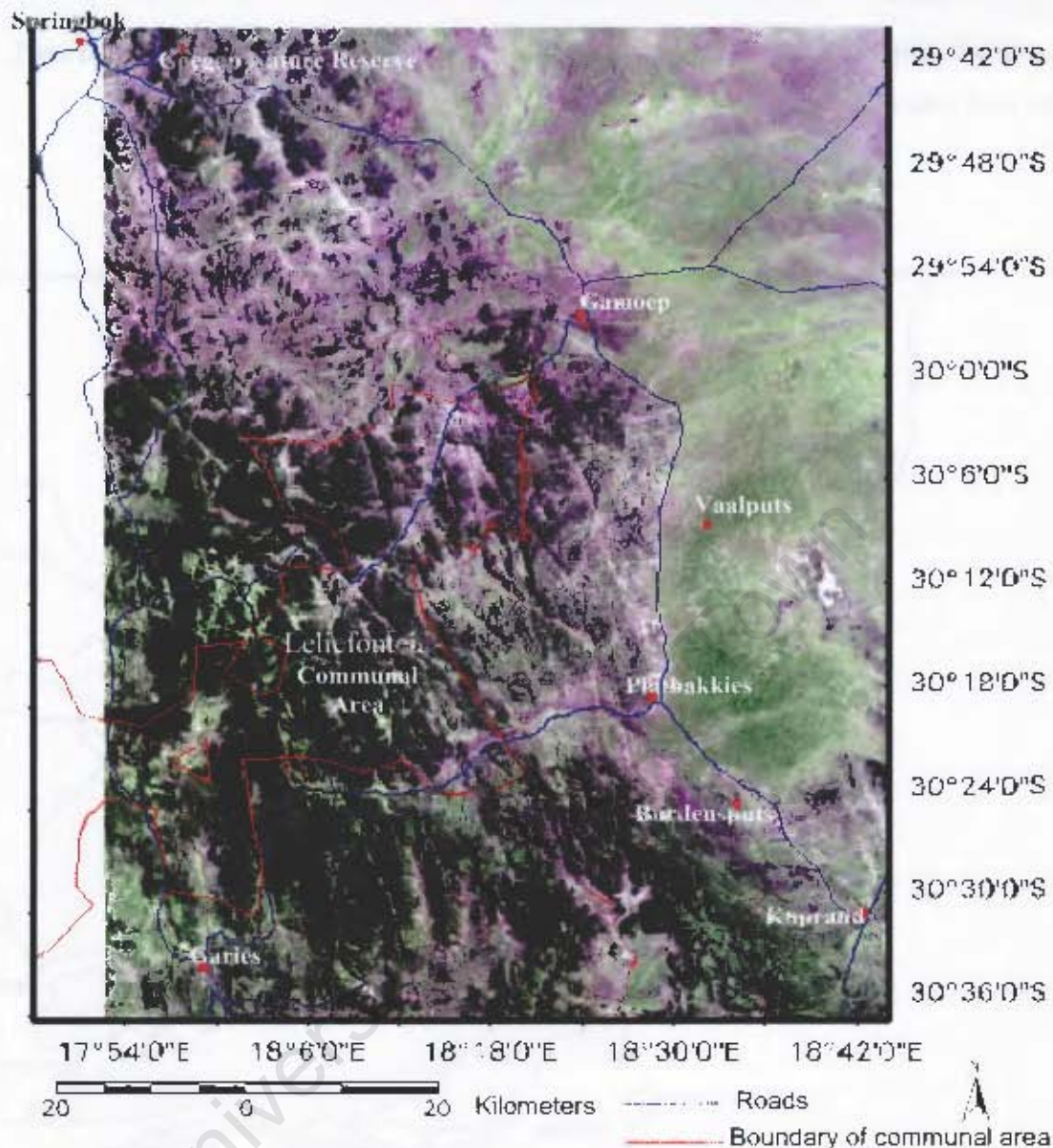


Figure 2.2 A 3-band colour composite of the study area, represented by the Landsat TM scene dated 04-02-2004. The band combination of 4-5-3 (Red-Green-Blue) is used. The roads and some major places are overlaid.

2.4 Geology and soils

Both Succulent Karoo and Nama-Karoo biomes share a similar geological history, which is sedimentary but influenced by folding along the southern and western edges of the Karoo, and by igneous intrusions in the northern and eastern parts (Watkeys 1999). Namaqualand and Bushmanland are underlain by highly deformed and metamorphosed rocks of the Namaqualand Metamorphic Province (Visser 1986; Watkeys 1999). Namaqualand is dominated by granitic gneisses which decay to form rich soils, whereas the quaternary sands and Karoo Sequence shales of Bushmanland give rise to weak and structureless clay and sandy soils (Watkeys 1999). Like other semi-arid and arid regions, lack of moisture results in less weathering and leaching

giving rise to soils that have weakly developed structure, freely drained soils and with little organic matter (Lloyd 1985; Ellis and Lambrechts 1986; Watkeys 1999).

Ellis and Lambrechts (1986) recognised morphologically four dominant soil types in the area: 1) the deep uniform coarse textured soils with minimal profile development, 2) shallow (less than 400 mm) coarse textured (sand to loamy sand) soils overlying a reddish coloured hardpan, 3) shallow (less than 400 mm) coarse textured (sand to sandy loam) soil overlying hardpan calcrete, and 4) medium textured (sandy loams to sandy clay loams) soils of varying depth overlying rock. These soils are generally sandy to very sandy soil texture, an important aspect in the karoo especially with regard to the capacity of the soil to hold water and withstand erosion (Ellis and Lambrechts 1986). In the Vaalputs area which also forms part of the study area Lloyd (1985) identified different types of soils. Light brown soil which characterise shrub communities, and occurring close to areas of rocky outcrop are possibly formed *in situ*. A red-brown aeolian sand is associated with the eastern and southeastern aspects of the dune-like structures in Bushmanland in grass communities, and consists predominantly of quartz and sand grains. Intermediate sands occur in the transition zone between light brown and red brown sands.

2.5 Land use

Small livestock production (goats and sheeps) is the main land use both in Namaqualand and Bushmanland but tenure arrangements differ between the two areas (Jonas 2004). Namaqualand has both communally and privately owned farms whilst Bushmanland is largely still privately owned. In addition to livestock grazing characterising the study area, the section of the Goegap Nature Reserve formerly known as the Hester Malan Nature Reserve has been under conservation since 1966, and the rest of the area was added in 1990 (Rosch 2001). Vaalputs farm which was also previously part of a commercial livestock grazing system has not been exposed to livestock grazing since 1983 when it was set aside for nuclear waste disposal site, but it is grazed by small indigenous antelope species (Lloyd 1985).

Communal and private tenure systems differ in the means of livestock production which is largely driven by farming objectives (Hoffman and Ashwell 2001). Communal livestock production is characterised by several herds individually herded on commons, in which the number of animals often increases above carrying capacity norms of the Department of Agriculture, but also falls below these in years of poor rainfall (Hoffman et al. 1999; Hoffman and Ashwell 2001). Lack of sufficient land means that herders are seldom able to rest large areas of the rangeland, although limited movements of herds occur in response to vegetation condition and seasonal climate fluctuations (Baker and Hoffman 2006). The livestock keepers have a range

of objectives of which selling for a steady income is not a major feature (Debeaudoin 2001; Hoffman and Ashwell 2001; Rohde, Hoffman and Allsopp 2003). With private livestock arrangements on the other hand, animals range freely in camps and are rotated between camps with numbers usually abiding by the Department of Agriculture recommendations and hence do not fluctuate as much as in communal areas (Hoffman and Ashwell 2001). This results in a high proportion of the rangeland being rested. There is a clear income generating objective and a high proportion of the animals are sold every year, and thus this form of livestock production in the area is often referred to as commercial livestock production (Todd and Hoffman 1999).

Cropping was more widespread than it is today, on both communal and private land and has had an important impact on the flatter deeper soils (Hoffman and Rohde 2007). It is believed that many of agricultural landscapes in Namaqualand today are a result of the slow recolonisation of old crop fields by pioneer shrubs that are now utilised as grazing lands (Mucina et al. 2006; Hoffman and Rohde 2007).

2.6 Precipitation

Namaqualand experiences cyclonic and orographic rainfall, which falls mainly in winter, whereas Bushmanland experiences convection rainfall falling mainly in late summer/early autumn (Desmet and Cowling 1999; Mucina et al. 2006). Rainfall along the ecotone varies between coastal lows and cold fronts to the rain from convective storms which occasionally occur in summer (Cannon 1924; Desmet and Cowling 1999). Rainfall thus may occur anytime of the year or may fail altogether due to the orographic influences of the Kamiesberg (Desmet and Cowling 1999). Rainfall patterns from different sites along the ecotone are presented in Figure 2.3. These graphs confirm the lack of defined rainfall seasonality that defines the main biomes. Goegap Nature Reserve which is located to the most eastern part of the study area has a rainfall peak from April to September, and it forms part of the winter rainfall Namaqualand (Rosch 2001).

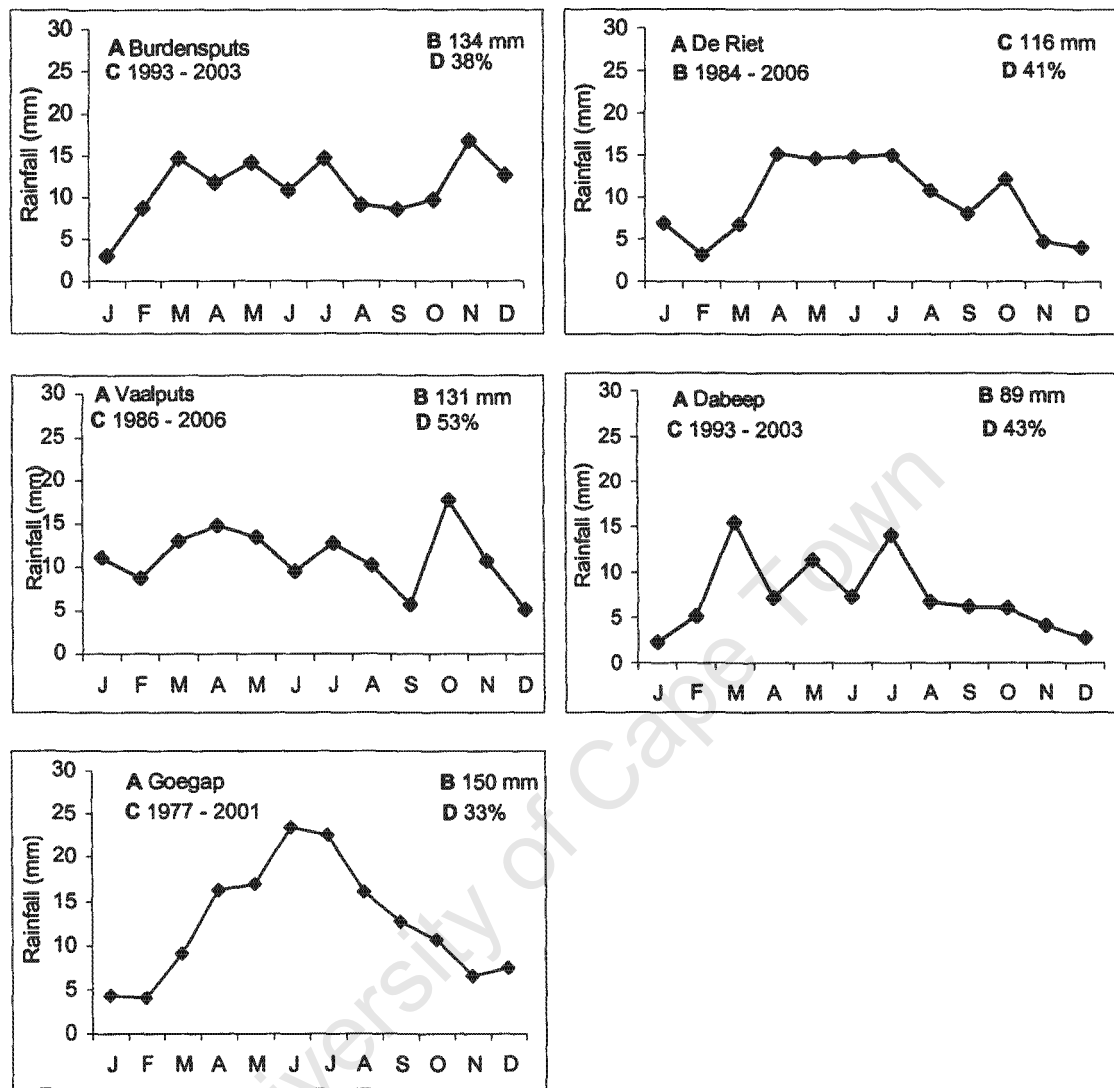


Figure 2.3 The mean monthly rainfall at different sites (A) along the ecotone. B mean annual rainfall, C period of rainfall data observation, and D Coefficient of Variation.

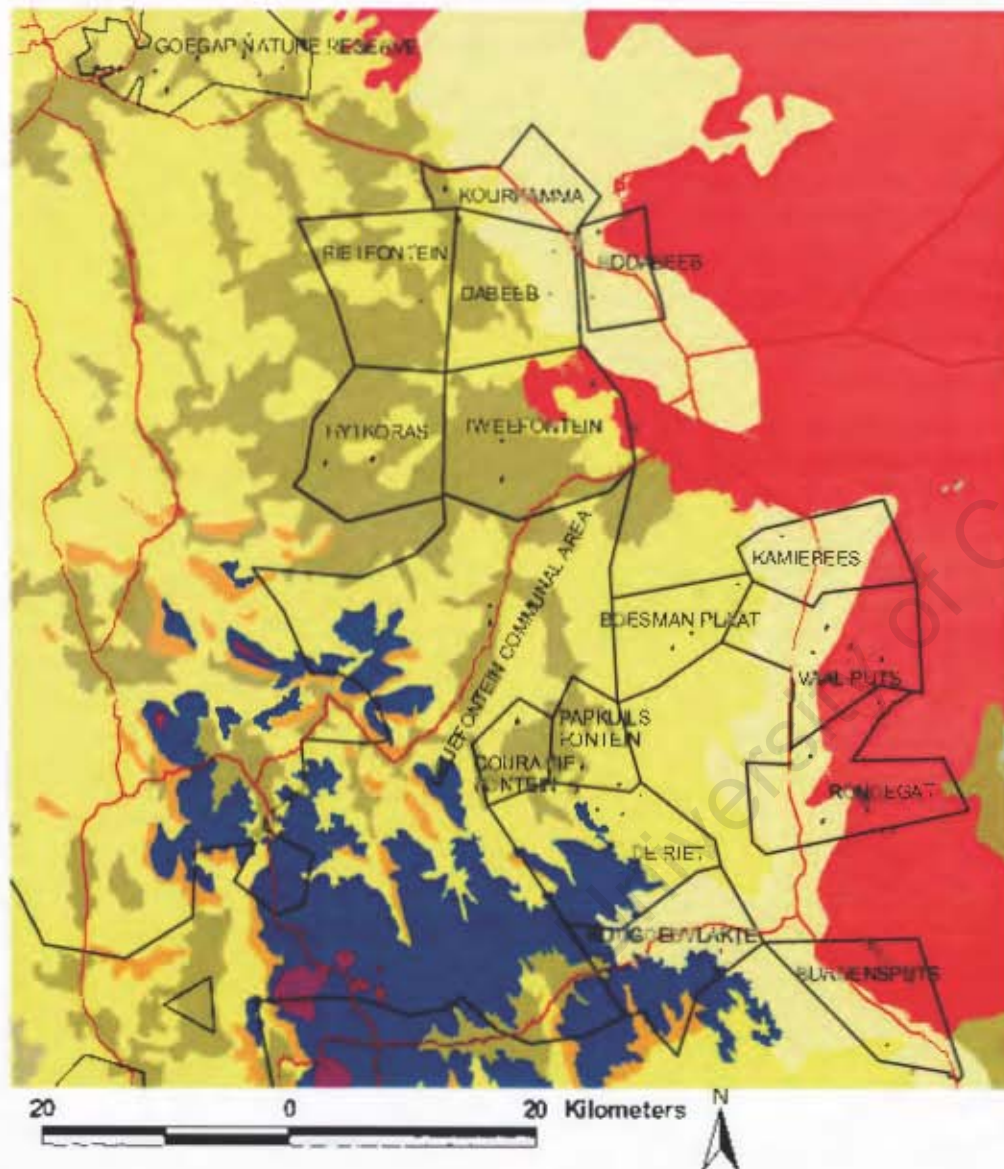
2.7 Vegetation

Vegetation in the study area has been described by several authors. It was described as the False Succulent Karoo veld type and the False Desert grassveld by Acocks (1975), and was later reclassified into the Upland Succulent Karoo and Bushmanland by Low and Rebelo (1996). The False Succulent Karoo veld type is succulent to non-succulent shrubland, whereas the False Desert grassveld is characterised by pure grassveld consisting of *Stipagrostis brevifolia*, *S. ciliata* and *S. obtusa* or by the dominance of the grass lifeform. Mucina and Rutherford (2006) offer the most detailed vegetation description of the study area, where four main vegetation types are recognised (Figure 2.4). The western part of the study area (west of the Kliprand-Springbok road) is dominated by the Namaqualand Klipkoppe shrubland mainly on flat or gently sloping rock

sheets, and the Namaqualand Blomveld in flatter areas and in the valleys between the rocky hills of the Escarpment (Mucina et al. 2006). These two types of vegetation are separated from the Bushmanland Arid grassland in the eastern part of the study area, by a relatively narrow belt of Platbakkies Succulent shrubland. The Platbakkies Succulent shrubland is dominated by low succulent shrubs e.g. *R. robusta* on loamy colluvial and rocky soil, and by *Stipagrostis brevifolia* grass on sandy soils (Mucina et al. 2006). Bushmanland Arid grassland which defines the eastern part of the study area is dominated by *Stipagrostis* grass species such as *S. ciliata*, *S. obtusa* and *S. brevifolia* (Mucina et al. 2006). Other vegetation types occurring in the surrounding area include the western Bushmanland Klipveld to the south east of the study site, Namaqualand Granite Renosterveld and isolated patches of Kamiesberg mountain shrubland (Figure 2.4).

The description of Platbakkies Succulent shrubland vegetation type, with affinity to both the Namaqualand Klipkoppe shrubland and Bushmanland Arid grassland vegetation types (Mucina et al. 2006) fits the general descriptions of ecotones (Gosz 1993). The Namaqualand/Bushmanland ecotone however, seems to be much wider than the Platbakkies Succulent shrubland as indicated by locations of grass and shrub communities further into the Bushmanland Arid grassland and Namaqualand Klipkoppe shrubland vegetation types where observations and investigations in this project were undertaken (Figure 2.4). The presence of elements of both the Bushmanland grass species and the Namaqualand succulent shrub species has been previously described to indicate that the vegetation is transitional between the Nama-Karoo and the Succulent Karoo biomes (Lloyd 1989; Rosch 2001). At Goegap Nature Reserve, Rosch (2001) identified four plant communities in the predominantly rocky hills and nine plant communities in the plains. The presence of certain species of *Stipagrostis*, particularly *S. brevifolia* which occur in certain communities of the plains at Goegap Nature Reserve indicates that the area lies in the transition zone between the Succulent Karoo biome and the more grassy Nama-Karoo biome (Rosch 2001). In a phytosociology study at Vaalputs nuclear waste disposal site on the western border of Bushmanland, Lloyd (1989) made a similar observation, identifying four major groups of plant communities representing elements of the Succulent Karoo and the Nama-Karoo biomes. These groups of communities ranges from dwarf/low semi-open shrublands on saline and calcareous soils, to low/short open grassy shrublands in areas of soils mixed with aeolian sand, to low open grasslands on deeper, strongly acid aeolian sands.

The two main species investigated in detail in the following chapters are *Stipagrostis brevifolia*, a perennial C₄ bunch grass, and *Ruschia robusta*, a leaf succulent dwarf shrub. *Ruschia robusta* belong to a group of the family Aizoacea called the mesembs.



Legends

- Bushmanland Arid Grassland
- Bushmanland Vloere
- Namaqualand Klipkoppe Shrubland
- Namaqualand Blomveld
- Namaqualand Granite Renosterveld
- Kamiesberg Granite Fynbos
- Kamiesberg Mountains Shrubland
- Platbakkies Succulent Shrubland
- Western Bushmanland Klipveld
- Roads
- Farm boundaries

Figure 2.4 Vegetation types at the ecotone and the surrounding area (Mucina, Rutherford and Powrie 2006). The text labels are the farm names where observations (black dots) have been conducted, selected in grass and in shrub communities at the interface between the two growth forms.

3. The influence of edaphic factors on vegetation distribution at the ecotone

Abstract: This study investigated the influence of soils on the distribution of grasses and shrubs at the ecotone between Bushmanland arid grassland and Namaqualand shrubland. Vegetation and soil data were collected along eight transects across gradients of grass and shrub communities along the ecotone. Nonmetric Multidimensional Scaling (NMS) ordination methods were used to analyse the relationship between vegetation and the soil variables. Axis 1 of the two dimensional ordination of the data showed a strong negative correlation with *Stipagrostis brevifolia*, a grass, and a positive correlation with *Ruschia robusta*, a succulent shrub ($r^2 = 0.74$ and $r^2 = 0.47$ respectively). Soil factors, however, showed no correlations ($r^2 < 0.08$) with both ordination axes. When statistical correlation analyses were applied to individual soil variables against abundance data for *S. brevifolia* and *R. robusta*, very weak significant correlations were obtained. Soil depth and sand content showed significant positive correlations ($r^2 = 0.06$ and $r^2 = 0.14$ respectively) with *S. brevifolia* abundance data, and significant negative correlations ($r^2 = 0.09$ and $r^2 = 0.11$ respectively) with *R. robusta* abundance data. Organic content and phosphorus concentration were also negatively correlated with *S. brevifolia* ($r^2 = 0.11$ and $r^2 = 0.14$), whereas silt content was positively correlated with *R. robusta* ($r^2 = 0.12$). The weak correlations between soil factors and ordination axes, as well as between soil factors and species data, suggest that soils have little influence on the distribution of *S. brevifolia* and *R. robusta*, the two abundant species at the ecotone.

3.1 Introduction

What determines vegetation distribution is one of the most important questions in community ecology, as it helps to understand patterns and behaviours of communities. Climatic variables largely control the species or life form that characterise a biome (large scale) (Neilson 1991), whereas at the smaller scale factors like soil properties, microclimate and competition become important (Gosz 1993; Milton et al. 1997; Rutherford 1997; Hochstrasser et al. 2002). Studies of vegetation patterns in arid ecosystems within relatively small areas have demonstrated relationships between vegetation patterns and site specific factors such as soil properties, microclimatic and water-balance factors (Bliss and Cox 1964; Bowers and Lowe 1986; Abd El-Ghani 1998, 2000; Buxbaum and Vanderbilt 2007).

The Succulent Karoo and the Nama-Karoo biomes are climatically differentiated based on a number of climatic variables such as the main rainfall season and the Summer Aridity Index (Rutherford 1997; Rutherford, Mucina and Powrie 2006). At the community scale, abrupt boundaries between plant communities along edaphic discontinuities have been demonstrated. For example, in the southern Succulent Karoo, dwarf succulents were found to be confined to the shallow saline soils of the slope, whereas non-succulent shrub communities were dominant on deeper soils (Milton et al. 1997). Similarly, plant communities in Vaalputs in Bushmanland were indicated to be defined by soil variables (Lloyd 1989). Along the ecotone between the Bushmanland arid grasslands, and Namaqualand shrubland, grass communities and succulent shrub communities form both abrupt and gradual boundaries with each other, forming gradients of communities.

Species that are positively or negatively associated are said to have a non-random distribution, and their patterns of association can be important in assessing the causal factors of species-distribution (Turkington and Harper 1979). The non-random distribution may reflect underlying patterns in edaphic conditions, but direct interference between neighbouring plants (competition) may also impose patterns on the vegetation (Turkington and Harper 1979). While the role of competition in structuring grass and shrub communities at the ecotone is addressed in the next two chapters, in this chapter, I have investigated the influence of soils on community gradients of grasslands and succulent shrublands along the ecotone. The occurrence of *Stipagrostis* grass species in relation to the succulent shrub communities is generally assumed to follow deeper and sandy patches of soils (see Mucina et al. 2006). Lloyd's (1989) investigation of the influence of edaphic factors on vegetation communities at Vaalputs revealed a gradient in soil depth and other soil factors, where *Stipagrostis ciliata* grass communities on deeper soils clearly separate from shrub communities on shallow soils. Along this soil gradient however, the distribution of *Stipagrostis brevifolia* and *Ruschia robusta* grades into each other, creating an overlap in the range of their distribution. *Stipagrostis brevifolia* and *Ruschia robusta* dominate communities of grass and shrubs respectively that occur adjacent to each other along the ecotone, and also communities in which both components co-occur. As a contribution to one of the main objectives of the project i.e determining the factors that influence the distribution of vegetation along the ecotone, the study presented in this chapter was aimed at investigating the role of soils in the distribution of grass and succulent shrubs at the ecotone.

3.2 Methods

3.2.1 Study area

The ecotonal study area is described in Chapter 2. This study focused on communities of grass and succulent shrubs, occurring adjacent to each other, forming community gradients. A total of eight of these community gradients were sampled across the ecotone, one at each of these sites: Burdensputs, De Riet, Boesmanplaat and Vaalputs, and two at Kougoedvlakte and at Goegap Nature Reserve (see Figure 2.4 for the locations of these sites). Burdensputs and Kougoedvlakte farms are managed under commercial management practices and are grazed by domestic livestock. The parts of De Riet and Boesmanplaat farms in this study, form part of the additional land added to the Leliefontein communal area as part of the national government's land reform programme during the late 1990s. The grazing system on this land is controlled by the Department of Agriculture. The section of the Goegap Nature Reserve formerly known as the Hester Malan Nature Reserve has been under conservation since 1966, and the rest of the area

(including the sites investigated in this study) was added in 1990 (Rosch 2001). Vaalputs farm which was also previously part of commercial livestock grazing system has not been exposed to livestock grazing since 1983 when it was set aside as a nuclear waste disposal site. It is grazed by small indigenous antelope species (Lloyd 1985). The average monthly rainfall at different sites is presented in Figure 2.3 (Chapter 2), in which Kougoedvlakte is represented by rainfall from De Riet.

3.2.2 Vegetation and soil sampling

Vegetation cover and composition were determined along a transect (100 m) placed across each of the eight community gradients of grass and succulent shrubs, based on a line intercept method (Canfield 1941). In this method, each time a perennial plant touched the transect line, its identity and canopy diameter along the transect was recorded. Total vegetation cover (projected canopy cover) was calculated for every 10 m interval along the transect. In this way, change in vegetation composition as one moves from one community to the other one is captured. Soil depth was measured in the middle of each 10 m intervals along the transects, by hammering a narrow steel stake into the ground until it hit bedrock. Soil samples were collected from a depth of 0 - 0.1 m, air dried and sieved through a 2 mm mesh before analysis of the following variables: soil texture (particle-size distribution), pH, elemental composition (exchangeable Ca, Mg, P, K and Na, and total N), electrical conductivity and organic content. Soil particle size was determined quantitatively using the hydrometer method (Bouyoucos 1962) to calculate the percentage of sand, silt and clay in the soil. Values for pH were determined from 10 g of soil in solutions of 0.01 M CaCl_2 using a pH meter. Macroelemental composition and electrical conductivity were determined at the soils lab at Elsenburg Agricultural Institute in Stellenbosch. Unfortunately, N analysis at this lab returned zero² values and this variable was removed from the analysis. Nitrogen content in the surrounding area is indicated at less than 1% (Carrick 2001). Total organic fraction was determined from the loss-on-ignition after 8 hours at 375°C, using 20 g of oven-dried (70°C for 48 hours) soil. The soil was pre-tested for CaCO_3 using HCl, but there was no sign of Calcium Carbonate. Sampling deeper than 10 cm might yield a comprehensive picture, but as the soil structure in the area lacks morphogenetic horizons, sampling in the top 10 cm as the zone most likely to reflect differences was selected (Allsopp 1999).

² The minimum range used for calibration at this lab is 2.58-2.64%.

3.2.3 Multivariate and correlation analysis

Ordination, a method of analysing field data in order to recognise factors which are likely to be most important in determining the distribution of vegetation (Gittins 1965) was employed in this study. Data were organised into matrices of sample units (10 m sub-transects) of species cover, and soil variables. A Nonmetric Multidimensional Scaling (NMS) ordination technique was used (using the Window's (4.25) PC-ORD (McCune and Mefford 1999)) to analyse patterns in species abundance, and to examine the relationship between vegetation and soil variables based on Bray-Curtis similarity. NMS produces ecologically interpretable ordinations which are superior to other available methods in their underlying assumptions, robustness and resistance to quantitative noise (Minchin 1987), and it is the most generally effective ordination method for ecological communities (McCune and Grace 2002). Species that were not well represented across transects (species occurring in 5 or less sample units for all the transects grouped together) were removed from the data set, to reduce noise and enhance the detection of patterns in the ordination. Correlation of the distribution of species in NMS ordination space to possible causal edaphic factors was performed using the joint-plot procedure in PC-ORD. This method plots correlated factors (cut off r^2 value for joint-plots was set at 0.20) as vectors radiating from the centroid of the ordination scores, where the angle and the length of the vector are proportional to the direction and strength of the relationship respectively (McCune and Mefford 1999). In addition to ordination, a correlation matrix was produced to test statistically significant correlations and determine the strength of relationships between individual soil variables and abundance of the most dominant species.

3.3 Results

3.3.1 Vegetation cover and composition among the transects

Vegetation cover in these transects ranged from 21% at De Riet to 69% at Vaalputs, as shown in brackets in Table 3.1. A total of 20 perennial species were recorded over all the sites. The first ten abundant species in all transects, and their vegetation cover (%) in each gradient transect, are presented in Table 3.1. The dominant grass species in each transect was *S. brevifolia*, whereas the dominant shrub species was *R. robusta* in each transect, and the two made up more than 80% of the total vegetation cover in most of the transects. Other dominant species included *Euphorbia decussata* at Boesmanplaat, *Lycium cinereum* at Kougoedvlakte A and Burdensputs, and *Ruschia aggregata* at Goegap A.

Table 3.1 Total % vegetation cover at each transect (shown in brackets), and vegetation cover of the ten most abundant species to occur in the survey of all transects.

	Vaalputs (69)	Goegap A (55)	Kougoed vlakte A (48)	Goegap B (47)	Kougoed vlakte B (43)	Burden sputs (32)	Boesman plaat (28)	De Riet (21)
<i>Stipagrostis brevifolia</i>	67	54	67	55	75	37	48	27
<i>Ruschia robusta</i>	19	25	21	41	19	34	29	57
<i>Euphorbia decussata</i>	5	-	-	< 1	3	-	14	8
<i>Lycium cinereum</i>	-	-	12	-	-	11	-	-
<i>Zygophyllum spp.</i>	-	-	-	3	-	4	8	-
<i>Aptosimum spinescence</i>	-	-	-	-	-	8	2	-
<i>Stipagrostis obtusa</i>	7	-	-	-	-	-	< 1	1
<i>Osteospermum sinuatum</i>	2	-	-	2	-	-	< 1	-
<i>Ruschia aggregata</i>	-	14	-	-	-	-	-	-
<i>Leipoldtia pauciflora</i>	-	3	-	-	-	-	-	-

3.3.2 Soils

The soil characteristics (mean, range and standard deviation) in the area are presented in Table 3.2, whereas a list of soil attributes by site is shown in Appendix A. Soils were sandy, with the total sand ranging between 82% - 96% of samples by weight, while the content of silt and clay were both less than 15%. The soils were slightly acidic to neutral in reaction and were low in organic content.

Table 3.2 Soil physical and chemical characteristics of the study area presented as mean, range and standard deviation

	Mean	Minimum	Maximum	Std.Dev
Soil depth (cm)	57	6	120	28
Total sand (%)	91	82	96	1.55
Silt (%)	4	0	10	1.59
Clay (%)	5	0	12	2.82
pH (in CaCl ₂)	6.40	5.58	7.40	0.35
Calcium (cmo kg ⁻¹)	1.62	0.54	3.84	0.75
Magnesium (cmo kg ⁻¹)	1.36	0.31	4.04	0.90
Phosphorus (mg kg ⁻¹)	36.89	13.00	118.00	20.29
Potassium (mg kg ⁻¹)	156.21	43.00	475.00	88.39
Sodium (mg kg ⁻¹)	27.60	9.00	105.00	17.58
Conductivity (Msm)	7.51	3.00	22.90	3.79
Organic matter (%)	0.8	0.2	2.4	0.36

3.3.3 Vegetation-environment relationships

The two-dimensional NMS ordination separated *S. brevifolia* and *R. robusta* dominated plots so that the two species are arranged diagonally opposite to each other in the ordination space (Figure 3.1). This is also explained by the strong negative correlation between *S. brevifolia* and the first axis ($r^2 = 0.74$), and a strong positive correlation between *R. robusta* and the same axis ($r^2 = 0.47$) (Table 3.3). *Ruschia robusta* was also negatively correlated with the second axis ($r^2 = 0.59$), while *S. brevifolia* was weakly positively correlated. None of the other common species showed correlations with the ordination axes.

None of the measured soil variables showed correlation with any of the ordination axes at the cut off level of $r^2 < 0.2$, but the first ordination axis showed vague correlations ($r^2 < 0.1$) with soil depth (negative correlation), and with Na and organic matter (positive correlation) (Table 3.4). When individual soil variables were analysed for correlations with vegetation cover for *S. brevifolia* and *R. robusta*, weak significant correlations were obtained (Table 3.5). Soil depth and sand content showed significant positive correlations ($r^2 = 0.06$ and $r^2 = 0.14$ respectively) with *S. brevifolia* abundance data, and significant negative correlations ($r^2 = 0.09$ and $r^2 = 0.11$ respectively) with *R. robusta* abundance data. Organic content and phosphorus concentration were also negatively correlated with *S. brevifolia* ($r^2 = 0.11$ and $r^2 = 0.14$), whereas silt content was positively correlated with *R. robusta* ($r^2 = 0.12$).

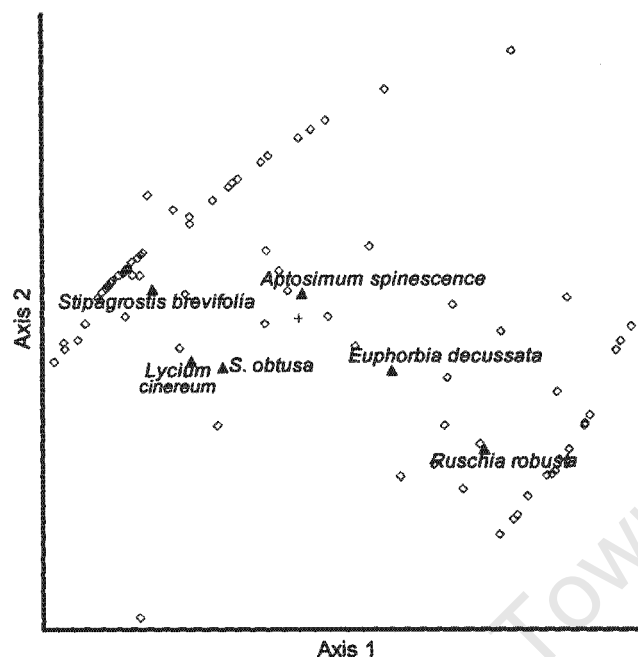


Figure 3.1 The two-dimensional NMS ordination analysis of 79 subtransects (open diamonds) in vegetation abundance of 6 species (solid triangles). Lack of joint-plot vectors at the centroid (the cross) indicates that none of the soil factors showed a correlation at $r^2 > 0.2$ level with ordination. The final solution had a stress value of 10.5. Ordination distances have a cumulative correlation coefficient of 0.70 (axis 1) and 0.00 (axis 2) with the original data.

Table 3.3 Pearson correlations (r-values) of species with ordination axes of a 2-dimensional NMS

	Axis 1	Axis 2
<i>Aptosimum spinescence</i>	0.01	0.06
<i>Euphorbia decussata</i>	0.18	-0.16
<i>Lycium cinereum</i>	-0.13	-0.08
<i>Ruschia robusta</i>	0.68	-0.77
<i>Stipagrostis brevifolia</i>	-0.86	0.27
<i>Stipagrostis obtusa</i>	-0.13	-0.13

Table 3.4 Pearson correlations (r-values) of soil variables with ordination axes of a 2-dimensional NMS

	Axis 1	Axis 2
Soil depth (cm)	-0.25	0.13
Sand (%)	-0.05	-0.11
pH (in CaCl)	0.07	0.20
Calcium (cmo kg ⁻¹)	0.18	-0.12
Magnesium (cmo kg ⁻¹)	0.17	-0.07
Phosphorus (mg kg ⁻¹)	0.11	0.00
Potassium (mg kg ⁻¹)	0.16	-0.10
Sodium (mg kg ⁻¹)	0.29	-0.08
Organic matter (%)	0.21	-0.13

Table 3.5 Pearson correlations (r-values) between soil variables and vegetation cover of the two most abundant species. The * marks significant values at $p < 0.05$

	<i>Stipagrostis brevifolia</i>	<i>Ruschia robusta</i>
Soil depth (cm)	0.24*	-0.31*
Clay (%)	-0.20	0.02
Sand (%)	0.37*	-0.33*
Silt (%)	-0.07	0.35*
pH	0.08	0.03
Calcium (cmo kg ⁻¹)	-0.22	0.02
Magnesium (cmo kg ⁻¹)	-0.19	0.10
Phosphorus (mg kg ⁻¹)	-0.38*	0.07
Potassium (mg kg ⁻¹)	0.01	0.12
Sodium (mg kg ⁻¹)	-0.12	0.06
Organic matter (%)	-0.33*	0.12

3.4 Discussion

A two-dimensional NMS ordination provided an ecologically interpretable solution with a stress value of 10.5. Stress values for most ecological community data range between 10 and 20, and a value of less than 15 is regarded as quite satisfactory (McCune and Grace 2002). A cumulative correlation coefficient of 0.70 in ordination distances with the original, n-dimension means that 70% of the variation in the data is represented by the two-dimensional ordination, and the original distances are therefore well preserved (McCune and Mefford 1999).

The arrangement of *S. brevifolia* and *R. robusta* (the two most abundant species) in ordination space shows a negative association as shown by opposite correlations with the first ordination axis. According to Gittins (1969), species occupy diagonally opposite points in the ordination when they are responding to a common influencing factor, but in opposite directions. Although the abundances of *S. brevifolia* and *R. robusta* showed strong trends in the current analysis, as indicated by coefficients of correlation with the ordination axes, soil parameters showed very weak trends. The weak correlations (all r^2 values were less than 0.1) between soil variables and ordination axes means that variation in the underlying soil factors explain less than 10% of the variation in the vegetation and thus contribute little to the observed vegetation patterns along the ecotone. These results were also confirmed by the weak correlations ($r^2 < 0.15$) between individual soil variables and species abundance data of *S. brevifolia* and *R. robusta* in these communities. Although very weak, the significant opposite correlations that *S. brevifolia* and *R. robusta* displayed with soil depth and soil texture (total sand content), indicate that these two species respond in opposite directions to the influence of soil depth and soil texture. Soil depth and soil texture are also among the important soil factors that separate the

grass communities of *Stipagrostis ciliata* on deeper sandy soils from communities of dwarf succulent or spinescence shrubs on shallow soils at Vaalputs Lloyd (1989). The close association between *S. brevifolia* and *R. robusta* may be an indication that these two species are ecotonal species, with high overlap in soil properties.

The importance of soil factors particularly those that influence local water balance in determining landscape vegetation pattern has been reported in arid areas and semi-arid ecosystems (Bliss and Cox 1964; Bowers and Lowe 1986; Abd El-Ghani 1998, 2000; Buxbaum and Vanderbilt 2007). At the desert grassland/shrubland ecotone between the Colorado Shortgrass steppe and the Chihuahuan desert, Buxbaum and Vanderbilt (2007) reported that soil texture and soil depth influence the plant dynamics by affecting local soil moisture regimes, and by inhibiting root growth of plants respectively. Soil moisture has been indicated to influence the distribution of fynbos species at the ecotone between the Succulent Karoo and the Fynbos biomes, but not the Succulent Karoo species (Lechmere-Oertel and Cowling 2001; Agenbag et al. 2004). Soil moisture variables were not tested in this study, but as these are highly influenced by factors such as soil depth and soil texture (Ellis and Lambrechts 1986), which displayed slight correlations with the two common species (*S. brevifolia* and *R. robusta*), a detailed analysis is required.

The weak relationships between the vegetation and soil variables revealed by both ordination and correlation analyses in this study suggest that the distribution of species may be controlled by interactions among the plants themselves. The role of competition in arid and semi-arid environments was initially questioned (e.g. Grime 1974, 1977), but it has been increasingly becoming clear that plant competition plays an important role in these environments (e.g. Tilman 1990; Goldberg and Novoplansky 1997). Plant competition has been reported in the broader Karoo (Cunliffe et al. 1990; Yeaton and Esler 1990; Esler and Cowling 1993; Carrick 2003), and is suggested as one of the factors limiting the distribution of Succulent Karoo species at the boundary between the Succulent Karoo and the Fynbos biomes (Lechmere-Oertel and Cowling 2001; Agenbag et al. 2004). The nature of competitive relationships between grass and shrubs in the Karoo however has not been explored before, but evidence of competitive interactions between neighbouring *S. brevifolia* and *R. robusta* adult plants along the ecotone were reported (Chapter 5). In the next chapter, a field experiment confirmed the role of competition in preventing the establishment of *R. robusta* in *S. brevifolia* grass community, whereas the influence of soils was negligible. From the current study, it emerged that soils contribute little to the distribution of *S. brevifolia* and *R. robusta* at the ecotone, and I hypothesise that the

distribution of these two components in the landscape may be determined by competition between species as further explored and discussed in the next two chapters.

University of Cape Town

4. Effects of root competition and soils on the establishment of grass and succulent shrub seedlings

Abstract: The establishment of grass and shrub seedlings, and the impact of root competition on seedling survival and growth were investigated in grass and shrub communities at the ecotone. The objective of the study was to determine whether grass communities and succulent shrub communities are spatially segregated as a result of competitive exclusion or soil differences between the two communities affecting the establishment of seedlings. Seedlings of *Stipagrostis brevifolia*, a perennial C₄ bunch grass and *Ruschia robusta*, a leaf-succulent shrub were transplanted into naturally occurring openings within *Stipagrostis brevifolia* and *Ruschia robusta* communities. The effects of competition were tested by exposing seedlings to roots of neighbouring adult plants or by excluding the influence of neighbouring roots by growing them within metal partitions. The influence of soil was tested by comparing seedlings of each species growing in their own community and in the community of the other species. Seedling survival and growth were monitored from May 2005, for 9 months through the winter, spring and summer seasons, until January 2006. Biomass was compared at the end of the experiment.

All *S. brevifolia* seedlings died within the first three months, irrespective of competition exclusion or community type in which they were growing, but initially survival was better in the grass community than in the shrub community. Competition affected the survival of *R. robusta* seedlings in the grass community, but not in the shrub community. In the shrub community, however, *R. robusta* seedlings exposed to competition exhibited reduced growth (height and leaf numbers) and lower biomass. When seedlings of *R. robusta* were not exposed to root competition, survival, growth and biomass in the grass community did not significantly differ from those in the shrub communities. Excluding root competition in the grass community provided favourable conditions for *R. robusta* seedlings to establish, suggesting that soil conditions were not affecting the establishment of this species in *S. brevifolia* communities.

4.1 Introduction

An ordination of soil factors and vegetation data between the grass *Stipagrostis brevifolia* and a succulent shrub *Ruschia robusta* communities characterising the ecotone has revealed little influence of soils on the vegetation pattern (Chapter 3). It is widely accepted that measurements of edaphic and climatic tolerances of plant species are imperfect predictors of their distributions, and inter-specific competition is regarded the most pervasive factor confining species distributions (Dunnett and Grime 1999). The role of competition is sufficiently emphasised in community and population ecology, where competitive and co-existence models have been postulated (see Gordon 2000). Multi-species habitat selection models, for example, reflect the general phenomenon that inter-specific competition tends to cause species to segregate into different habitat types but allow for co-existence in some cases (Rosenzweig 1981). Whether species would co-exist or exclude each other competitively therefore depends on competition coefficients, which largely govern inter-specific dynamics (Hardin 1960; Brown 1971; Gordon 2000).

From the previous chapter, it was hypothesised that the distribution pattern of *S. brevifolia* grass communities and *R. robusta* shrub communities at the ecotone may be determined by competition. Competition should however be confirmed through experiments, in order to distinguish between the effects of habitat preferences and competitive exclusion

(Gurevitch 1986). Such experiments focus on seedlings establishment, which is the critical life history stage for population persistence (Harper 1977; Snaydon and Howe 1986; Reader 1990; Aguilera and Lauenroth 1993; Davis, Wrage and Reich 1998; Gordon 2000; Lechmere-Oertel and Cowling 2001; Peltzer and Kochy 2001; Sanchez and Peco 2004). In arid and semi-arid environments where light availability is not a frequent limiting factor, belowground competition is believed to be the principal form of competition (Fowler 1986), and thus the current study focuses on the effects of root competition.

Plant competition experimental studies make use of among other methods, removal experiments and root exclusion techniques to suppress interferences between plants (Fonteyn and Mahall 1981; Ehleringer 1984). Removal experiments are appropriate in areas of high vegetation density, and the method is common in areas of high herbaceous coverage with no available openings. It involves the removal of both aboveground and belowground biomass of neighbouring vegetation (e.g Reader 1990; Sammul et al. 2000; Peltzer and Kochy 2001; Midoko-Iponga, Krug and Milton 2005). Root exclosures involve the isolation of the belowground environment of openings using metal barriers sunk into the soil (Snaydon and Howe 1986; Aguilera and Lauenroth 1993; Sanchez and Peco 2004). In this study, the root exclusion method was combined with reciprocal seedling transplanting (e.g Esler and Cowling 1993) in a field experiment in communities of *S. brevifolia* and *R. robusta* at the ecotone, in order to investigate the influence of soil and root competition on the establishment of seedlings of each species. In this way, two hypotheses were tested simultaneously by transplanting seedlings, with and without the exclusion of root competition from the established adult plants in the two communities: 1) seedlings of *S. brevifolia*, or of *R. robusta* will establish better in their own community than when growing in a community of each other species, and 2) root competition from established adult plants inhibits the establishment of seedlings. The first hypothesis is a measure of the influence of soils in different communities on seedling establishment. The two hypotheses address the question whether the occurrence of disjunctive communities of grass and of succulent shrubs along the ecotone is due to exclusive competition in these communities or soil preferences for establishment. This information contributes to the overall understanding of the determinants of the vegetation along the ecotone.

4.2 Materials and methods

4.2.1 Study site

The study was carried out on the farm Kougoedvlakte (18°26' E and -30°20' S), in the area along the border between Namaqualand and Bushmanland in the Northern Cape. Climatically, this

farm lies in the zone separating the predominantly winter rainfall Succulent Karoo and the predominantly summer rainfall Nama-Karoo biomes (Chapter 2). Annual average rainfall from De Riet, which is the farm adjacent to Kougoedvlakte to the north, is 116 mm (1984-2006), and rainfall between years is extremely variable (Coefficient of Variation of 41%, Figure 4.1). The rangeland at the study site is privately owned and is used for commercial sheep farming. The vegetation is also transitional between Bushmanland arid grassland and Namaqualand succulent shrublands, and is composed of grass communities, succulent shrub communities and grass/shrub mixed communities. *Stipagrostis brevifolia* is the dominant perennial grass species in these communities but other grasses such as *S. obtusa*, *S. ciliata* and *Cladoraphus spinosa* were also frequently observed, together with isolated *Lycium cinereum* shrubs (personal observation). *Ruschia robusta* is the dominant shrub in succulent or mixed communities. Kougoedvlakte was chosen because it carried the community types of interest and was easily accessible. Two communities dominated by *S. brevifolia* and *R. robusta* respectively were selected for the present study. Vegetation cover and composition in these two communities are presented in Figure 4.2. Similar species dominance and vegetation cover were observed in similar communities along the ecotone, and soil properties were also comparable (Chapter 3).

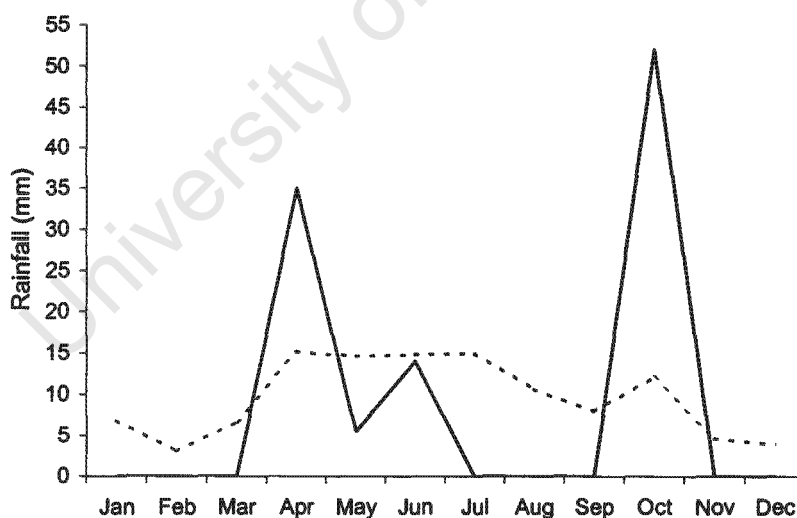


Figure 4.1 The mean monthly rainfall (dotted line) at De Riet, a farm adjacent to the study site for the period 1984-2006, and the monthly rainfall (solid line) during 2005. (Mean annual rainfall = 116 mm; Coefficient of Variation =41%).

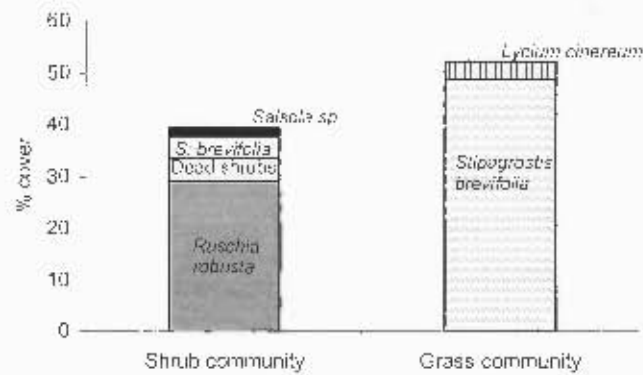


Figure 4.2 Percentage vegetation canopy cover along 50 m transects in shrub and grass communities at Kougoedvlagte farm.

4.2.2 The seedlings transplant experiment

Seeds of *Stipagrostis brevifolia* and *Ruschia robusta* were collected from the field and sown on the 16 February 2005 in seedling trays comprised of compartments measuring 3 x 3 cm wide and 6 cm deep. Three seeds of each species were sown in each compartment, and the trays were kept in a glasshouse at the University of Cape Town. The seedling trays were well-watered to encourage germination. Germination commenced two days after sowing for *R. robusta*, and after four days for *S. brevifolia*. In cases where more than one seedling emerged, the first seedling was maintained and the rest were removed. The seedlings were watered daily for two weeks after which watering was reduced to every second day. After four weeks, watering was reduced to every third day until they were transplanted in the field on the 28 April 2005.

In the field, the transplanted seedlings of each species were either exposed or excluded from the roots of adult plants in a *Stipagrostis brevifolia* community or a *Ruschia robusta* community. This experimental design allows the effects of competition to be distinguished from those arising as a result of differences in soils between the two communities. The experiment was a fully factorial design with two treatments: root competition from adults, and identity of neighbouring adult/or surrounding community, which resulted in four treatment combinations. Each treatment combination was replicated 5 times. In both *S. brevifolia* and *R. robusta* communities, (which will be referred to as grass and shrub communities respectively in this study), 10 naturally occurring gaps between established plants of at least 50 x 40 cm in size were identified. Five of these gaps were randomly allocated to 'neighbour roots exclusion plots' and five to 'neighbour root-competition plots' as explained below.

For seedlings that were assigned to grow without root competition, steel boxes 50 x 40 x 30 cm with open top and bottom were carefully sunk into the ground with as little soil disturbance

as possible. These structures excluded roots in the surface 27 cm of the surrounding vegetation from competing with the seedlings for soil resources such as water and nutrients. Similar boxes but which were only 3 cm deep (50 x 40 x 3 cm), and protruded above the ground to a similar height as the 'root exclusions boxes' were used in plots where seedlings grew in the presence of neighboring roots. Similar root exclusion structures have been used to test below-ground competition (Snaydon and Howe 1986; Aguilera and Lauenroth 1993; Sanchez and Peco 2004). The soil inside the plots was watered and seedlings of both species were randomly transplanted into each plot, in regular patterns 10 cm apart, and a minimum of 5 cm from the edge of the box. Surviving seedlings from the glasshouse allowed only for a maximum of eight seedlings of *S. brevifolia* to be transplanted in each box, whereas sufficient seedlings for *R. robusta* were available to allow 10 seedlings per box as initially planned. The position of each species within the boxes was predetermined randomly.

The seedlings were watered immediately after transplanting, although the soil was also still moist from heavy showers received two weeks prior to transplanting. A chicken wire fence (with a mesh size of 1.5 x 2.0 cm) was erected around each box to prevent damage to seedlings by domestic livestock and other animal disturbances. Seedlings were watered on the following two days, and then at two days intervals until the 11th day after transplanting the seedlings when they were counted and measured for the first time. Thereafter the transplants were watered after two weeks for the last time, and were counted and measured for the second time. The monthly rainfall during the year 2005 is superimposed with the average rainfall in Figure 4.1.

Seedlings were monitored for growth and survival on the following dates: 09 May 2005, 23 May 2005, 11 June 2005, 27 July 2005, 07 September 2005 and 21 January 2006. Growth was monitored in terms of height of the seedlings for both species and number of leaf pairs for *R. robusta*. At the end of the experiment (21 January 2006), aboveground and belowground biomass of surviving seedlings were harvested, washed free of sand and dried for 48 hours at 70°C for dry biomass determination.

4.2.3 Data analysis

All statistical analyses described below were done using STATISTICA Vers. 7, (StatSoft 2004). Normality was tested using the Kolmogorov-Smirnov and Lilliefors tests and homogeneity of variance was tested with Levene tests. Where data were not normally distributed, appropriate transformations were employed. The data on the proportion of seedlings surviving were Arcsin transformed. Number of leaf pairs and biomass data were square-root-transformed while height data were log-transformed to meet normality and homogeneity of variance assumptions.

Two-way ANOVA was performed on survival data at 44 days after transplanting for *S. brevifolia* seedlings (there were not enough survivals for statistical analysis after this period) and at 268 days (the end of the experiment) for *R. robusta* seedlings, with root competition and soil type (identity of adult neighbour) as the main factors. The identity of adult neighbour, or community type is used here to represent the measure of soil type. As there were no surviving seedlings of *S. brevifolia* at the end of the experiment, there was no biomass data for this species. Surviving seedlings in both species also did not provide sufficient replicates in each of the four combinations of factor levels for a factorial ANOVA of growth data (leaf count, height) and biomass (in the case of *R. robusta*) and thus one-way ANOVAs were applied between the group pairs.

4.3 Results

Stipagrostis brevifolia seedlings had almost all died out 90 days after transplantation, and only one seedling has survived up to the end of the experiment (Figure 4.3). In the first 44 days of monitoring, survival of *S. brevifolia* seedlings was initially better in their own community (the grass community) than in the shrub community (Figure 4.3). The importance of soil type during this period of monitoring was also revealed in a factorial ANOVA as indicated by the significant effect of soil on the survival of *S. brevifolia* seedlings (Table 4.1). At this period, competition did not have a significant effect on seedling survival of *S. brevifolia* (Table 4.1). A one-way ANOVA which was applied on height data has revealed that *S. brevifolia* seedlings in their own community were significantly taller than in the shrub community (with the exclusion of root competition in both cases) ($F_{(1,8)} = 11.02$, $P = 0.01$), but root competition did not have a significant influence on the height of the seedlings growing in *S. brevifolia* community ($F_{(1,8)} = 1.96$, $P = 0.199$) (Figure 4.4).

Both soil type and root competition influenced the survival of *R. robusta* seedlings, and there was a significant interaction between the two factors (Table 4.1). Competition thus affected survival of these seedlings only in the grass community but not in the shrub community (Figure 4.3). In the grass community, seedlings of *R. robusta* exposed to competition were reduced to only one seedling at the end of the experiment. In the shrub community however survival of *R. robusta* seedlings was not affected, a one-way ANOVA has revealed significant effects of competition on seedling height ($F_{(1,8)} = 19.57$, $P = 0.002$), number of leaves ($F_{(1,8)} = 15.49$, $P = 0.004$) and biomass ($F_{(1,8)} = 22.42$, $P = 0.001$) (Figure 4.4 and Figure 4.5). At the end of the experiment, *R. robusta* seedlings growing without the presence of roots of neighbouring adult vegetation were significantly taller, had higher biomass and more leaves than seedlings growing

in the presence of roots (Figure 4.4 and Figure 4.5). *Ruschia robusta* seedlings growing in grass community were significantly taller ($F_{(1,8)} = 22.33$, $P = 0.002$) than those growing in *R. robusta* community (with the exclusion of root competition in both case), although leaf count and biomass did not differ significantly between the two community types ($F_{(1,8)} = 1.85$, $P = 0.063$ and $F_{(1,8)} = 4.65$, $P = 0.068$ respectively) (Figure 4.4 and Figure 4.5). There was no significant difference in root mass fraction of *R. robusta* seedlings between the two communities ($F_{(1,8)} = 3.18$, $P = 0.118$) or between competition treatments in the shrub community ($F_{(1,8)} = 0.26$, $P = 0.062$) (Figure 4.5).

Table 4.1 Results of ANOVA for seedling survival of **A:** *Stipagrostis brevifolia* 44 days after transplanting and **B:** *Ruschia robusta* at the end of the experiment (268 days after transplanting). Significant differences are indicated by * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

A	Factor	d.f.	F-ratio	P	B	Factor	d.f.	F-ratio	P
	Soil	1	47.6	<0.001***		Soil	1	10.97	0.005**
	Competition	1	0.09	0.772		Competition	1	8.17	0.012*
	Soil x Competition	1	3.89	0.066		Soil x Competition	1	8.26	0.012*
	Error	16				Error	16		

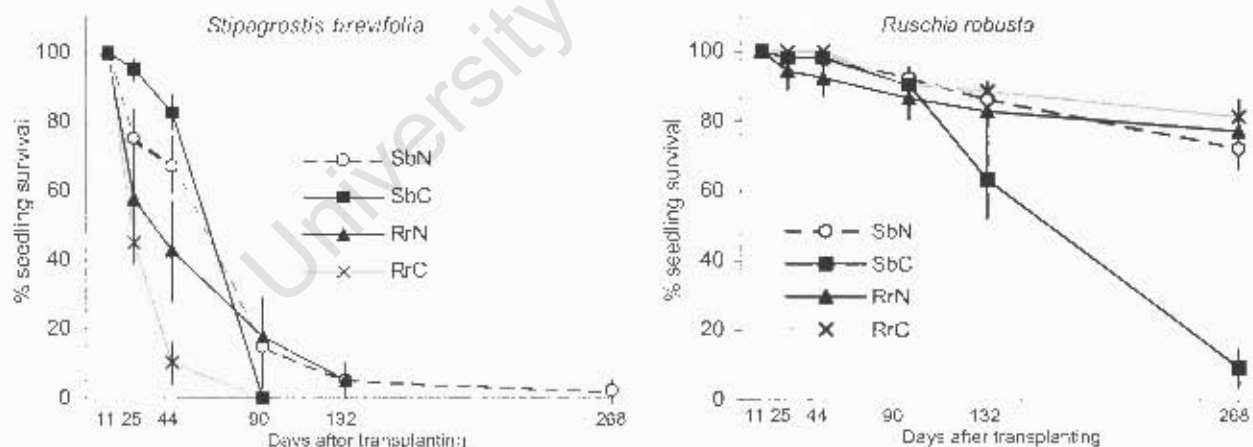


Figure 4.3 Survival of *S. brevifolia*, and *R. robusta* seedlings in both communities and in competition treatments. Data are means ($\pm$ 1 S.E.). SbN = no competition in the grass community, SbC = Competition in the grass community, RrN = no competition in the shrub community, RrC = Competition in the shrub community.

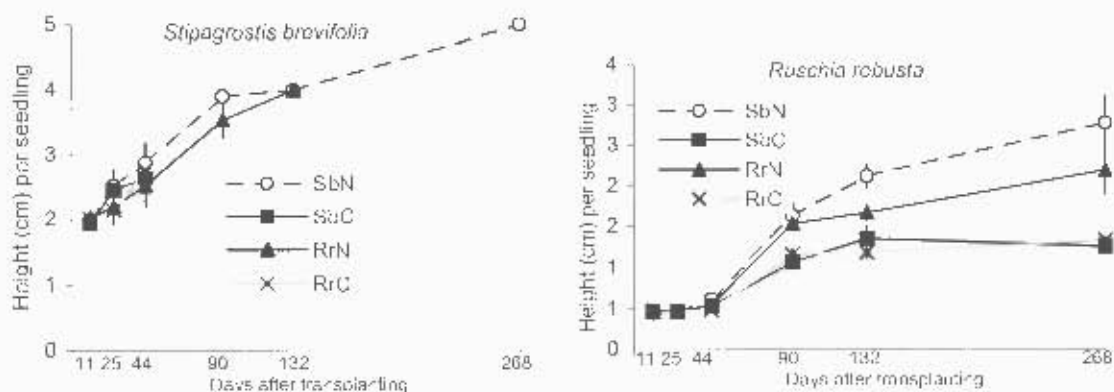


Figure 4.4 Height of surviving seedlings (top row) for *S. brevifolia* and *R. robusta*, and number of leaf pairs for *R. robusta* seedlings over time (to the right). Values are means ($\pm$ 1 S.E.).

SbN = No competition in the grass community,
SbC = Competition in the grass community,
RrN = No competition in the shrub community,
RrC = Competition in the shrub community

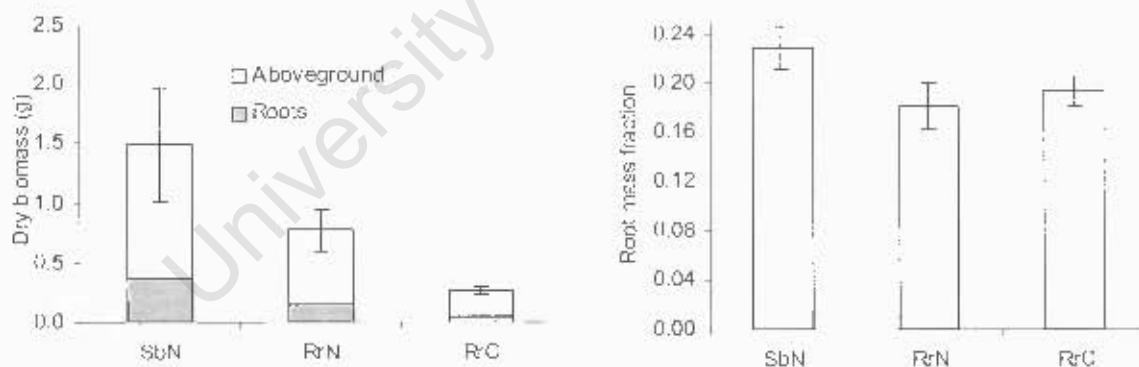
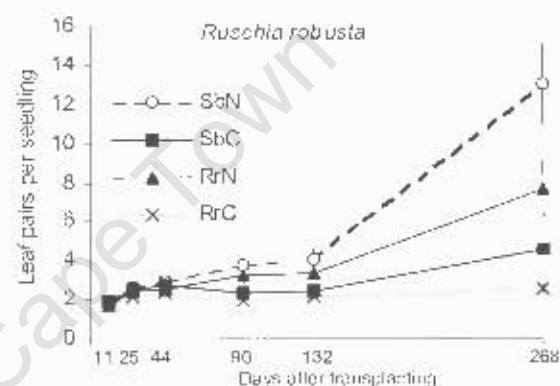


Figure 4.5 Dry biomass and root mass fraction of seedlings of *Ruschia robusta* 268 days after transplantation. Values are means ($\pm$ 1 S.E.). Label codes are as in previous figure.

4.4 Discussion

4.4.1 The establishment of *S. brevifolia* seedlings

Results from the establishment of *S. brevifolia* seedlings were inconclusive, as all the seedlings died early on in the experiment irrespective of treatment or soil type. Different factors might have contributed to the observed high mortality of *S. brevifolia* seedlings, but the results may be important regarding the resilience of *S. brevifolia* seedlings, and especially comparing to *R. robusta* seedlings which had higher survival under similar conditions. Rainfall during the year of

the experiment was fairly above average for most of the time the experiment was running, and thus it is unlikely that transplanting the seedlings at different time would improve the seedlings survival. *Stipagrostis brevifolia* is possibly a difficult species to grow, and it apparently cannot establish as fast as the other two *Stipagrostis* species i.e. *S. ciliata* and *S. obtusa* (Barnard and Louw 1984 in Lloyd 1989).

During the initial stage of the experiment (44 days period of monitoring, at which statistical comparisons were made), soil type had a significant influence on both the survival and the height of *S. brevifolia* seedlings, while competition showed no effects. I would be cautious however to conclude upon these results, as the time period might be too short even for competition to start having effects. The role of soils in preventing the establishment of *S. brevifolia* in *R. robusta* shrub communities is unlikely, given the greater overlap in soil properties between the two community types (Lloyd 1989; Chapter 3). The potential for belowground resource competition between grass seedlings and the mesembs³ exists, given the dense mesh of shallow root system characterising most of the later (Esler and Rundel 1999; Carrick 2001; Chapter 5).

4.4.2 The establishment of *R. robusta* seedlings

The importance of root competition on the establishment of *R. robusta* seedlings in grass community was clearly indicated by high mortality of the seedlings exposed to the roots of adult *S. brevifolia* vegetation. *Ruschia robusta* established well in *S. brevifolia* grass community provided the seedlings were not exposed to root competition from the surrounding grass vegetation. Moreover, neither survival nor biomass or the number of leaves differed between seedlings growing in the grass community and in the shrub community, confirming that root competition from established grass vegetation is the main factor regulating colonisation of grass community by *R. robusta*, and not soil type associated with *S. brevifolia* communities. Competition from *S. brevifolia* vegetation was strong enough to cause high mortality of *R. robusta* seedlings, supporting the exclusive competition models (Hardin 1960; Brown 1971) in this case whereby *S. brevifolia* communities competitively exclude *R. robusta* from colonising these communities. The presence of pure grasslands at the ecotone may thus be a result of these strong competitive effects. Grass with their fibrous roots are generally considered to be capable of taking up more available soil resources and successfully compete against short woody plants, e.g. seedlings or low shrubs (Kochy and Wilson 2000). This however does not explain the

³ A group of leaf succulent plants in the family Aizoaceae, which formerly constituted a separate family, the Mesembryanthemaceae, and which are colloquially referred to as 'mesembs'

presence of mixed grass/shrub communities along the ecotone. Evidence of competitive interactions between *S. brevifolia* and *R. robusta* was reported between the adult individuals in mixed communities at all four sites investigated along the ecotone (Chapter 5). From this we can infer that *S. brevifolia* is able to competitively exclude *R. robusta*, but competition may also not be strong enough to cause competitive exclusion of the later species and the two co-exist, supporting the multi-species habitat selection models (Rosenzweig 1981; Gordon 2000; Krivan and Sirot 2002).

It was not entirely surprising that competition rather than soil type emerged as the main factor preventing the establishment of *R. robusta* seedlings in the grass community, given the reported overlap in the soil factors between the two community types (Lloyd 1989; Chapter 3). The mesembs, including *R. robusta* established well over a wide range of microhabitat types (Carrick 2001). Carrick (2001) thus concluded that the failure of these species to colonise sites dominated by deeper rooted non-succulent shrub, *Galenia africana* was not due to changes in soil chemistry or to a lack of microhabitat suitable for establishment. These results are thus in line with Grime (1974; 1979) that the limits of a plant's distribution are not simply set by the environmental limitation of resources, but competition can act to further influence vegetation patterns. Excluding the roots of established grass vegetation in this study facilitated access to soil resources by *R. robusta* seedlings, allowing them to survive and grow, reaching the same biomass as those growing in their own community (*R. robusta* shrubland). The importance of competition in controlling Succulent Karoo species was also reported at the boundary between Fynbos and the Succulent Karoo biome in Matjiesrivier Nature Reserve, whereas abiotic environment was indicated as unimportant in limiting the Succulent Karoo species (Lechmere-Oertel and Cowling 2001). The current study and the existing reported evidence of competition between the Succulent Karoo species (Cunliffe et al. 1990; Yeaton and Esler 1990; Esler and Cowling 1993; Carrick 2003) indicate the importance of competition in structuring Succulent Karoo vegetation, and contrast Esler et al., (1999) and Cowling and Hilton-Taylor, (1999) who suggested that competition among plants has a negligible influence on structuring the Succulent Karoo vegetation.

The effects of competition experienced by *R. robusta* seedlings differed depending on the type of community they were growing in. *Ruschia robusta* seedlings exposed to inter-specific root competition from *S. brevifolia* vegetation have died out, but intra-specific competition in *R. robusta* community did not have any effect on seedlings survival. Surviving *R. robusta* seedlings exposed to root competition of their own conspecific adults were significantly smaller, and the average number of leaves per seedling was three times fewer than when seedlings were not

exposed to root competition. Similar observations whereby intra-specific competition allows shrub seedlings to continue surviving as stunted and with no noticeable growth have been previously reported (Fenner 1978; Howe and Snaydon 1986; Aguilera and Launroth 1993). In mixed-grass prairie, the seedlings of the shrub *Elaeagnus* species experience much lower competition intensity in the shrub dominated habitat than in a grass dominated habitat (Peltzer and Kochy 2001). Higher inter-specific competition effects than intra-specific effects experienced by *R. robusta* seedlings in the current study is ecologically important for the regeneration of these communities. Higher intra-specific than inter-specific competitive relationships on the other hand have been commonly reported in other studies in arid areas (Yeaton and Cody 1976; Yeaton et al. 1977; Fonteyn and Mahall 1981; Briones, Montana and Ezcurra 1996). Stronger competitive interactions within species than between species is reportedly important for co-existence between species (Scholes and Archer 1997), as shown between *R. robusta* and *S. brevifolia* adult individuals in mixed communities where the two species co-exist (Chapter 5).

4.4.3 Implications for ecotone dynamics

Results of this experiment were based on a nine months' study, and within only one example of each community type. Year-to-year variability in water availability may affect competition between seedlings and established vegetation (Aguilar, Soriano and Sala 1992). Variation in the results may thus occur if high rainfall years for example characterised the year of the experiment, as it may be a case in years of exceptionally above average rainfall years such as El Niño events which are reported to be associated with high seedling establishments (e.g. Marone, Horno and Gonzalez del Solar 2000). The intensity of competition is also shown in some cases to vary across environmental gradients (Grime 1979; Davis et al. 1998; Sammul et al. 2000). Although debate regarding competition across environmental gradients still continues (Welden and Slauson 1986; Tilman 1987; Campbell and Grime 1992; Craine 2005), extrapolating results of a once off and a single site competition study should be done unequivocally. It is reasoned that the ecological importance of competition, defined as the relative impact of competition on processes such as community composition or population dynamics (Welden and Slauson 1986; Goldberg 1994) is likely to remain the same across temporal and spatial environmental gradients which may alter competition intensity (Grime 1977; Reader 1990; Foster 1999). An example of this is demonstrated in a seedling experimental study in the Patagonian steppe, where root competition has resulted in a decreased growth and increased mortality of grass seedlings during both a dry and rainy year, but the effect was greater during the dry year (Aguilar et al. 1992). It is thus most

likely that even though the magnitude or intensity of competition may change between the years, competition will have the same effects in terms of importance as observed from the current study.

Two hypotheses were investigated in this study: whether seedlings of either species could establish in each other's communities (the influence of soil), and the influence of root competition in the establishment of seedlings. One of the main findings from the study was the initial better performance of *S. brevifolia* seedlings in their own community than when growing in the shrub community, and the ultimate mortality of all grass seedlings in both communities irrespective of competition treatments. Whereas these findings do not provide concluding evidence on the role of competition and soils on the establishment of this species, they provide insights into the resilience of the seedlings of *S. brevifolia*. Compared to *R. robusta*, *S. brevifolia* might be more competitive as is explored further in the next chapter, but the seedlings of *R. robusta* seem to establish better as suggested in this study. A trade-off between high rates of colonization (shrub's strategy) and strong competition (grass' strategy) could facilitate the coexistence of grass and shrubs at the ecotone. The second main finding was that under no competition from established vegetation, *R. robusta* seedlings did not distinguish between the grass community and the shrub community, but the seedlings did not survive when exposed to root competition of *S. brevifolia* vegetation. *Ruschia robusta* can thus successfully establish in the soils of *S. brevifolia* communities in the absence of competition from neighbouring established grass. This highlights the role of competition in these communities, and supports Dunnett and Grime (1999) and Gordon (2000) who described competition as the most pervasive factor confining species distributions. Competitive exclusion (Hardin 1960; Brown 1971; Armstrong and McGehee 1980) is supported in the current study, whereby *S. brevifolia* communities competitively exclude *R. robusta* from colonising these communities.

5. Competitive relationships between grass and succulent shrubs at the ecotone

Abstract: Nearest-neighbour analysis was used to examine the competitive interactions between *Stipagrostis brevifolia*, a C₄ perennial grass and *Ruschia robusta* and *Leipoldtia pauciflora*, leaf succulent shrubs in mixed communities along the ecotone between Bushmanland arid grassland and Namaqualand succulent shrubland. The vertical and horizontal distribution of roots was also compared to assess the potential degree of overlap in the use of soil resources. Regressions between the sum of sizes of nearest-neighbour comparisons and the distance between them showed significant positive correlations for *S. brevifolia* and *R. robusta*, indicating the presence of competition. Intra-specific competition in both of these species was stronger than inter-specific. There was a stronger relationship between the size of *R. robusta* and the distance from *S. brevifolia*, than between the size of *S. brevifolia* and the distance from *R. robusta*, indicating that grass exerted a stronger competitive force on the succulent *R. robusta* shrub than *R. robusta* on *S. brevifolia*. There was no evidence of a competitive relationship between *S. brevifolia* and *L. pauciflora* or intra-specific relationship among *L. pauciflora* plants. Among the three species, the grass had deeper roots, exceeding 60 cm deep. *Ruschia robusta* had second deepest root system, with a taproot recorded as deep as 55 cm, although most of the roots were found in the first 20 cm. *Leipoldtia pauciflora* had the most shallow roots, most of which occurred in the top 10 cm of the soil.

5.1 Introduction

Plant competition is one of the important factors determining the structure and the dynamics of natural plant communities in arid and semi-arid environments (Yeaton and Cody 1976; Harper 1977; Fonteyn and Mahall 1981; Yeaton and Esler 1990; Damgaard 1998; Weigelt and Jolliffe 2003; Damgaard 2004). Species may co-exist or they may segregate into different communities, which is largely moderated by competition coefficients among them (Rosenzweig 1981; Scholes and Archer 1997; Gordon 2000). The vegetation along the ecotone between the Bushmanland arid grassland and the succulent shrubland of Namaqualand is characterised by communities of segregated grassland and succulent shrubland but also communities in which grasses and succulent shrubs co-occur. The previous two chapters have established that soil factors have little influence on communities of *S. brevifolia* and *R. robusta*, and that competition from the established grass vegetation plays an important role in preventing the establishment of *R. robusta* seedlings in *S. brevifolia* community. The study presented in this chapter focused on communities in which grass and succulent shrubs co-exist, to investigate the nature of competitive relationship between the two components along the ecotone.

Competition theories to explain co-existence between plant species or life forms are mainly based on the principle of niche differentiation through resource partitioning, both in space and in time as the main mechanism (Yeaton et al. 1977; Walker and Noy-Meir 1982; Knoop and Walker 1985; Cody 1986; Sala et al. 1989). A classic example is a vertical root separation model to partition soil resources between co-existing plant species (Walter 1971), which is widely explored in arid and semi-arid savanna systems (Walker and Noy-Meir 1982; Knoop and Walker 1985), Patagonian steppe (Sala et al. 1989) and in humid savannas (Le Roux et al. 1995;

Mordelet et al. 1997). Schenk and Jackson (2002) for example have recently proposed that Walter's two-layer model appears to be more appropriate in drier areas with substantial winter precipitation. Excavations of roots of a number of species have demonstrated that species in arid and semi-arid regions are characterised by several different patterns of root distribution resulting in separation of water use sufficient to permit co-existence (see Fowler 1986). In the Succulent Karoo, perennial species are reported to co-exist through spatial and temporal partitioning of resources and microsites (Milton 1990; Esler and Cowling 1993). Carrick (2003) has reported evidence of competition between the two leaf succulent Aizoaceae shrubs *Leipoldtia schultzei* and *Ruschia robusta* (the 'mesembs'), and the absence of competition between these succulents and a non-succulent Asteraceae shrub *Hirpicium alienatum*. Carrick (2003) ascribed these results to vertical separation in the rooting morphologies.

The root systems of the perennial grass in the broader Karoo region have not really been studied, and it is not clear how species within this growth form interact or co-exist with other growth forms such as succulent shrubs. Midgley and van der Heyden (1999) have proposed that perennial grasses and succulent shrubs might be competing for water in the same horizontal plane, due to the shallow-rooted nature of succulent shrubs. Focused studies on competitive interactions between grass and shrubs in the Karoo are also lacking. In the eastern Karoo, where perennial grasses and dwarf shrubs co-exist, Hoffman, Barr and Cowling (1990) have proposed that the abundance of grasses regulates the abundance of dwarf shrubs through competition, but current debate on the co-existence of the two growth forms in the area is centred around the importance of seasonal distribution of rainfall in regulating the vegetation (Roux and Vorster 1983; Hoffman et al. 1990; O'Connor and Roux 1995). The aim of this study was to determine the nature of competitive interactions between a grass *Stipagrostis brevifolia*, and two leaf succulent shrubs, *Ruschia robusta* and *Leipoldtia pauciflora* in mixed communities at the ecotone. Vertical partitioning in root systems was studied to explain the nature of possible belowground interactions between these two life forms.

The occurrence of plant competition in arid or semi-arid regions is inferred via studies of spatial patterns (Fowler 1986). In the current study, evidence of competition was inferred from the relationship between distance and size of neighbouring plants. This technique, the nearest-neighbour analysis, first described by Pielou (1960) has been widely used to study plant interactions in arid and semi-arid areas (Yeaton and Cody 1976; Yeaton et al. 1977; Welden, Slauson and Ward 1988; Yeaton 1990; Esler and Cowling 1993; Carrick 2003). It is based on the premise that significant positive linear correlations between the sum of neighbouring plant sizes and the distance that separates them indicate competition, while the lack of such correlations is

interpreted as the absence of competition. Studies have also compared the distribution of roots in the soil, in order to study the degree at which species are likely to interact (Cable 1969; Pelaez et al. 1994; Briones et al. 1996; Casper and Jackson 1997; Nobel 1997; Carrick 2003).

5.2 Methods

5.2.1 Study sites

The study was carried out at Burdensputs, Kougoedvlakte, Vaalputs and Goegap Nature Reserve along the ecotonal border between Bushmanland and Namaqualand, which is described in details in Chapter 2. The study focused on communities in which both grass and shrubs co-occur. At each of these sites, a community co-dominated by *S. brevifolia* and *R. robusta* was selected for sampling, but at Goegap Nature Reserve in the northern part of the study area, *Leipoldtia pauciflora* also co-existed with *S. brevifolia* and a community of this combination was also sampled.

5.2.2 Sampling of the nearest neighbours and vegetation cover

Vegetation composition and projected canopy cover in each of the communities were estimated using a line intercept method (Canfield 1941), to obtain the percentage cover and the relative abundance. Dead shrub cover in these communities was also recorded. For the nearest neighbour sampling, I walked along a 1 m-wide transect and whenever one of the studied species was encountered and its nearest neighbour was either a conspecific or one of the other studied species, then the distance between them, two perpendicular diameters (one of which was the longest possible) and height of each individual were recorded. At least 50 pairs of each combination of plants were sampled within each community, except in the *S. brevifolia* – *L. pauciflora* community in which *S. brevifolia* – *S. brevifolia* combinations did not occur frequently. Insufficient *S. brevifolia* combinations were encountered and therefore intra-specific interactions could not be analysed for this species in this community.

5.2.3 Roots excavation

The root systems of three isolated adult plants of *S. brevifolia* and *R. robusta* were excavated at Kougoedvlakte, and *L. pauciflora* at Goegap Nature Reserve. Excavation was done by hand using a pointed wooden stick marked at five cm and 10 cm to loosen the soil which was then hand removed, leaving the root system intact. Excavation progressed by extracting the soils, and recording the root architecture and lateral extent. Diagrams were made and photographs were taken as excavation progressed. At the recorded depths (see below), roots were collected into

separate paper bags, washed off excess sand, then dried and weighed. In the grass community, it was particularly difficult to find isolated adult grass plants because the grass density was high, and so young adults were excavated. The root data for *S. brevifolia* were collected at the following depth categories: 0-5, 5-10, 10-20, 20-30, 30-40, 40-50 and 50-60 cm. Excavation continued up to 65 - 70 cm; but roots from below 60 cm were only used for total root mass value. *Ruschia robusta* and *L. pauciflora* root data were collected at these depths: 0-5, 5-10, 10-20, 20-30, 30-40 and 40-50 cm, and were grouped into fine roots (with diameter < 2 mm) and course roots (with diameter > 2 mm). The taproot of *R. robusta* extended below 50 cm, but it was cut at this depth because the bedrock became too hard for excavation to continue. One plant was followed up to the end of the root system at 55 cm, but this extra data was not included in the analysis. To determine whether the root depths of *S. brevifolia* and *R. robusta* vary along the ecotone, confirmatory rapid excavations of plants were also done at the northern part of the study area, next to Goegap Nature Reserve.

5.2.4 Data analysis

The sizes of the plants were represented by an area of a ellipse calculated from the canopy diameters as:

$$A = \pi(ab/4)^2,$$

where: *A* is the area of the plant, *a* and *b* are the two diameters.

According to Kolmogorov-Smirnov and Liliefors tests, size data were not normally distributed, and, therefore, were square root transformed. Size data were then standardised by dividing the size of each plant by the mean size for that species, in a particular pair combination, in order to minimise the effect of different sizes of plants in each pair. Linear correlations between the sums of transformed and standardised size data and the distance between combined pairs were calculated. In inter-specific combination, the relative contribution of each species to the interaction was tested by regressing the individual sizes of plants of the two species against distance. Significant positive correlations (*r*) were interpreted as an indication of competition among plants.

The proportions of roots in different depth classes were described. The ratio of mean rooting diameter to mean canopy diameter, and the root mass proportion (root dry mass/ total dry mass) between the three species were compared using a one-way ANOVA followed by a Scheffe's test for post hoc comparison where necessary (STATISTICA Vers. 7, StatSoft 2004).

5.3 Results

5.3.1 Vegetation cover and composition

The total vegetation cover in the communities ranged between 41% at Burdensputs to 75% at Goegap Nature Reserve (Table 5.1). The co-dominance between the grass *S. brevifolia* and the leaf succulent shrubs *R. robusta* or *L. pauciflora* varied between the sites, and comprised more than 80% of the total vegetation cover. This cover included dead shrub cover, which was the third most important cover class in all cases.

Table 5.1 Vegetation canopy cover (%) at the five communities sampled for Nearest-Neighbour analysis.

Site	Total	<i>S. brevifolia</i>	<i>R. robusta</i>	<i>L. pauciflora</i>	Dead shrubs
Burdensputs	41	16	15	-	5
Kougoedvlakte	58	39	9	-	5
Vaalputs	58	16	23	-	10
Goegap <i>Ruschia</i>	75	46	22	-	5
Goegap <i>Leipoldtia</i>	75	24	-	42	3

5.3.2 Root distributions in the soil

The vertical distribution of roots and rooting structures of the three species are schematically represented in Figure 5.1 - Figure 5.3. *Stipagrostis brevifolia* had the deepest roots, extending below 60 cm in the soil. The top 10 cm of the root system of *S. brevifolia* was made up of a dense tuft of thick and tough non-fibrous roots. These roots contributed 30% to the total root mass, but they did not spread horizontally (Figure 5.1). The root system then became more fine and fibrous, spreading both horizontally and vertically going as deep as the excavation continued, but more than half of the total root mass were found between 10 and 40 cm deep (Figure 5.1). Exploratory rapid excavation near Goegap Nature Reserve and Dabeep farm confirmed this general root structure of *S. brevifolia*.

Ruschia robusta had the next deepest roots, with a taproot recorded as deep as 55 cm. The roots of *R. robusta* were primarily coarse, with about 70% of the root mass greater than 2 mm in diameter. More than 90% of the total roots occurred in the top 20 cm in the form of secondary roots that spread horizontally more than a meter away (Figure 5.2). In all three *R. robusta* plants excavated at Kougoedvlakte, the taproot split into two at about 30 cm, of which one branch continued deep down vertically in cracks in the bedrock, and the other becomes a lateral root. Since the ground hardened at about 40 cm, excavation was only possible up to 50 cm, and taproots were cut at this depth and only one of the three excavated *R. robusta* plants was followed up to the end of the root system, measured at 55 cm. Rapid root excavations further in the north of the study showed similar structure in the first 20 cm, but lack the taproot and thus the rooting system was shallower. *Leipoldtia pauciflora* had the most shallow root system and

only 3% of the total root mass was found below 10 cm, and none below 20 cm (Figure 5.3). The roots were also predominantly fine, with about 80% of the total dry root mass less than 2 mm in diameter.

The ratios of mean rooting diameter to mean canopy diameter were significantly different between the three species $F_{(2,6)} = 67.65$, $p < 0.0001$, of which *R. robusta* had the higher relative root diameter (5.77 ± 0.36 , mean $\pm$ 1SE) than *S. brevifolia* (2.19 ± 0.21) $p = 0.0002$, and *L. pauciflora* (2.08 ± 0.24) $p = 0.0001$. The root mass fraction (root dry mass / total dry mass) on the other hand was not significantly different $F_{(2,6)} = 2.38$, $p = 0.17$ between the species *S. brevifolia* (0.19 ± 0.023 , mean $\pm$ SE), *R. robusta* (0.26 ± 0.01) and *L. pauciflora* (0.32 ± 0.07).

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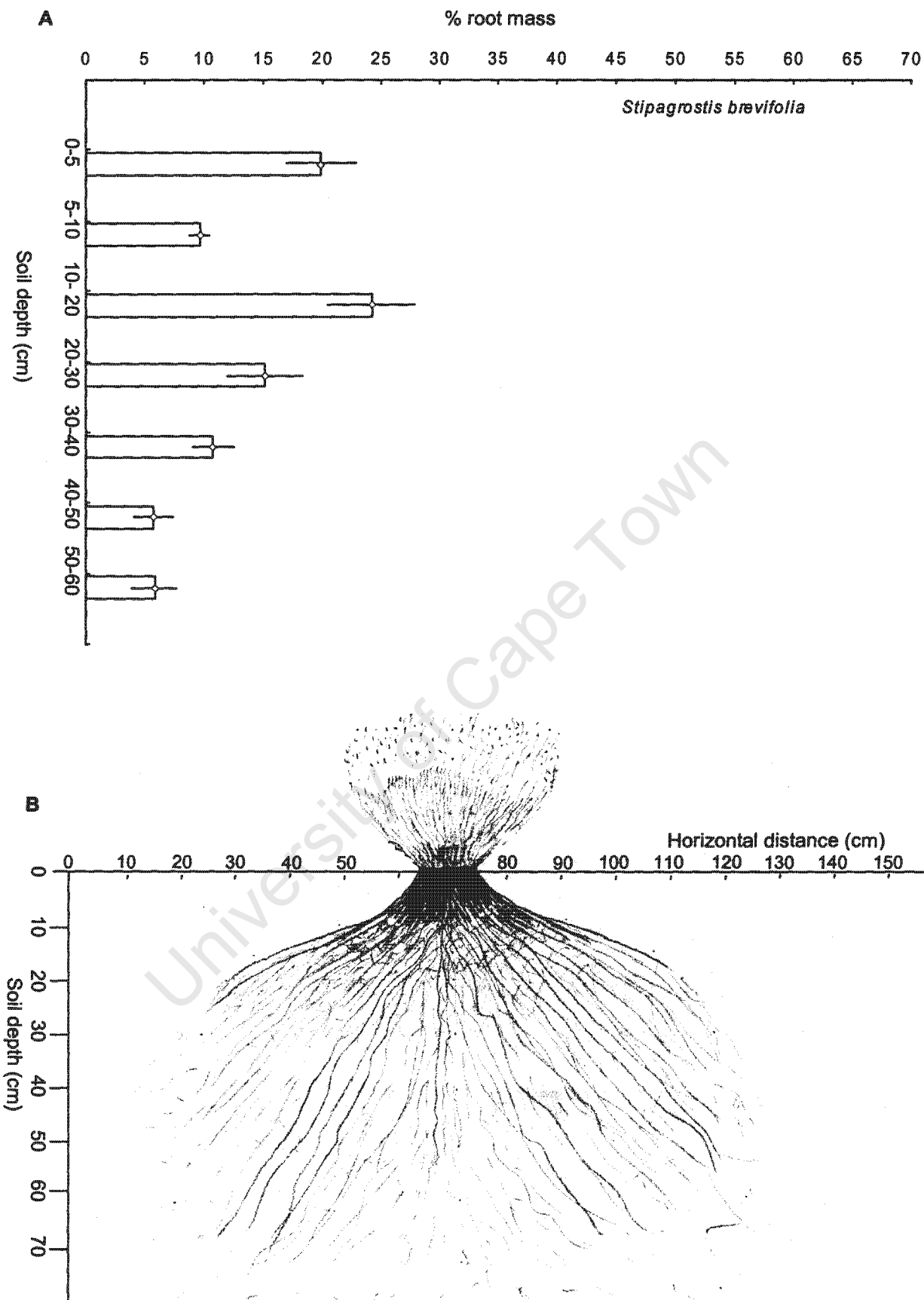


Figure 5.1 **A** Mean ($\pm$ 1S.E.) root mass at different soil depths and **B** the plant architecture showing the root system for *Stipagrostis brevifolia*, at Kougoedvlakte, $n = 3$.

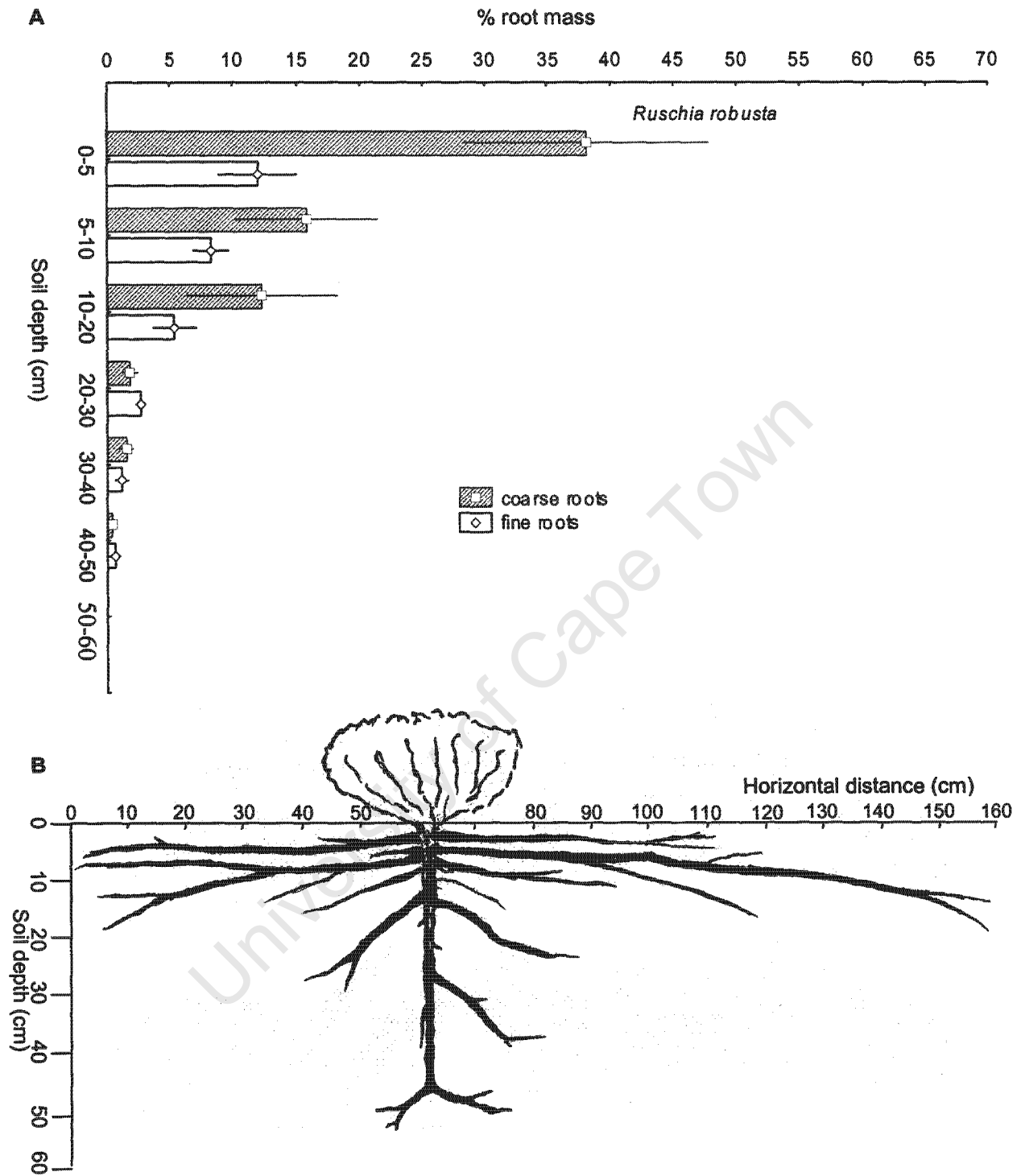


Figure 5.2 **A** Mean ($\pm$ 1S.E.) root mass at different soil depths and **B** the plant architecture showing the root system for *Ruschia robusta*, at Kougoedvlakte, $n = 3$.

In **A**: coarse roots > 2 mm, fine roots < 2 mm

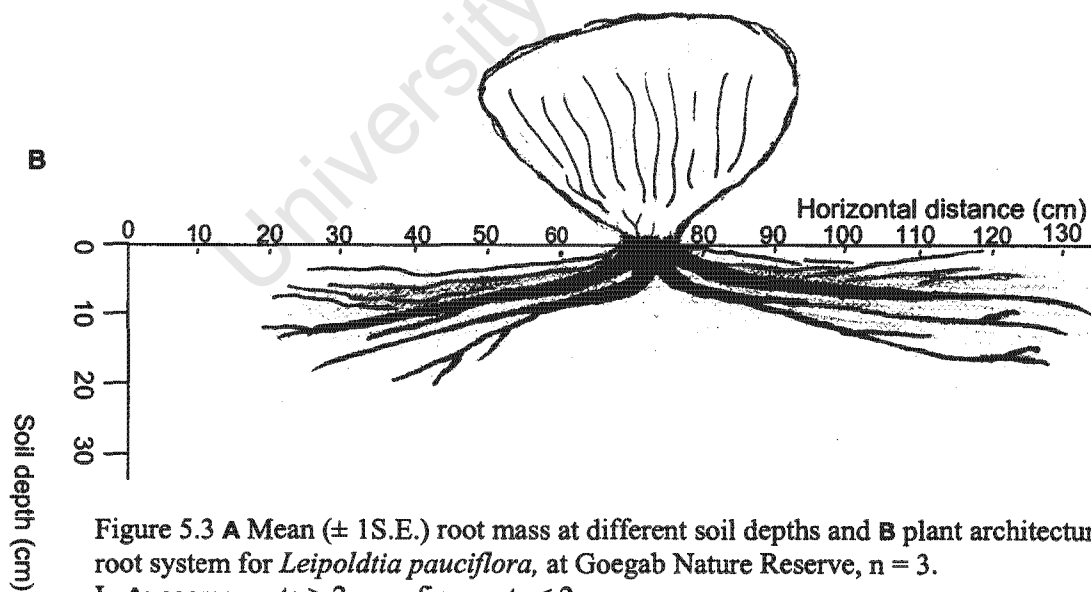
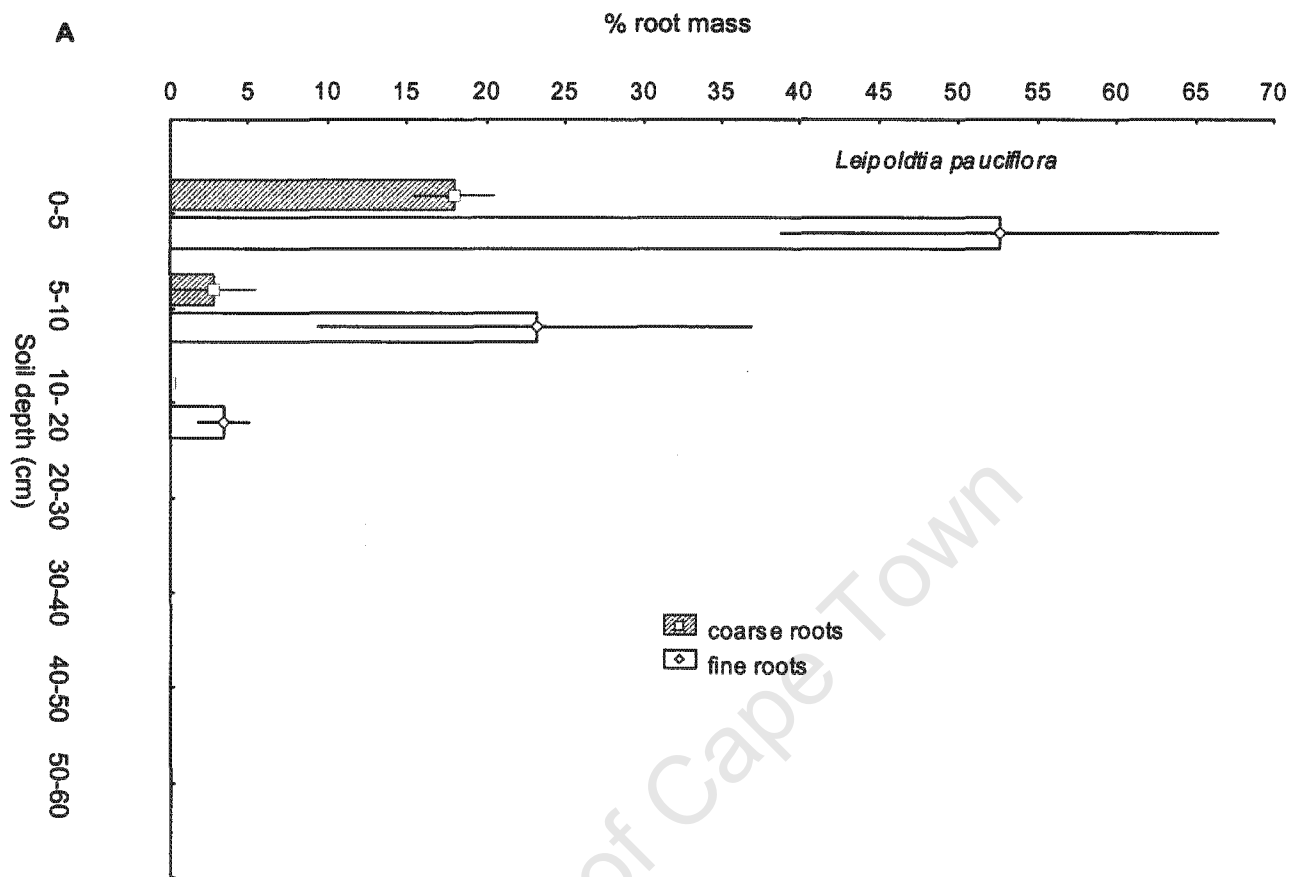


Figure 5.3 **A** Mean ($\pm$ 1S.E.) root mass at different soil depths and **B** plant architecture showing the root system for *Leipoldtia pauciflora*, at Goegab Nature Reserve, $n = 3$.
In **A**: coarse roots > 2 mm, fine roots < 2 mm

5.3.3 The nearest neighbours

Intra- and inter-specific nearest-neighbour pairings between *S. brevifolia* and *R. robusta* in all communities showed significant positive linear correlations between nearest-neighbour distances and the sums of sizes of the two neighbours (Figure 5.4 and Figure 5.5). Intra-specific comparisons yielded stronger correlations than inter-specific comparison. For inter-specific pairs, the correlation between the size of *R. robusta* and the distance from *S. brevifolia* was stronger, than the correlation between *S. brevifolia* and the distance from *R. robusta*. There was no relationship between the sizes of *L. pauciflora* plants and the distances between them ($r = -0.001$; $p = 0.99$), or between *L. pauciflora* and *S. brevifolia* ($r = 0.031$; $p = 0.80$).

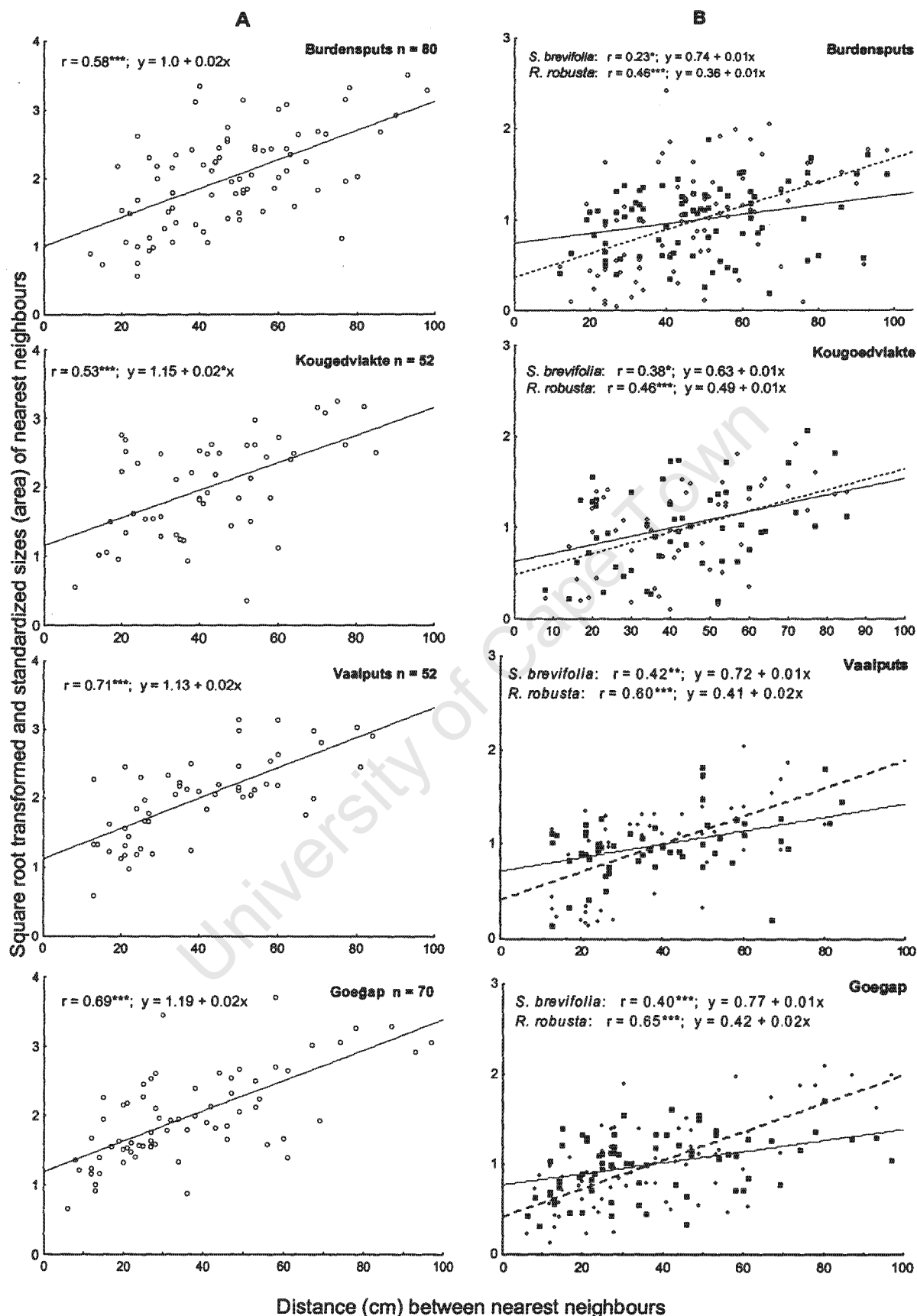


Figure 5.4 Correlations between the sizes and the distance between nearest neighbour plants between inter-specific comparisons using **A** combined sizes, and **B** individual species sizes where each line shows the effects of one species on the other species. * $P < 0.05$, ** $P < 0.001$ *** $P < 0.0001$. In **B**: *Stipagrostis brevifolia* *Ruschia robusta*

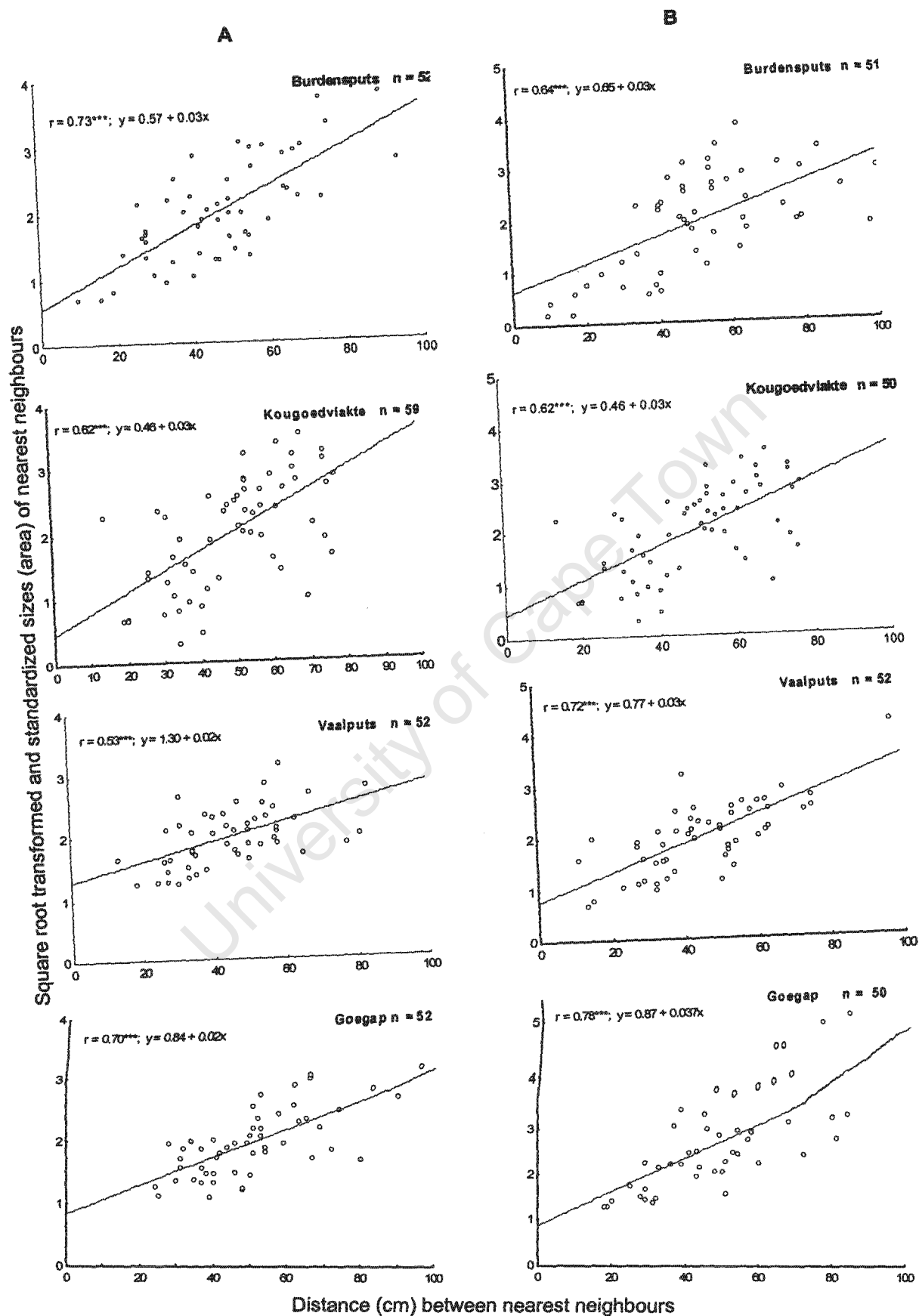


Figure 5.5 Correlations between the size and the distance between nearest neighbour plants between intra-specific comparisons using combined sizes between **A** *Stipagrostis brevifolia* pairs, and **B** *Ruschia robusta* pairs. *** $P < 0.0001$

5.4 Discussion

5.4.1 Competitive relationships

Results of nearest-neighbour analyses in this study suggest that competitive interactions occur between adjacent individuals within *R. robusta* – *S. brevifolia* communities, as indicated by positive significant correlations in both intra-specific and inter-specific nearest-neighbour comparisons. The relative strengths of intra- and inter-specific competition are relevant to species co-existence and stability (Scholes and Archer 1997). Thus the higher ratios of intra-specific to inter-specific competitive relationships reported in this study between *R. robusta* and *S. brevifolia* facilitate co-existence between the two species along this biome ecotone. Stronger competitive interactions within species than between species have been commonly reported in other studies in arid areas (Yeaton and Cody 1976; Yeaton et al. 1977; Fonteyn and Mahall 1981; Briones et al. 1996), since conspecific individuals are expected to compete among each other, owing to the similarities in the individual's resource requirements (Yeaton and Cody 1976; Turkington et al. 1979). Both intra- and inter-specific competitive relationships have been reported previously among species of *Stipagrostis* genus in the Namib desert (Yeaton 1990). Carrick (2003) has also reported intra-specific interactions among *R. robusta* plants in Namaqualand.

Leipoldtia pauciflora on the other hand, displayed no neighbour interactions either among the individuals or towards *S. brevifolia* plants. Unfortunately, not enough pairs of *S. brevifolia* occurred to assess their intra-specific behaviour in this particular community, but it is possible that this infrequent occurrence was a result of strong intra-specific competition among this grass species. Previous studies on *Leipoldtia constricta* (Cunliffe et al. 1990) and *L. schultzei* (Carrick 2003), species in the same genus, in the Succulent Karoo have reported evidence of intra-specific competition. Therefore what brings about lack of intra-specific interactions among *L. pauciflora* is not clear and requires further investigation. Evidences of negative interactions were also reported between these species and their neighbouring plants of different species; *L. constricta* towards an annual *Gorteria diffusa* (Cunliffe et al. 1990) and *L. schultzei* towards *R. robusta* plants, but not with the deeper rooted *Hirpicium alienatum*, an Asteraceae shrub (Carrick 2003). Carrick (2003) ascribed lack of competitive relationships between the shallow rooted *L. schultzei* and a deeper rooted *H. alienatum* to their vertical separation in the root system.

The distribution of *S. brevifolia* roots recorded in the soil profile in this study is comparable to the root distributions recorded for other grass species from other deserts. The two grass species studied in semi-arid Argentina have root systems mainly distributed in the top 10 - 40 cm of the soil profile (Pelaez et al. 1994). In the Chihuahuan desert, the perennial bunch grass

Hilaria mutica had roots through the entire excavated profile of 75 cm, and 70% of these occurred between 5 and 30 cm (Briones et al. 1996). *Ruschia robusta* in the present study has displayed differential rooting depth, with a taproot at Kougoedvlakte and lack the taproot near Goegap Nature Reserve. However, even where a taproot is present, most of the roots of *R. robusta* occurred in the first 20 cm of the soil as shown from this study, and previously at Paulshoek in Namaqualand (Carrick 2003). With a small proportion of the root mass extending beneath 20 cm soil layer, Carrick (2003) described this as unusually deep among the mesembs. The root structure of *L. pauciflora* reported in this study resembles that of *L. schultzei* described by Carrick (2003) with a very high proportion of the root mass made up of fine roots forming a dense mesh of roots in the shallow soil.

The shallow root structure for *L. pauciflora* recorded in this study confirms the perception of succulents in the Succulent Karoo as being extremely shallow rooted (Esler and Rundel 1999; Esler et al. 1999; Midgley and van der Heyden 1999; Carrick 2003). Shallow roots and succulent leaf tissue are reported as the two common morphological characteristics for the Succulent Karoo perennial shrubs in a winter rainfall Namaqualand area as adaptations to compete for water uptake and store water (Von Willert et al. 1992; Cowling, Esler and Rundel 1999). The dominance of shallow rooted succulents in the Succulent Karoo is related to high incidences of small rainfall events over much of the area (Cowling et al. 1994; Carrick 2001), providing the mesembs with the ability to take advantage of these small winter rainfall events which only penetrate the top few centimetres of the soil (Esler and Rundel 1999). After a rainfall event of less than 10 mm at the end of a long dry summer, *R. robusta*, *L. schultzei*, and *R. aggregata* were able to fill their leaves to apparent maximum turgidity within 24 hours (P.J. Carrick unpublished data). The evolution of the taproot in *R. robusta* may thus be an adaptation to access deeper soil water during seasons of insufficient winter rains at the ecotone as rainfall becomes less seasonal and less predictable relative to the main winter rainfall Succulent Karoo. One other mesemb species that displays a taproot is *Ruschia spinosa*, which is widespread in the summer rainfall Nama-Karoo biome (P.J. Grubb and P.J. Carrick, unpublished data).

Distribution of vertical root structure has been widely advocated to explain co-existence and competition between species (Walter 1971; Yeaton et al. 1977; Knoop and Walker 1985; Fowler 1986; Briones et al. 1996). The relative dominance of roots between the species is presented in a hypothetical illustration in Figure 5.6 to explain the observed competitive relationships. Lack of competitive relationships between *L. pauciflora* and *S. brevifolia* can be ascribed to a clear vertical differentiation in the root systems between the two species. *Leipoldtia pauciflora* with most of the roots in the top 10 cm is expected to utilise water in this layer,

facilitating co-existence with *S. brevifolia* which has most of the absorbing roots between 10 and 40 cm. For *S. brevifolia* and *R. robusta*, the degree of partial overlap in the vertical root distribution may explain the observed inter-specific competition between these species. The stronger competitive impact by *S. brevifolia* on *R. robusta* may be explained by the fact that *S. brevifolia* has a deeper vertical area to extract water and other soil resources, comparing to *R. robusta* whose root system is concentrated on the top 20 cm. The net competition by *S. brevifolia* which showed a greater competitive impact on *R. robusta*, is however not strong enough to cause complete competitive exclusion of *R. robusta* in these communities, and these two species co-exist over a wider area along the ecotone. The partial overlap in the vertical root distribution may account for the observed competition, but each species dominates in a different layer, in a similar manner to the two layer-hypothesis (Walter 1971) proposed for the savanna systems between the shallow-rooted grasses and the deep-rooted trees. *Ruschia robusta* with high proportion of the root mass in the first 20 cm of the soil is expected to dominantly utilise soil water in the first 50 cm of the soil, and in a way reduces the net competition from the grass.

The form of competitive relationship between grass and succulent shrub vegetation obtained in this study is unique in that, contrast to savanna competition models where grass is proposed to obtain water from the top layer and shrubs from the bottom soil layer (Knoop and Walker 1985; Kochy and Wilson 2000; Snyman 2005), the succulent shrubs are shallower rooted comparing to grass and are thus expected to utilise water from the top layer. Grasses have generally high root mass fraction compared to trees and non-succulent woody plants (Waisel, Eshel and Kafkafi 1991; Kochy and Wilson 2000; Snyman 2005), but a contrasting observation from the current study indicated that succulent shrubs have comparably greater root mass proportion as shown for *L. pauciflora* (this study), *R. robusta* and *L. schultzei* (Carrick 2003; this study) than grass.

Whereas the differences in root distribution obtained in this study are proposed as a mechanism that facilitates species coexistence at the ecotone, grasses and shrubs dominate biomes dominated by summer rainfall and winter rainfall respectively. This may suggest that a certain degree of temporal segregation in plant growth among the species is likely, as previously hypothesised (Van der Heyden 1992). Variations in rainfall patterns have been indicated to have profound effects on the response of the grass and Karoo shrubs in the eastern Karoo (Hoffman, Barr and Cowling 1990; Hoffman and Cowling 1990; Bousman and Scott 1994; O'Connor and Roux 1995). Therefore, a detailed investigation of the phenological patterns of grass and shrubs at the ecotone will yield useful information.

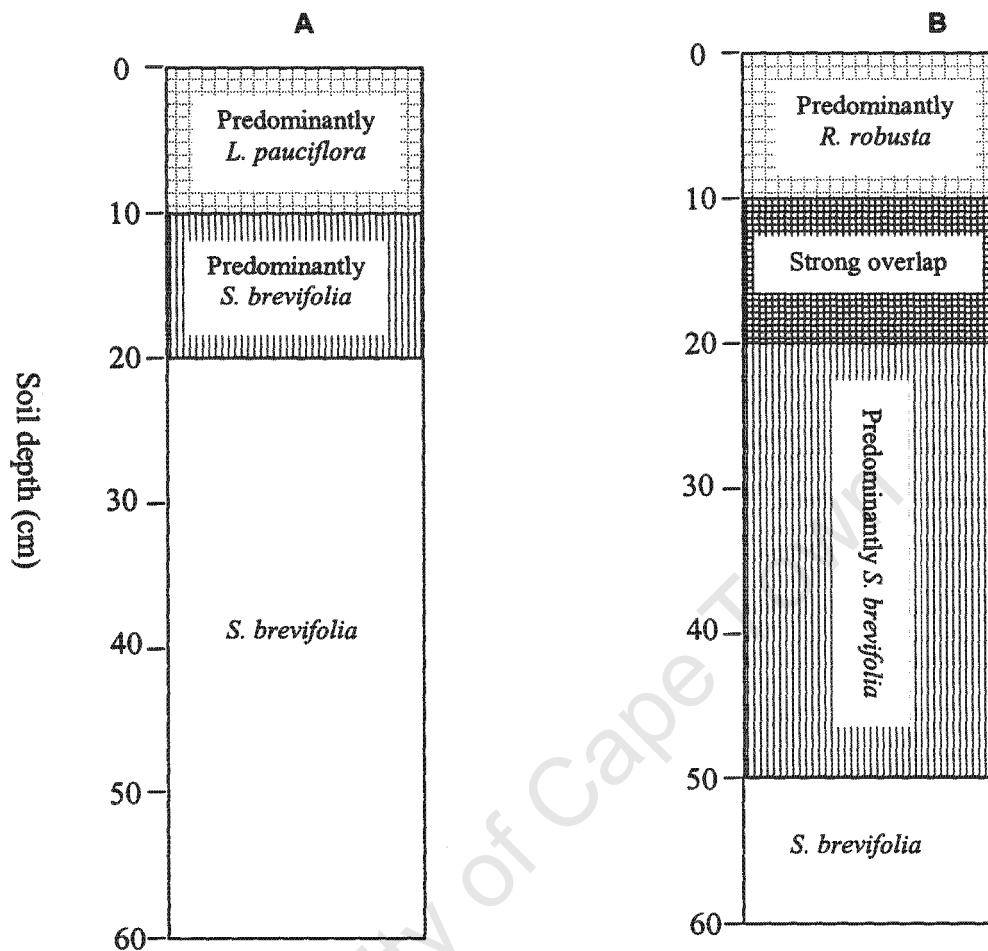


Figure 5.6. Hypothetical presentation of relative dominance of roots of *Stipagrostis brevifolia* and **A**, *Leipoldtia pauciflora* and **B**, *Ruschia robusta*. The clear vertical separation in root proportion in **A** avoids competition, whereas the partial overlap in **B** allows for competition between the species.

5.4.2 Competition and community dynamics

The asymmetric competitive relationship between *S. brevifolia* and *R. robusta* is ecologically important for the dynamic of these species, and particularly that in all the communities studied the direction of competition seemed to be consistently in favour of *S. brevifolia*. A slight disturbance at the expense of the *R. robusta* can therefore put the grass at an advantage, following Hardin's (1960) expression that even a small competitive difference will result in a rapid extermination of the species. The decreasing winter rainfall which is observed over the past 50 years (MacKellar et al. 2007) and predicted by climate change scenarios (Rutherford et al. 1999; Hannah et al. 2002) is one factor which is likely to reduce the competitive ability of *R. robusta*, as mesembs with their root system dominantly in the upper soil layer are suggested to depend on light winter rainfall events (Cowling et al. 1994; Carrick 2001). *Ruschia robusta* at the ecotone may be threatened if shallow water becomes less available and the net competition

from the grass, whose root system is proportionally more evenly distributed at other depths increases. This is in line with Esler and Rundel (1999) who have proposed that an increased summer rainfall will lead to a rapid increase in grass cover and thus an increased competitive pressure.

It is clear from this study that both intra- and inter-specific competition are important for co-existence between *R. robusta* and *S. brevifolia* in these communities. Competitive relationships (observed in *R. robusta* - *S. brevifolia* combinations) as well as lack of thereof (in *L. pauciflora* - *S. brevifolia* combination) were explained by the vertical distribution of the root systems in the soil. The root distribution between the shrubs and the grass species described in this study have indicated the possibility of two different water obtaining strategies similar but opposite to the two-layer hypothesis proposed in the savanna. However, further investigations towards understanding ecotonal species co-existence should look at plant water relations between succulent shrubs and the grass species at the study area. Competition was also established as an important factor preventing the establishment of *R. robusta* seedlings in *S. brevifolia* community and not soils (Chapter 4). These studies demonstrate that competition play a role in the distribution of species at the ecotone, both in mixed communities where grass and succulent shrubs co-exist, and in segregated communities. The results may not provide long-term investigation of vegetation dynamics, but they offer ecological insights into explaining observed or expected changes in vegetation distribution along the ecotone. However, other other unexplained or uninvestigated factors may also regulate this vegetation. The following two chapters make use of remote sensing technology to establish the current distribution of grass and shrub vegetation along the ecotone, and to detect how the vegetation might have changed over the past years.

6. The spatial distribution of grass and shrubs at the ecotone as determined from remote sensing data

Abstract: The objective of this study was to map the current spatial distribution of grasslands and shrublands at a climatic ecotone between Succulent Karoo and the Nama-Karoo biomes, using remote sensing data and techniques. ASTER (Advanced Spaceborne Thermal Emission and Reflection Radiometer) satellite data were used due to their high spatial resolution (15 – 30 m). A nonparametric decision tree classification method was applied on single ASTER bands, band combinations and enhanced data using field data, to produce four vegetation classes; grassland, shrubland, mixed vegetation and bare ground. The first three classes were best discriminated using a combination of the first band, band ratio 4:2 and the second component of a Principal Component Analysis (PCA) of the 9 bands composite. Bare ground was discriminated from all other surfaces by having high reflectance values in bands 5 to 9. The final classification maps had overall accuracies of more than 90%, and kappa coefficients above 0.90 when tested against validation datasets acquired on the ground.

6.1 Introduction

Studies focussing on spatio-temporal changes in vegetation require the derivation of thematic maps for future vegetation monitoring and for assessing past vegetation changes. This is particularly true along regions such as ecotones, which are perceived as highly sensitive to environmental changes (Shmida and Wilson 1985; Gosz 1993; Neilson 1993; Risser 1993; Hochstrasser et al. 2002). In this study, the spatial distribution of grass and shrubs at the ecotone was determined, using a combination of field data and recent satellite imagery.

In the national vegetation classification of Acocks (1953), the vegetation in the study area was classified as the False Desert grassveld of the Namaqualand Broken Veld, and the False Succulent Karoo veld type. The False desert grassveld is characterised by pure grassveld consisting of *Stipagrostis brevifolia*, *S. ciliata* and *S. obtusa* or by the dominance of this growth form, whereas the False Succulent Karoo veld type is succulent to non-succulent shrubland. Low and Rebelo (1996) later reclassified the area into Upland Succulent Karoo, and Bushmanland. In the recently completed Vegetation Mapping project of southern Africa (Mucina et al. 2006), the study area is characterised by four vegetation types, namely Bushmanland Arid grassland, the Namaqualand Blomveld, Namaqualand Klipkoppe shrublands, and the Platbakkies Succulent shrublands vegetation types as described in Chapter 2. While these works provide a broad classification of the vegetation in the area, detailed information required in monitoring grass and shrub distribution at the ecotone is missing. Large patches of grasslands occurring west of the Springbok-Kliprand road, for example were not detected in the previous mapping approaches. In this study, high spatial resolution satellite data are applied to produce high resolution vegetation maps depicting the spatial distribution of the ecotonal vegetation (grasslands and shrublands).

6.1.1 Remote sensing of vegetation

Vegetation exhibits characteristic spectral properties in the visible and near infra-red regions of the electromagnetic spectrum, allowing the distinction of different vegetation types with multispectral remote sensing sensors (e.g. Jensen 2000; Lillesand, Kiefer and Chipman 2004). Multispectral satellite data have been used for ecological applications since the early 1970 with the launch of Landsat MSS sensors (Jensen 2000; Lillesand et al. 2004). Their spatial and spectral resolution allowed vegetation investigation on the regional scale. With recent advances in spatial and spectral resolutions, the availability of remotely sensed data, and improved computation power, the utility of remote sensing for ecological applications such as vegetation assessments and monitoring has greatly improved (e.g. Wallace et al. 2000; Langley et al. 2001; Kerr and Ostrovsky 2003; Turner et al. 2003). Remote sensing technology provides the possibility to acquire data over time and from broad spatial extents, which is otherwise difficult or impossible to achieve using field-based methods.

Satellite imagery are processed into thematic vegetation maps, during a computer-assisted classification process which involves grouping the contents of an image into classes depicting the same vegetation type (Jensen 2000; Foody 2002). Supervised classification processes require a set of user defined sampling areas known as training areas (that have been spectrally characterised by ground reference data), to be collected for each class of interest to be mapped. Image pixels are then clustered on the basis of their similarity to such training areas, following a confined statistical algorithm (Jensen 2000; Foody 2002). The commonly used supervised classification algorithms such as Minimum-Distance- and Maximum-Likelihood-Classifiers, require complex calculations and demand that distinct sites used as training samples in the image should enclose a homogenous area of sufficient spatial extent, and represent the unique spectral properties of the target class (Jensen 2000). Statistically, it is also required that the histogram of such training set areas is normally distributed.

Nonparametric classification methods such as decision trees and neural networks were developed as alternatives beyond the commonly used parametric supervised classifiers, since training data often tend towards non-Gaussian distribution in spectral or temporal feature space (Hansen, Dubayah and DeFries 1996; Friedl and Brodley 1997; Shupe and Marsh 2004). These methods are being used increasingly because they make no assumptions about data distribution and independency (McIver and Friedl 2002; Brown de Colstoun et al. 2003). The use of nonparametric classification algorithms have also been motivated by the increased accuracy that these algorithms provide (Friedl and Brodley 1997; Rogan et al. 2002; Brown de Colstoun et al. 2003). A unique strength of decision tree algorithms lies in their flexibility and simplicity for

partitioning data sets as a function of the input feature space, and their ability to adapt to the noise of remotely sensed data (Friedl and Brodley 1997). Decision tree classification methods use a hierarchical framework to sequentially partition and label observation, based on empirically estimated specific values of the decision boundaries, from the training data (Friedl and Brodley 1997). Following this argumentation, a decision tree classifier was developed in this study to obtain the best accuracies in the detailed distribution map of grasslands and shrublands along the ecotone. This chapter presents the process involved in producing the map, and the accuracy of the product thereof.

6.2 Methods

6.2.1 Study area

The area covers the extent of the study area described in Chapter 2.

6.2.2 Ground vegetation sampling

For accurate remote sensing vegetation mapping, a reliable set of ground truth data is required to train and to validate the classification process. Vegetation assessments in the field were conducted along the ecotone. This included GPS (Global Positioning System; in decimal degrees with WGS 1984 geodetic datum) annotation for accurate geo-referencing of the collected data. Vegetation surveys were done using a line intercept method (Canfield 1941), which offers a rapid assessment of vegetation cover and composition and thus allows for large area to be covered. One GPS point was recorded at each end of the 50 m vegetation survey transects. A total of 49 transects in nine cadastral units were surveyed in grass communities, shrub communities and mixed grass/shrub communities. GPS points were also taken along the ecotone in grasslands, shrublands and in mixed communities without vegetation surveys, to increase the set of ground truth data. Homogeneity within stand, and a minimum stand size of approximately 30 m x 30 m which is at least twice the spatial resolution of the satellite data to be used, were considered. For spectral comparison in the satellite imagery, areas characterised by bare or open ground were also surveyed and marked with the GPS. Altogether this adds up to more than 900 points. Ground truthing was conducted during separate field visits during the period May 2004 - September 2005. Locations of the sampled sites were selected subjectively based on accessibility, and are presented in Figure 6.1.

6.2.3 Satellite datasets and pre-processing

ASTER (Advanced Spaceborne Thermal Emission and Reflection Radiometer) products were acquired as 'Level 2' surface reflectance dataset (AST07), via ASTER On-Demand Data

Gateway (<http://imsweb.aster.ersdac.or.jp>). The spatial extent of the study area was covered by three ASTER scenes, acquired on 19-10-2003 in the north-eastern part of the study area, 07-01-2004 north-west, and 18-01-2005 in the south, and were selected as the most recent available data (Figure 6.1). Each of the ASTER scenes is composed of three reflective bands (1, 2 and 3) in the visible and near infra-red (VNIR), and six reflective bands (4, 5, 6, 7, 8 and 9) in the short wave infra-red (SWIR) regions, at spatial resolutions of 15 m and 30 m respectively.

All image processing and handling, described in this study, were done using Erdas IMAGINE 8.7 software package. The steps involved in the pre-processing of the data as described in this section are illustrated in the flow chart in Figure 6.2. First the visible and near infra-red bands, and the short wave infra-red bands from each date scene were stacked into one image file (9-layer stack) to optimise the extraction and analysis of training samples as explained in the next section. 'Level 2' ASTER products are geometrically and radiometrically corrected prior to distribution, but the standard geometric accuracy provided by the distributor turned out not to be sufficient for the 2004 and the 2005 images. As a result, in the second step of image pre-processing, these images were newly geo-referenced on the basis of the national topographic data (1:50 000) obtained from the Chief Directorate of Survey and Mapping in Cape Town as reference for the geo-rectification process. The 2nd order of polynomial transformation on the base of 60 and 62 control points showed substantial geometrical improvement for the scenes of 2004 and 2005 respectively. As the area of interest concentrated on the non-mountainous vegetation, it was necessary to mask out the areas covered by mountains from the data to reduce noise and prevent shadow-effect caused by mountains in remote sensing analysis. Masking out areas representing mountains from the data was achieved by using a combination of unsupervised clustering, and thresholds in SRTM-X-band derived Digital Elevation Model (DEM) data, which was made available by the German Aerospace Centre (DLR) within the BIOTA South project.

A Principal Component Analysis (PCA) transformation of the nine reflective bands of each ASTER scene was conducted, creating the first three principal components of the transformation. The PCA is a mathematical transformation that decorrelates the data into fewer uncorrelated bands referred to as principal components, which are linear combinations of the original images (Byrne, Crapper and Mayo 1980; Armenakis et al. 2003). The first three principal components of each scene described more than 98% of the total variance in the input data, and were stacked together with the nine reflective bands, as additional three layers (bands 10 to 12). The Normalised Difference Vegetation Index (NDVI), which is one of the most commonly used vegetation indices, was also calculated. Vegetation indices provide a

quantitative assessment of green biomass and aid in the monitoring of vegetation (Jensen 2000; Jensen 2004). NDVI is based on the vegetation characteristics in the red and near infra-red bands, by taking advantage of the different absorbance and reflectance characteristics of the vegetation between those bands depending on different vegetation states and types (Jensen 2000; Jensen 2004). NDVI was calculated in this study using the formula:

$$NDVI = (band\ 3 - band\ 2) / (band\ 3 + band\ 2),$$

where band 3 represents the near infra-red band, and band 2 represents the visible red band. With these additional layers (the three principal components and the NDVI image), the resultant multilayer stacks contain a total of 13 layers each; including the nine spectral reflective bands (layers 1-9), the first three principal components (layers 10 - 12) and the NDVI image (layer 13). The spectral properties of these layers are presented in Table 6.1.

Table 6.1 The spectral properties of individual layers in the multilayer stack of each of the three scenes.

Name	Band No.	Spectral range (μm), or the band definition
Visible (Green)	1	0.520 - 0.600
Visible (Red)	2	0.630 - 0.690
Near Infra-Red	3	0.780 - 0.860
Short Wave Infra-Red	4	1.600 - 1.700
	5	2.145 - 2.185
	6	2.185 - 2.225
	7	2.235 - 2.285
	8	2.295 - 2.365
	9	2.360 - 2.430
Derivatives	10 (PC1)	PCA
	11 (PC2)	PCA
	12 (PC3)	PCA
	13 (NDVI)	(Band 3 - band 2) / (Band 3 + band 2)

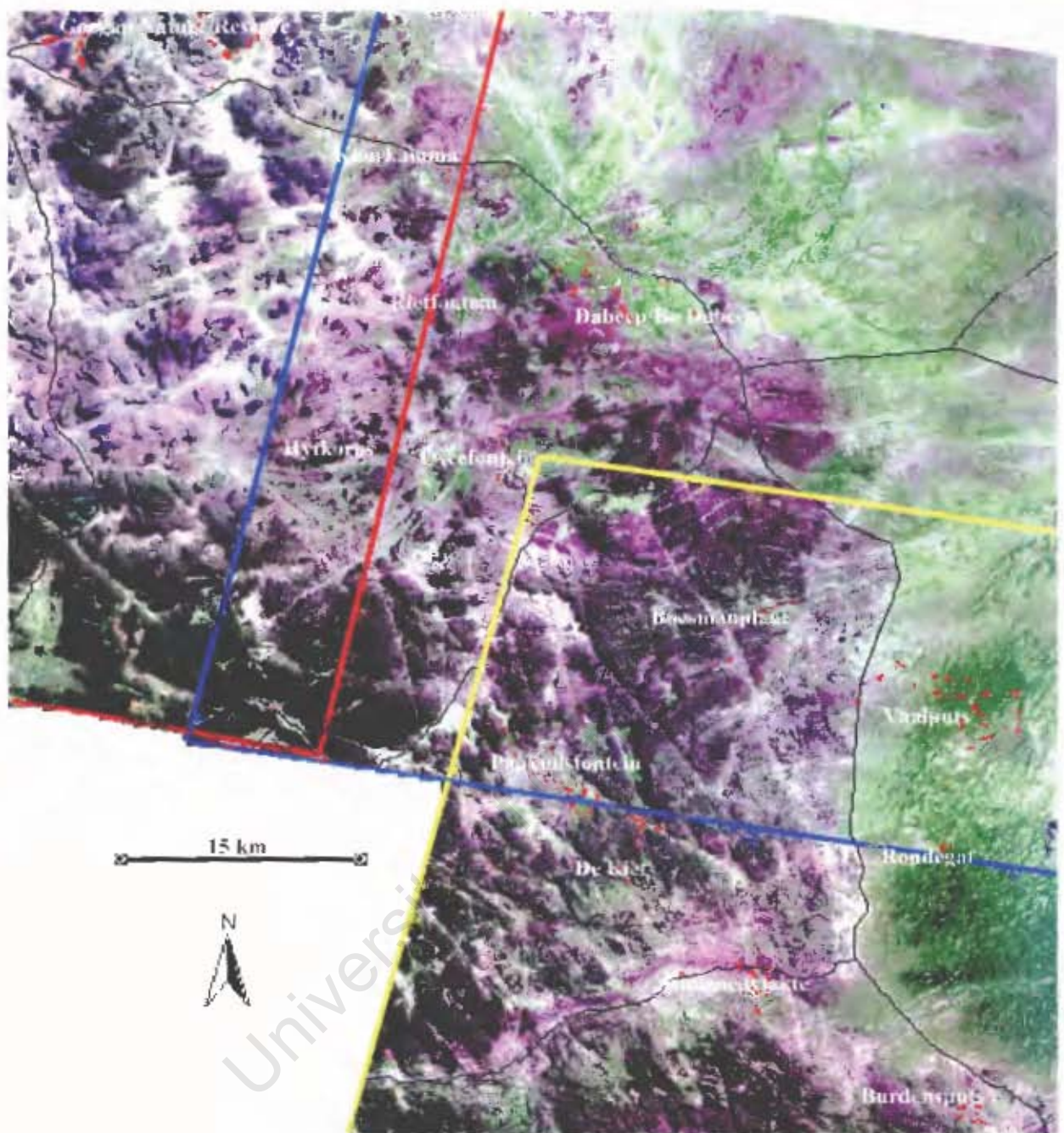


Figure 6.1 Locations of the reference field data (red dots) overlaid in the three ASTER scenes: 19-10-2003 (north west image, brown border), 07-01-2004 (north east image, blue border) and 18-01-2005 (southern image, yellow border) covering the study. Band combination in each scene is 3-4-2 (Red-Green-Blue), in which green shade indicates dry vegetation and fresh vegetation appears red. The three scenes are subset to cover the extent of the study area. The black line represents the road network.

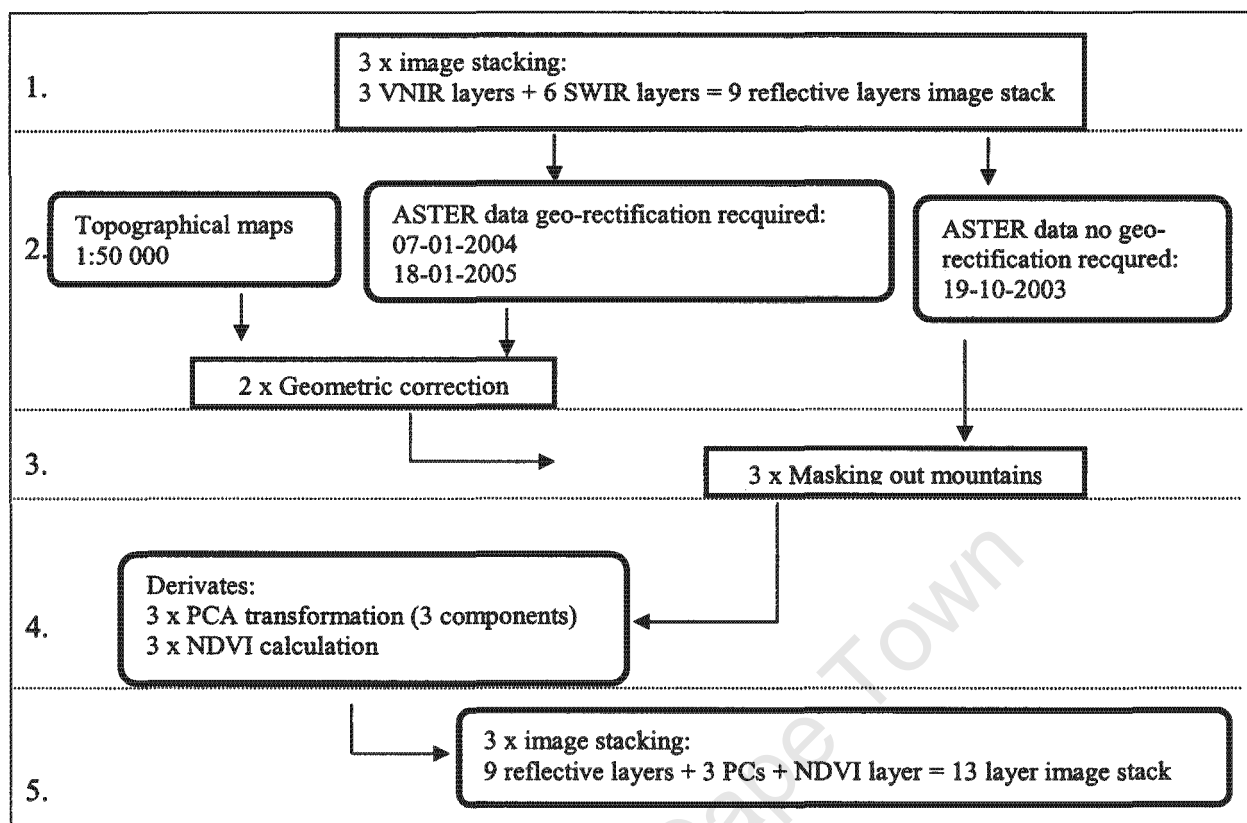


Figure 6.2 Steps involved in the pre-processing of the multispectral ASTER datasets.

6.2.4 Vegetation classification

The relative cover of grass and of shrub components in the sampled mixed communities was not always 1:1, but ranged between 30 and 70%. Mixed grass/shrub communities were thus divided into communities which were predominantly grass (grass cover between 60 and 70% of the total vegetation cover); predominantly shrubs (shrub cover between 60 and 70% of the total vegetation cover) and intermingled vegetation in which each growth form makes up between 40 and 60% of total cover. A part of the vegetation ground reference data (about 60%) were then used as input to derive multispectral training samples from the image stacks, using the region growing seed pixel method (Woodcock and Harward 1992), and the rest were reserved for accuracy assessment of the classification. The region growing seed pixel method makes use of a selected target 'seed' pixel, and analyses the spectral properties of pixels and uses these to merge the pixels into homogeneous regions. The merge tolerance, which specifies the Euclidean distance in feature space within which adjacent pixels would be allowed to merge, was set to 10. As the vegetation in the current study area is very patchy and heterogenous, the region growing seed pixel tool underestimated class variance (Erdas 2003), resulting in too small merged regions with insufficient pixels per training sample for parametric supervised classification algorithms. Often less than 5 neighbouring pixels were merged at each seed pixel selected for training

samples. A training sample contains the name of the vegetation class represented, and the spectral information (spectral signature value) derived from each layer in the multilayer image data. With a minimum of three pixels per training sample, a total of 292 training samples were obtained for the whole study area, representing spectral signatures of shrubs, grass, grass dominated, shrubs dominated, and grass/shrub intermingled vegetation as defined above.

As the extensions of the training samples showed not to be sufficient for using parametric supervised approaches such as Minimum-Distance- and Maximum-Likelihood-Classifiers, the training samples were then used to specify decision boundaries for a nonparametric decision tree classification method based on spectral signatures that grouped into separable classes of similar vegetation types. Conditional Boolean expression of the form

either [a] if [x > b] or [0] otherwise

in the spatial modeller module of Erdas IMAGINE 8.7 was used to map a vegetation class *a*, conditioned by the set threshold *b* in the observed range of *x* (a given image layer or band ratio). The threshold *b* is defined after spectral analysis of the training data, to maximise spectral dissimilarity between classes. The thresholds were determined separately for each of the three ASTER subscenes. Mean spectral signatures of non-succulent shrubs, a class less represented in the training samples, clustered inseparably together with signatures from succulent shrubs in one class. The second principal component of the PCA (which will be referred to as PC2 or the second component hereafter), together with the first reflective band, and the band ratio 4:2 have shown maximum discrimination between the classes. These three layers were used in the decision tree classification model to discriminate between the vegetation classes. Firstly, four classes were separated as presented in the decision boundary thresholds table (Table 6.2), and in Figure 6.3.

Table 6.2 Applied classification rules for the vegetation classes 1 to 4 per ASTER scene in the three layers used in the decision tree model. Values are surface reflectance for the reflective bands (B1, and B4:B2), and eigenvalues for the PC2.

Veg. class	Date of ASTER scene acquisition								
	19-10- 2003			07-01-2004			18-01-2005		
	Thresholds for bands or ratios								
	B1	B4:B2	PC2	B1	B4:B2	PC2	PC2	B1	B4:B2
1. Grassland		1.12 - 1.18	39 - 56	< 164	> 1.33	> 235	< 179	> 1.33	> 109
2. Shrubland		1.00 - 1.10	-34 - 12		< 1.19	< 210		< 1.17	< 308
3. Grass, grass-dominant and intermingled			8.5 - 39		1.26 - 1.31		180 - 192	1.23 - 1.3	
4. Shrubs, shrubs-dominant and intermingled		1.13 - 1.18		166 - 183			119 - 214		

Grass spectral signatures (class 1) separated from shrub spectral signatures (class 2), but there were overlaps from both classes with signatures from mixed vegetation, producing classes 3 and 4 (Table 6.2). These overlaps (classes 3 and 4) were refined subsequently, using subtractions and combinations of classes in the spatial modeller module, to hierarchically in two-level steps, further break down classes 3 and 4 into more specific classes as illustrated in Figure 6.3. In the first level, class 1 (grass) was subtracted from class 3 (grass, grass dominated, intermingled) to separate off the grass and produce class 5 (grass dominated and intermingled). Similarly, class 2 (grass) was subtracted from class 3 (shrubs, shrubs dominated, intermingled) to separate off the shrubs and produce class 6 (shrubs dominated and intermingled). In the second hierarchical level, class 5 (grass dominated and intermingled class) and class 6 (shrub dominated and intermingled class) were split into three separate classes; class 7 (intermingled), class 8 (grass dominated) and class 9 (shrubs dominated), using conditional expression and subtractions as follows:

either [class 7 (intermingled)] if [class 5 equals class 6] or [0] otherwise,
class 8 (grass dominated) = class 5 - class 7,
class 9 (shrubs dominated) = class 6 - class 7.

The end resulting classes are: grass (class 1), shrubs (class 2), intermingled (class 7), grass dominated (class 8) and shrubs dominated (class 9) (Figure 6.3). Finally, classes 7, 8 and 9 were merged into **class 10 (mixed vegetation)** for the accuracy assessment as explained in the next section.

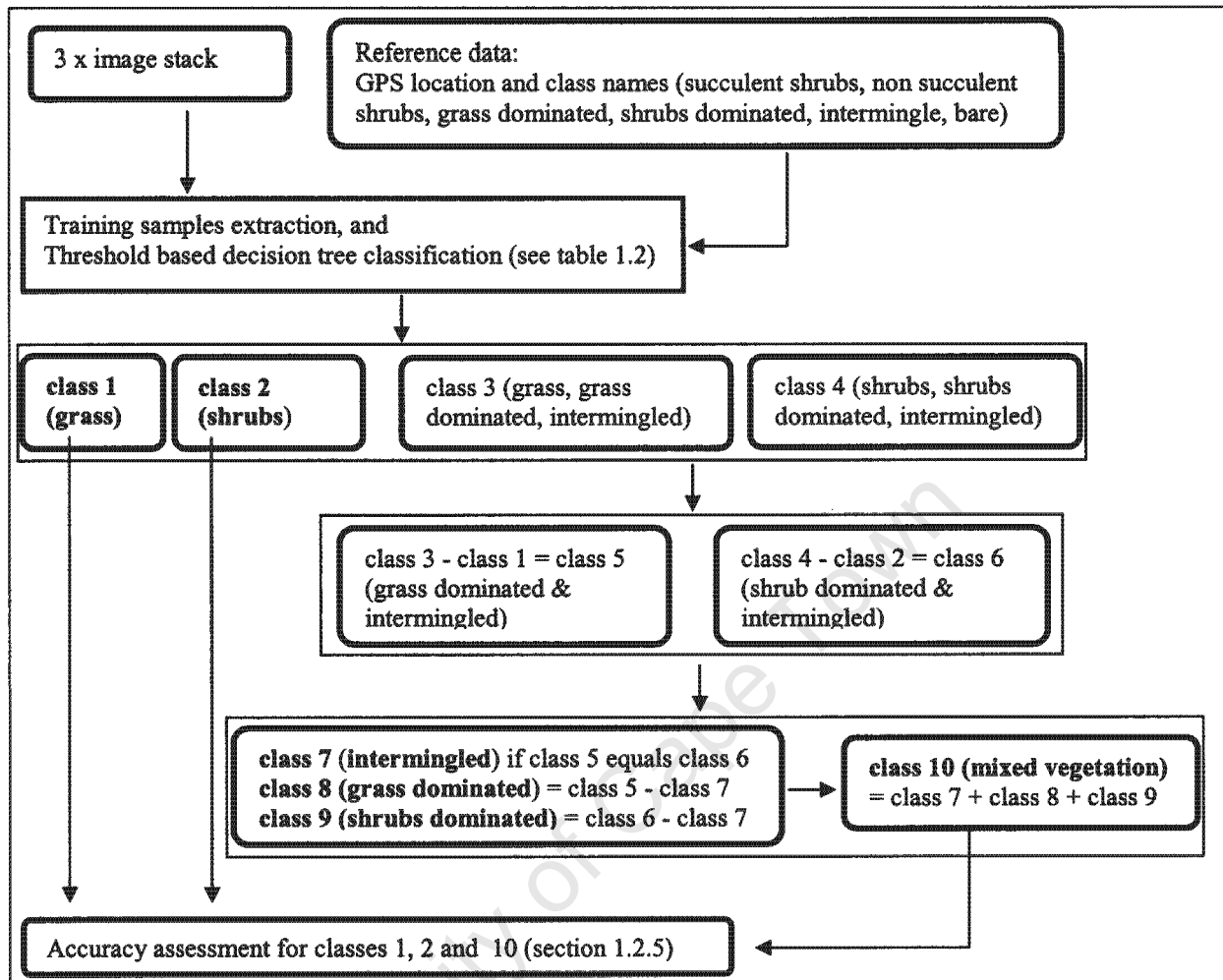


Figure 6.3 Flowchart displaying the steps for the decision tree classification used in the extraction of vegetation classes from the image stacks.

Examining the threshold values used in discriminating between classes, (Table 6.2), grass and shrubs discriminated from each other, based on higher eigenvalues of PC2 in grass areas, and lower eigenvalues of the PC2 values in shrub areas. Similarly, the ratios of the reflectance values in bands 4:2 were higher for grass areas and lower for shrubs. Mixed grass and shrubs were detected using a combination of PC2, band 1 and band ratio 4:2 (Table 6.2). The eigenvector matrices of the PCA transformations in all the three ASTER scenes revealed similar structures. The second principal components used in the classification were in all cases strongly loaded negatively in the visible, and near infra-red channels (1 - 3) and positively loaded by the short wave infra-red channels (bands 4 - 9), meaning that they contain similar spectral information. Bare ground which was not well discriminated using the above mentioned input layers was separated from the rest by having very high reflectance values in bands 5 - 9.

6.2.5 Map accuracy assessment

The three mixed classes (grass dominated, shrub dominated and the intermingled classes) were merged into one class, the grass/shrub mixed class, to obtain sufficient number of reference points because individual classes did not have sufficient reference points for accuracy test as separate classes. To verify the derived vegetation classification in terms of usefulness and limitations (Stow, O'Leary and Hope 1993), an accuracy assessment was conducted for each map. This assessment tests how likely a particular mapping unit labelled as vegetation type x will actually be that type when surveyed on the ground. As only a portion of ground truth data was used to derive training samples, ground truth data that were not used in deriving training samples were used as reference data in the accuracy assessment. In the Accuracy Assessment module of Erdas IMAGINE, the vegetation label assigned to a class in the map (mapping unit attribute) is compared with the label assigned to the same class using ground-truthing/field sampling information. This module produces an error matrix which is used for evaluating classification accuracies, reporting four measures of classification accuracy: producer's accuracy, user's accuracy, overall accuracy and Kappa (k) statistic (Congalton 1991; Stow et al. 1993; Stehman and Czaplewski 1998). Producer's accuracy gives the number of correctly classified pixels per total number of reference pixels per class, and it is an indication of how well training set pixels were classified. Accordingly, the error of omission is defined as:

$$\text{Error of omission} = 100 - \text{Producer's accuracy.}$$

User's accuracy is the number of correct classified pixels per class, and gives the probability that a classified pixel actually represents that category in reality. Accordingly the error of commission is defined as:

$$\text{Error of commission} = 100 - \text{User's Accuracy, (Lillesand et al. 2004).}$$

Overall accuracy is the percentage of correctly classified reference pixels. The Kappa (k) coefficient is a standard statistic to evaluate overall classification accuracy, providing a more conservative estimation than simple percent agreement value or overall accuracy (Rogan et al. 2002). This is because k statistic takes into account different class sizes whereas in overall accuracy, spatially small classes are given the same weight as spatially extended classes (Foody 2002). The k statistic tests if a produced map is significantly better than a map generated by randomly assigning labels to areas (Ortiz, Formaggio and Epiphonio 1997; Giri and Jenkins 2005).

6.2.6 Evaluation using Landsat TM imagery

The process of training sample extraction, and classification procedures as described above for the ASTER imagery were applied on the Landsat TM image, using the same field data. The aim was to transfer the above described mapping approach to Landsat TM data. In contrast to ASTER data which have been collected only since 2000, Landsat TM data have been acquired since 1982 with a slightly lower spatial resolution of 30 m compared to ASTER. The spatial coverage of Landsat data with about 180 x 180 km is about nine times higher than the ASTER coverage with 60 x 60 km. Landsat TM data have 6 reflective bands containing spectral information which is comparable to the spectral range of ASTER (Jensen 2000; Lillesand et al. 2004). So a direct transfer of ASTER derived mapping approaches to Landsat imagery would allow a long term retrospective vegetation change analysis. As a first step for a development of such an approach, the transferability of the vegetation mapping method developed on the ASTER data on a recent Landsat scene was tested in this study. In spite of the availability of historical data, a scene from 2004 was chosen as for that date, the gathering of field data and validation of classification results was feasible. The atmospherically and geometrically corrected Landsat 5 TM scene dated on 14 December 2004, and located on path 181 and row 76 of the Worldwide Reference System (WRS-2) was used for this work.

The second principal component of the PCA of the six reflective bands in the Landsat image, together with the first reflective band, and the band ratio 5:3 layers were used in the decision tree classification model to discriminate between the vegetation classes. As in ASTER data, there were overlaps from both classes with signatures from mixed vegetation, and this overlapping class was subtracted from grass and from shrub classes, to eliminate the overlap. Band ratio 5:3 Landsat TM (like the ratio 4:2 for ASTER data used in the classification) represents the ratio infra-red to the red energy in the electromagnetic spectrum. The infra-red region (Landsat TM band 5, ASTER band 4) is sensitive to the amount of water in plants, and it is where plant species show their greatest differentiation (Eastman 2001; Erdas 2003). Like the second principal components in ASTER transformations, PC2 of the PCA transformation in Landsat TM was negatively loaded in the visible bands 1-3, and the near infra-red (NIR) band 4, and positively loaded by the mid infra-red (MIR) bands 5 and 7. The same reference dataset used in the accuracy assessment of ASTER data classification, were used to calculate the accuracy statistics i.e. user's accuracy, producer's accuracy, overall accuracy and the Kappa statistics.

6.3 Results

The results of the ASTER and Landsat classifications are presented as vegetation maps, depicting the distribution of vegetation types (Appendix A1 and A2 respectively). The maps show the dominance of grass along the eastern part of the study area, east of the Springbok-Kliprand road, and the dominance of shrubs along the western part of the study area. There are patches of grass vegetation within the shrub dominated area, as well as patches of shrub vegetation within the grass dominated eastern part of the study area. These results coincide with the visual observations in the field.

The presented classification model classified at least 98% of the area covered by each ASTER scene, excluding mountainous areas (Table 6.3). The percentages for the vegetation types in terms of numbers of classified pixels of the ASTER images differed widely between the single classifications, depending on the geographical position of the ASTER images (Table 6.3). The overall map accuracies were greater than 90%, with the Kappa statistics greater than 0.9, both for ASTER scenes and Landsat TM scene (Table 6.4 - Table 6.7). Points in the reference data, which fall in the unclassified area of the image, are indicated in the unclassified category in the accuracy tables.

Table 6.3 The areas (as % number of pixels) covered by each class in each of the ASTER classification results.

	NW image (2003)	NE image (2004)	S image (2005)
Grassland	17.0	45.5	36.7
Shrubland	42.6	45.4	39.6
Mixed	38.4	8.0	23.0
Total classified	98.0	98.9	99.3
Unclassified	2.0	1.1	0.7

Table 6.4 Contingency matrix of the decision tree classification of ASTER scene acquired on the 19th October 2003. class 1 = grass; class 2 = shrubs; class 3 = all mixed grass/shrubs

	Unclassified	Class 1	Class 2	Class 3	Classified Total	User's Accuracy
Unclassified	6	0	1	1	8	—
Class 1	0	39	0	0	39	100%
Class 2	1	0	51	1	53	96%
Class 3	0	1	1	26	28	93%
Referenced Total	7	40	53	28	128	
Producer's Accuracy	—	98%	96%	93%		
Overall Classification Accuracy					91%	
Overall Kappa (k) Statistics					0.91	

Table 6.5 Contingency matrix of the decision tree classification of the ASTER scene acquired on the 7th January 2004. class 1 = grass; class 2 = shrubs; class 3 = all mixed grass/shrubs

	Background	Class 1	Class 2	Class 3	Classified Total	User's Accuracy
Unclassified	13	0	1	0	14	—
Class 1	0	76	0	1	77	99%
Class 2	0	0	46	1	47	98%
Class 3	0	1	1	18	20	90%
Referenced Total	13	77	48	20	158	
Producer's Accuracy		99%	96%	90%		
Overall Classification Accuracy					97%	
Overall Kappa (k) Statistics					0.95	

Table 6.6 Contingency matrix of the decision tree classification of the ASTER scene acquired on the 18th January 2005. class 1 = grass; class 2 = shrubs; class 3 = all mixed grass/shrubs

	Unclassified	Class 1	Class 2	Class 3	Classified Total	User's Accuracy
Unclassified	13	0	0	3	16	—
Class 1	0	96	4	1	101	95%
Class 2	0	0	85	1	86	99%
Class 3	0	3	1	76	80	95%
Referenced Total	13	99	90	81	283	
Producer's Accuracy	---	97%	94%	94%		
Overall Classification Accuracy					95%	
Overall Kappa (k) Statistics					0.93	

Table 6.7 Contingency matrix of the decision tree classification of Landsat TM scene acquired on the 12 December 2004. class 1 = grass; class 2 = shrubs; class 3 = all mixed grass/shrubs

	Unclassified	Class 1	Class 2	Class 3	Classified Totals	User's Accuracy
Unclassified	37	0	0	0	37	—
Class 1	2	221	2	9	234	95%
Class 2	2	0	163	10	175	93%
Class 3	2	1	2	86	91	95%
Referenced Totals	43	222	167	105	537	
Producer's Accuracy	---	99%	98%	82%		
Overall Classification Accuracy					94%	
Overall Kappa (k) Statistics					0.91	

6.4 Discussion

The overall map accuracy from this classification for the ASTER scenes and the Landsat TM scene (> 90%) exceeded the commonly recommended target accuracy of 85% proposed by Foody (2002). These results are also reflected by the Kappa coefficient of more than 0.9,

exceeding the interval of good classifications delineated by this metric. According to Ortiz et al., (1997) who proposed a benchmark system for the evaluation of thematic classifications based on the Kappa coefficient, values ranging from 0.60 to 0.80 characterise a very good classification. The Kappa coefficient in the current study explains that the observed classification is more than 90% better than a random classifier applied to the same dataset. These results are among the few with high accuracies reported in the literature, for arid and semi-arid vegetation mapping (e.g. Langley et al. 2001; Shupe and Marsh 2004). In the Jornada Experimental semi-arid grassland Range in New Mexico, classification reached an overall accuracy of 94%, and a kappa coefficient of 0.92 (Langley et al. 2001). High accuracies reported in the current study made sense given that only a few classes (grass, mixed and shrubs) needed to be delineated. A classification accuracy as high as 99.5% (overall accuracy) when considering only forest vs. nonforest classes was reported in the National Park vegetation mapping of the United States, using decision tree classifiers (Brown de Colstoun et al. 2003).

While all classes achieved high accuracies, the lowest accuracy was achieved in the grass/shrub mixed class (class 3) of the 2004 ASTER scene, which also had relatively few observations in the training sample data (Table 6.5). Friedl and Brodley (1997) have suggested that decision tree algorithms have a tendency to penalise classes with fewer observations in the training data. It was also noted that most of the reported errors in the classification were associated with confusion between grass and mixed vegetation classes, or between shrubs and mixed vegetation classes, but confusion due to errors between grass and shrub areas was minimal. Mixed vegetation communities are patchy and thus more heterogeneous, with clumps of grass and of succulent shrubs (personal observation). Due to this heterogeneity, often ground points referenced in the field as representing mixed vegetation community came out in the classification either as grass or as shrub class. This was most evident in the Landsat TM scene, where 10 referenced points for the mixed vegetation class were mistaken for shrubs in the classification, as reflected in the relatively low producer's accuracy (82%) obtained for the mixed vegetation class, and in the user's accuracy for the shrubs class. The spatial correlation of classification errors at vegetation class boundaries has been pointed out in the literature (2002). There were also errors due to a number of reference points that fall in the unclassified areas in the classified imagery, both in ASTER and in Landsat data. This occurred when a point in the reference data did not fall within any of the set threshold of the decision tree boundaries in the classification, and is assigned to the unclassified category in the accuracy tables.

The input data used in the decision tree classification in the present study were selected accordingly, to best discriminate between the target vegetation classes as indicated by high

accuracies. According to Friedl and Brodley (1997), high classification accuracy indicates the ability to distinguish between classes of interest with the input data used in a classification. At least 98% of the area covered by the input image data was classified by the set threshold boundaries, leaving only less than 2% unclassified. Unclassified category relates to areas which spectrally do not fall within any of the set boundaries representing the main classes in the input data. An example was an area of isolated *Lycium* sp. shrubs (vegetation cover < 10%) in an otherwise bare patch at Burdensputs farm, which in the classification came out as unclassified category. Isolated tussocks of heavily grazed grass characterising certain communities were also observed, which may lead to altered grass vegetation which differ spectrally to the typical grass signatures.

The use of decision tree classification methods for high spatial resolution mapping was supported in this study. Although decision tree classification methods were initially developed for coarse scale land cover applications (Foody 2002; McIver and Friedl 2002), the non-Gaussian behaviour of training data has also been encountered at finer scales, considering a common bare soil category (Brown de Colstoun et al. 2003). The challenge in attempting parametric supervised classification in the present study lay in obtaining training sites of adequate size, particularly in areas of low vegetation coverage and in transition vegetation between grass and shrub communities. This has rendered decision tree classification method as an ideal approach for this work. High accuracies acquired in this study confirm the significant potential of decision tree classification algorithms for land cover mapping problems (Friedl and Brodley 1997; Rogan et al. 2002; Brown de Colstoun et al. 2003; Im and Jensen 2005).

Agreements in classification results and the maps produced using ASTER data and Landsat TM data, provided confidence in the mapping exercise. The advantage of Landsat data is their longer temporal history, providing source of data for assessing past change in the vegetation. The spectral properties of grasses and shrubs developed in this classification will be tested on multirate Landsat data for change detection in the next chapter.

The maps produced in the present study have however shown a level of discrepancy with the vegetation data of the new vegetation map of southern Africa (Mucina et al. 2006), particularly the grasslands west of the Springbok-Kliprand road which were mainly classified as Namaqualand Blomveld or Namaqualand Klipkoppe shrubland vegetation type. With reference to both field knowledge and the maps produced in this study, the large grassland patches at Papkuilsfontein, and at Goegap Nature Reserve for example were classified as Namaqualand Blomveld, which is described as a sparse dwarf shrubs with succulent or ericoid leaves dominated shrublands (Mucina et al. 2006). Similar examples include grasslands at Burdensputs,

Boesmanplaas and De Riet farms which were classified as Namaqualand Klipkoppe shrubland vegetation type, described as an open shrubland vegetation unit dominated by shrubs of dwarf to medium stature and with ericoid or succulent leaves (Mucina et al. 2006).

The mapping and detection of the spatial distribution of grass and shrub vegetation at the ecotone was successfully conducted, using high spatial multispectral satellite data. A remote sensing based classification scheme to discriminate between grass communities and shrub communities was developed using ASTER data, and successfully applied on Landsat TM data. One of the strengths in this study is the low level of classification errors reported, rendering the produced maps with an increased confidence as important tool in supporting the vegetation assessment along the ecotone. Room for improving vegetation mapping of the area lies in mixed vegetation communities, with the focus on delineating different levels of intermingling considering relative abundance of each growth form. Mixed vegetation represents the core area of concern where change in vegetation distribution is expected to be more evident, and should be the main focus in future mapping exercises. With further investigations, there might also be potential in the use of radar imaging to improve the vegetation assessment in this area, especially if dual-polarisation or multi-polarisation is available for characterising different scatter mechanisms of grassy and shrubby vegetation and of rough surfaces of bare soil (Imhoff et al. 1997; Menges, Hill and Ahmad 2001; Menges et al. 2001). Nevertheless the results are useful as a base for multi-temporal comparisons and deliver some local improvement for existing national vegetation maps.

University of Cape Town

7. Remote sensing change-detection for vegetation change at the ecotone

Abstract: Two independent change detection methods were used in this study, first to identify areas of change in terms of vegetation cover as obtained from an existing change detection method, and secondly to determine whether there has been changes in vegetation types. In the first method, a classification independent change detection method (Vogel 2006) was applied to multitemporal Landsat TM and ETM+ acquired between 1986 and 2005 to detect spectral changes that are related to an increase or decrease in vegetation cover. This method derives change information by spectral thresholds and band ratios of bi-temporal difference images and modified selective Principal Component Analysis datasets independently from explicit vegetation maps as input information. In the second method, spectral properties of grasslands and shrublands as determined from the previous chapter were used in an image differencing change-detection technique, to derive spectral changes reflecting vegetation shifts between grasslands and shrublands.

According to the analysis, most of the detected areas of change were characterised by fluctuations in the direction of vegetation change, and only a small area showed signs of directional vegetation change. Where directional change was detected, it was related either to a decrease in general vegetation cover or to an increase in grass cover. Evidence of increasing grassiness is of significance to the ecotone, but the high fluctuations that dominated the detected change areas indicate that the vegetation has been relatively stable in terms of directional change, over the last 20 years.

7.1 Introduction

The potential link between ecotones and climate (Shmida and Wilson 1985; Delcourt and Delcourt 1988; Holland 1988; Hansen and di Castri 1992; Gosz 1993; Risser 1995; Lloyd et al. 2000; Hochstrasser et al. 2002) has led to the current investigation on the status of vegetation change at the climatic ecotone between the Bushmanland arid grassland and the Namaqualand shrublands. This is of particular importance under climate change scenarios and predictions in the region. Both climate change projections (Rutherford et al. 1999; Hannah et al. 2002), and the analysis of the past rainfall trends (MacKellar et al. 2007) point towards a decreasing winter rainfall, and an increased summer rainfall regime over the region. Accordingly, it is expected that this climate shift would have negative impacts on plant populations which characterise the winter rainfall, Succulent Karoo biome (Rutherford et al. 1999; Midgley and Thuiller 2007).

Research on vegetation change in the Karoo has reported the impacts of grazing on the vegetation (Roux and Vorster 1983; Milton 1994; Todd and Hoffman 1999; Riginos and Hoffman 2003; Archer 2004; Anderson and Hoffman 2007). Vegetation changes have also been linked to rainfall amount and seasonality (Milton et al. 1995; O'Connor and Roux 1995), but much of the research on vegetation change in the region has focused on understanding the relative influence of grazing and climate on vegetation composition (Hoffman and Cowling 1990; Bousman and Scott 1994; Dean and Macdonald 1994; O'Connor and Roux 1995; Hoffman et al. 1999). There has been little research on detecting vegetation change on a broad spatial scale in the area.

Remote sensing technology provides data through time and from broad spatial areas, and serves as a valuable tool for evaluating dynamics at broad scales (Schmidt and Karnieli 2000;

Kerr and Ostrovsky 2003; Turner et al. 2003). As a result, temporal comparisons of spectral signals of satellite imagery that reflect aboveground vegetation cover or standing biomass are used to detect changes in aboveground vegetation cover. Remotely sensed change detection techniques are based on the fact that natural or induced disturbances in land cover produce detectable variations in the spectral response of ground targets (Singh 1989; Fung 1990; Mas 1999; Almeida-Filho and Shimabukuro 2002). Thus, many different change detection techniques have been developed and used for a variety of different change detection purposes (Singh 1989; Fung 1990; Mouat et al. 1993; Mas 1999; Kaufmann and Seto 2001; Rogan et al. 2002; Cakir et al. 2006). Most of these methods have been limited to detecting abrupt land cover changes such as the common types of detectable changes associated with the clearing of natural vegetation, increased cultivation, postfire vegetation regeneration and animal overgrazing (Price et al. 1992; Cakir et al. 2006; Vogel 2006). However, environmental impacts that result in gradual change in vegetation type allow one to test the sensitivity and utility of remotely sensed data for monitoring subtle changes (Ehleringer et al. 1991; Price et al. 1992) which are much more challenging to detect than standard land cover change analysis (Frank and Menz 2003).

The application of remote sensing technology was explored in this study, to detect changes that have occurred at the ecotone between the Bushmanland arid grassland and the Namaqualand shrublands, as a baseline for vegetation change and monitoring studies in the area. Two independent remotely sensed change detection techniques were applied on the same multi-temporal satellite data, to detect spectral change information related to vegetation change in terms of vegetation cover, and vegetation shift between grassland and shrubland vegetation. In the first approach, an existing change detection method, which has been developed and tested in different vegetation types in Namibia to detect spectral changes related to change in vegetation cover, was applied (Vogel 2006). This method derives spectral change information using a combination of band-wise image differencing and a modified selective Principal Component Analysis (mod. sPCA). Image differencing involves image subtraction of time 1 and time 2, pixel by pixel to produce a further image representing the change between the two times (Singh 1989; Coppin et al. 2004; Cakir et al. 2006). This is a commonly applied technique for change detection and it is described to deliver accurate results in many applications on land cover change (e.g. Singh 1989; Fung 1990; Price et al. 1992; Coppin and Bauer 1996; Lyon et al. 1998; Mas 1999; Coppin et al. 2004; Cakir et al. 2006). Additional spectral change information for this method is also derived from mod. sPCA (Vogel 2006). Selective Principal Component Analysis differs from the classical Principal Component Analysis in that the same algorithm is not applied to a multi-layer stack of all the bands when calculating sPCA, but selectively on single band

pairs of corresponding spectral ranges, i.e. on band 1 (old dataset) and band 1 (new dataset) and so on. The resulting first principal component reflects spectral similarities between the bands for the two dates, whereas spectral differences are displayed within the second component and thus can be used for the detection of spectral change between the datasets (Chavez and Kwarteng 1989; Chavez and Mackinnon 1994). Vogel (2006) modified the sPCA results for the second component with fuzzy logic rules as suggested by Weiers et al. (1999) and Weiers et al. (2001). This leads to a conversion of the values in a way that the resulting data range from 0 to 1 indicates a probability of change for the respective pixels in the analysed image pair, i.e. values near 1 indicate a high change probability, values near 0 a low probability.

The spectral classification of the resultant difference image and sPCA image between the two dates into change classes is conducted in a decision tree, using characteristic spectral change signatures that reflect different classes of vegetation change in the difference image bands 5 and 7 and in the ratio of modified sPCA bands 5:7. The definition of the thresholds was developed by an iterative test series using field data from a Savanna vegetation type and they were demonstrated to work in different types of vegetation with high accuracy levels (Vogel et al. in prep). Therefore in this study, a different but also semi-arid ecosystem, provides an opportunity to test this semi-automatic change detection method.

In addition to the method described above to detect land cover changes in the area, the challenge specific to the objectives of this thesis was to determine how the spatial distribution of grass and shrub vegetation at the ecotone has changed over time. Therefore, the spectral properties of grasslands and shrublands as determined from the previous chapter were used in an image differencing approach to detect spectral changes related to shift in vegetation types in grasslands and shrublands. This method is based on the logic that when different vegetation types can be spectrally distinguished, then the spectral properties used in a classification scheme to map such vegetation can be applied to multi-date datasets to monitor the direction of change.

7.2 Methods

The method section is subdivided into three subsections. First, the source and the type of satellite data used, and the associated criteria of consideration in selecting remotely sensed data for change detection analysis are described. Secondly, a detailed description of pre-processing performed on the data is presented. In the final subsection, a detailed description of the methodology and techniques used to derive spectral change over time, and the classification of these changes into appropriate vegetation change classes is presented.

7.2.1 Data acquisition

Landsat Thematic Mapper (TM) and Enhanced Thematic Mapper (ETM) data used in this study were obtained from the United States Geological Survey (USGS) through the website (<http://landsat7.usgs.gov/index.php>), as well as from the CSIR Satellite Application Center in Pretoria (www.sac.co.za), under the umbrella of the BIOTA project. The study area was covered by the scenes located on path 181 and row 76 of the Worldwide Reference System (WRS-2) (NASA 1999) and were delivered registered to a Universal Transverse Mercator (UTM) projection, zone 34 S, using a WGS 84 datum. In terms of processing level these data were acquired as radiometrically and geometrically corrected “level-1G” datasets (Jensen 2000).

Numerous system and environmental parameters should be considered in the selection of available datasets to be used for change detection analysis, in order to prevent false change detection (Mouat et al. 1993). The use of images acquired by the same sensor acquisition system is emphasised so as to minimise the influence of the system factors due to differences in spatial, spectral and radiometric resolutions which can occur when using mixed datasets (Singh 1989; Cakir et al. 2006). The work in this study was thus based on the long term available Landsat TM and ETM data, as these provide largely comparable spectral and spatial properties, e.g. with a spatial resolution of 30 m x 30 m each. A detailed description of the spectral and spatial properties of Landsat TM and ETM+⁴ is given in Table 7.1. The first Thematic Mapper (TM) sensor on board Landsat 4 satellite was launched in 1982, with a spatial resolution of 30 x 30 m, and 7 spectral bands. The Enhanced Thematic Mapper (ETM+) sensor on board the Landsat 7 satellite was introduced to continue the TM data series and enhancing it by adding a 15 x 15 m ground resolution panchromatic band as well as to improve the geometrical resolution of the thermal infra-red from 120 m to 60 m. Furthermore ETM+ possesses an in-flight sensor calibration system, which provides constant sensor properties even over long sensor operational periods. As the ETM+ sensor evolved from the TM sensor series, their almost complementary design makes them ideal for change detection studies.

⁴ ETM+ is the complete name of the sensor, where “+” denotes the additional panchromatic band. ETM is often used to refer to the multi-spectral bands of the ETM+ sensor, without the panchromatic band, as often used in land cover investigations.

Table 7.1 Specifications for the TM (Landsat 4 and 5) and ETM+ (Landsat 7) sensors. Source: <http://www.eurimage.com/products/landsat.html>, modified following Jensen (2000).

	TM and ETM+						ETM+	
Band	1	2	3	4	5	6	7	8
μm	0.45-0.52	0.52-0.60	0.63-0.69	0.76-0.90	1.55-1.75	10.42-12.50	2.08-2.35	0.52-0.90
Pixel size (m)	30	30	30	30	30	120 (ETM+: 60)	30	15
Spectral range	Blue	Visible: Green	Red	Near Infra-Red	Mid Infra-Red	Thermal Infra-Red	Mid Infra-Red	Panchromatic

The appropriate selection of imagery acquisition dates is as crucial to change detection as is the choice of the sensors and change detection algorithms (Singh 1989; Coppin et al. 2004; Cakir et al. 2006). A challenge in land cover change studies, particularly in arid and semi-arid environments is to distinguish change in land cover from variability within land cover types (Bradley and Mustard 2005). Vegetation in these environments is highly dependent upon precipitation, and thus there is a high probability of detecting seasonal vegetation responses, or inter-annual variability rather than directional change (Lambin 1996; Bradley and Mustard 2005). Ideally, anniversary or near anniversary dates are selected to minimise the influence of exogenous factors such as sun angle or environmental distortions caused by atmospheric conditions, soil moisture and vegetation phenological cycles (Singh 1989; Lambin 1996; Coppin et al. 2004; Cakir et al. 2006).

Due to high rainfall variability, and variations in local precipitation in the area investigated in the present study, selecting image pairs based on anniversary dates alone does not account for the effect of rainfall variability, (Lambin 1996; Coppin and Bauer 1996; Coppin et al. 2004). Rainfall patterns between the years were thus compared in terms of total annual rainfall as well as at least three months of comparable rainfall patterns prior to image acquisition. However, the ability to control all of the distortions presents a challenging problem especially if image selections are limited (Cakir et al. 2006). In the current study, spatial variations in local rainfall patterns at different sites presented an additional challenge.

Broad-scale time frame comparison of the Landsat images was considered to take into account changes that are slow and take a long time such as change in vegetation type. Fine-scale comparison (image pairs in adjacent years, or at 6 months intervals) was also considered in the detection of spectral changes related to vegetation cover. This was done to account for the seasonal variations which are generally not considered when analysing broad-scale temporal series (Lambin 1996). Considering the selection criteria described above, and the data

availability, Landsat image pairs listed in Table 7.2 were considered for bi-temporal change detection analysis. A series of pairs allows areas of change showing the same direction of change between all pairs to be distinguished from areas that fluctuate in the direction of change between the years. Images acquired in May (early winter), as well as from the summer months (November, December, February) also provide a variety of seasons to be evaluated. Rainfall patterns at the ecotone are described as non-seasonal and can occur any time of the year (Chapter 2).

Table 7.2 Acquisition dates of the Landsat TM and ETM data pairs used in the change detection analysis.

Long term comparisons	Time lag (years)
15 Dec 1986 - 19 Dec 2002	16
15 Dec 1986 - 17Nov 2005	19
24 Nov 1990 - 19 Dec 2002	12
24 Nov 1990 - 17Nov 2005	15
16 May 1990 - 03 May 2000	10
16 May 1990 - 30 May 2001	11
16 May 1990 - 09 May 2005	15
17 Feb 1993 - 04 Feb 2004	11
Short term comparisons	
16 May 1990 - 24 Nov 1990	0.5
03 May 2000 - 30 May 2001	1
04 Feb 2004 - 17 Nov 2005	1.8
09 May 2005 - 17 Nov 2005	0.5

7.2.2 Data pre-processing

Geometric and atmospheric calibration form an important part of pre-processing in the analysis of multi-temporal remotely sensed images for change detection (Mouat et al. 1993; Chavez and Mackinnon 1994). Geometric registration ensures that multi-date images from the same path and row are registered to each other within one-half a pixel, in order to prevent changes due to mis-registration on the final change map (Singh 1989). For this reason, image-to-image control points were used to geometrically co-register all the selected scenes to the Landsat ETM+ image of 2003-08-22 (as master image). This scene has been geo-corrected at the beginning of the BIOTA project on ground-control-points obtained from the 1: 50 000 South African national topographic maps. The panchromatic ETM band of the 2003 image was used as the master image due to its spatial resolution of 15 x 15 m that allows the selection of ground correction points with higher accuracy than the multi-spectral composite with 30 m resolution. Geometric correction of each

image involved at least 50 ground control points, and an average RMS (Root Mean Square) error of less than 0.5 pixel. Images were resampled using a nearest neighbour algorithm with a second order of polynomial transformation, to preserve integrity (Almeida-Filho and Shimabukuro 2002). All geometrically corrected data were visually checked for apparent distortions against the reference used for absolute registration of the master image in the first place, and against the images used for relative registration.

The second pre-processing step involved an atmospheric correction of the dataset, which is undertaken to provide radiometric comparability of the data, and ensures that detected spectral changes are not the result of differences in atmospheric conditions between the two dates of imagery (Singh 1989). Atmospheric correction was conducted using the calibration parameters provided in the dataset, considering sun azimuth, sun zenith and BRDF (Bidirectional Reflectance Distribution Function) effects, and the influence of standard dry desert atmospheric conditions, using the ATCOR-3 atmospheric correction tool developed by Richter (see Richter 1996 and <http://www.op.dlr.de/atcor>). The corrected images were then subset to clip out the area of interest from each scene, and were ready for bi-temporal comparison to detect spectral changes in the study area over time. The steps involved in the pre-processing described above are illustrated in Figure 6.2.

It was established from the previous chapter, that the second component of a Principal Component Analysis (PCA), the first reflective band, and the band ratio 5:3 of the tested Landsat TM scene of December 2004 contained the information of interest, which were used to discriminate between grassland and shrubland vegetation. Since these layers contain the spectral information of interest for a temporal comparison of different vegetation types, a PCA was computed in the current study for all single datasets given in Table 7.2, to derive a second principal component layer needed as input in the change detection analysis described in the following section. Accordingly, image data that are used as input to the change detection procedure should contain the spectral information of interest (Chavez and Mackinnon 1994). Since PCA is scene dependent, a careful comparison between the individual PC images derived and their eigenstructures (eigenvalues and eigenvectors) is essential before any other change detection techniques such as image differencing can be applied (Fung and Ledrew 1987). Image differencing with Principal Components (PCs) assumes that the PCs represent similar spectral information, and if such techniques are applied using components of different information content, considerable error would be involved (Fung and Ledrew 1987). In the present study, analysis of the derived eigenstructures for single date data showed that the second Principal Components had similar information content in that they were all negatively loaded in the visible

bands 1-3, and the near infra-red (NIR) band 4, and positively loaded in the mid infra-red (MIR) bands 5 and 7 of Landsat TM or ETM scenes (refer to Chapter 6 for the spectral interpretations of different bands). Therefore applying image differencing to these Principal Components for change detection was reasonable for this dataset.

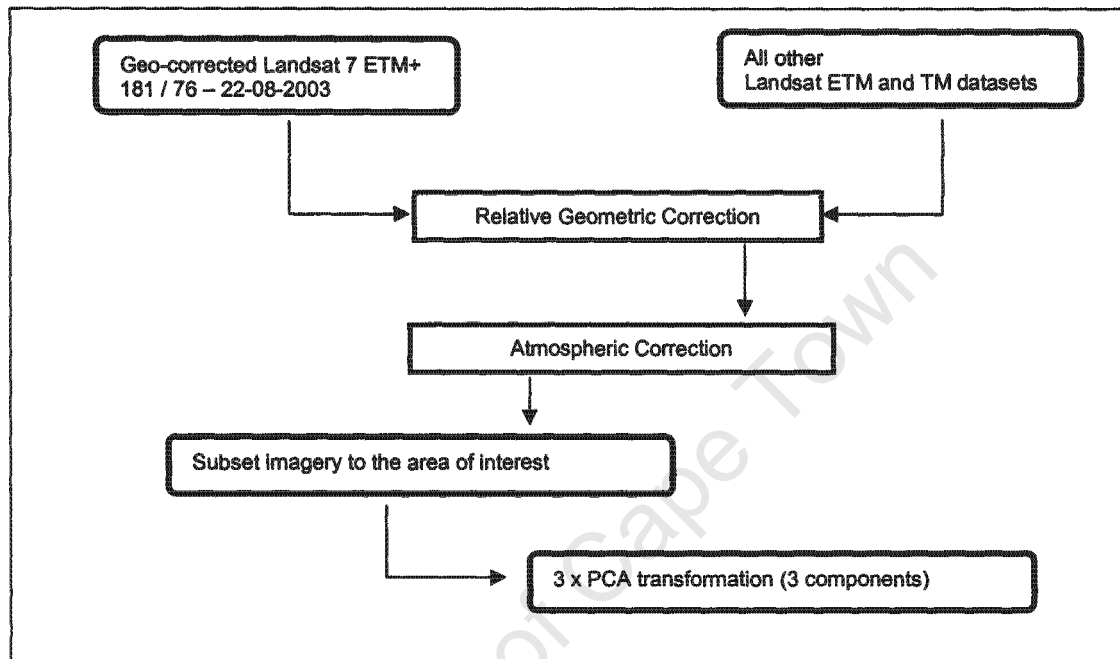


Figure 7.1 Steps involved in the pre-processing of the multi-spectral Landsat datasets.

7.2.3 Spectral change detection

To detect spectral changes that reflect vegetation change in terms of increase or decrease in vegetation cover, a bi-temporal comparison of the pre-processed data was conducted, following a change detection method that was developed by Vogel (2006) and outlined in the introduction section of this chapter. Using the differencing image and the second principal component of the mod. sPCA as inputs in a rule-based classification, four change classes were derived:

- a) increase in vegetation cover, or vegetation become denser,
- b) revegetation of previously bare or open area,
- c) decrease in vegetation or vegetation become less dense, and
- d) conversion to bare or open areas.

The second change detection approach was aimed at targeting specific spectral changes that represent changes from one vegetation type to another between grasslands and shrublands. The method is based on the spectral enhancement of grass and shrub vegetation in selected bands and band ratios as determined from the previous chapter. The input image layers (PC2, Band 1 and Band ratio 5:3), containing distinguishing spectral information for grass and shrub

vegetation (see Chapter 6) were tested individually and in combinations in an image differencing change detection technique. The second principal components of the PCA were selected preferably as input layers over the other two layers (Band 1 and Band ratio 5:3), which produced change images that were noisy and less interpretable. As in the band-wise image differencing technique described in the first method, image differencing of the second Principal Component of one date from another created a new image representing spectral difference in PC values. In an image differencing technique, areas of change are detected at the lower end and higher end tails of the difference-image pixel distribution histogram (Cakir et al. 2006). The critical part of using an image differencing technique is in selecting the appropriate threshold (cut off) values in the lower and upper tails of the distribution representing change pixel values in the difference image, that could be set to separate changes of interest (Cakir et al. 2006). Since there were no reference data for areas of known change to assist in deriving thresholds for the classification of change image into change classes, an unsupervised classification was applied on the change images, and only the end changes (classes with a highest change intensity) both in the low end and the high end of the difference distribution were considered, and the remaining classes were labelled as no change. Using only the end change classes provides a conservative approach to minimise the commission error in the interpretation of change classes given the lack of validation data, and the change maps produced mainly indicate the centre of areas that are subjected to change rather than delineating the exact boundaries of the change areas (Serneels, Said and Lambin 2001). This, however, means that mid-range values that tend to carry more subtle information about the nature of change are compromised (Cakir et al. 2006). The target output number of classes of the unsupervised classification was set to ten, at which homogeneity within classes was optimised at less than ten standard deviations.

It was established from the previous chapter that shrubs occupied the lower end of the second principal component space, whereas grass occupied the high end of the space with some overlap (see also Figure 7.2). Thus, considering the illustration in Figure 7.2, a change class with the largest decrease in PC2 reflects a change from a grass spectral signature to a shrub spectral signature, and a class with the largest increase in PC2 reflects a change from a shrub spectral signature to a grass spectral signature. These classes are thus labelled 'change to shrubs' and 'change to grass' respectively. Short time frame comparisons between images were not used for this approach, as the method is aimed at modifications that are believed to be subtle and take a long time. As there were no historical ground truth data, a direct estimation of the classification errors was not possible. However, since the method is dependent on the spectral information used in the classification of grass and shrub vegetation, the resulting accuracy is expected to be

dependent on the accuracy of the classification scheme on which it is based. The work was facilitated through the use of the current vegetation maps which are derived within this work (Chapter 6).

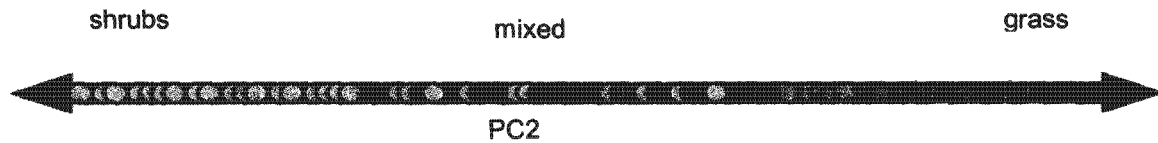


Figure 7.2 Graphical representation of the spectral distribution of grass and of shrubs along the 2nd axis (PC2) of the PCA of the 6 reflective bands of Landsat datasets.

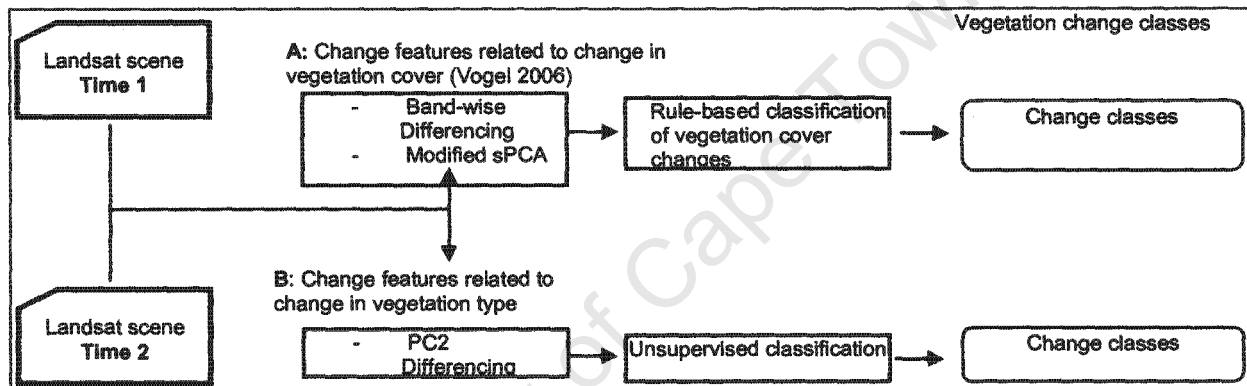


Figure 7.3 The steps involved in detecting spectral change areas related to **A** change in vegetation cover, and **B** change in vegetation composition.

7.3 Results

7.3.1 Overall changes

The individual change maps between different years are presented in Figure 7.4 and Figure 7.5 as a time sequence between the summer month's comparisons and the winter month's comparisons. In the top rows (images *a - d*) in both figures, the results from Vogel's approach are given for the subset of the study area, and in the bottom rows (images *e - h*) the respective results for the classification-based approach are illustrated. Viewing these change maps as a time sequence, no directional change is visible, and very often changes detected over a certain time period seem to be reversed in the following change images as summarised in Table 7.3 for the changes in vegetation cover (the top rows). The detected changes in vegetation cover between December 1986 and December 2002 were predominantly those related to vegetation decrease and conversion to bare or open areas, but between December 1986 and November 2005, the detected areas of change were dominated by signs of increase in vegetation cover particularly in the northern part of the image (Figure 7.4 *a* and *b*; Table 7.3). Again, the change images between

November 1990 and December 2002, and between November 1990 and November 2005 were dominated by signs of decrease in vegetation cover, and conversion to bare or open areas (Figure 7.4 *c* and *d*; Table 7.3). Contrasting change information was also observed between May 1990 and May 2000 showing a combination of signs of vegetation recovery, vegetation decrease and conversion to bare areas, and between May 1990 and May 2001 with mostly signs of vegetation recovery (Figure 7.5 *a* and *b*; Table 7.3). On the shorter time frame comparisons, spatial variations in the direction of the detected spectral change were also observed between individual image pairs (Table 7.3). The total annual rainfall, and that of three months prior to image acquisition date are also given in the summary table (Table 7.3) and will be used to discuss the observed pattern in the detected changes related to vegetation cover in the discussion section.

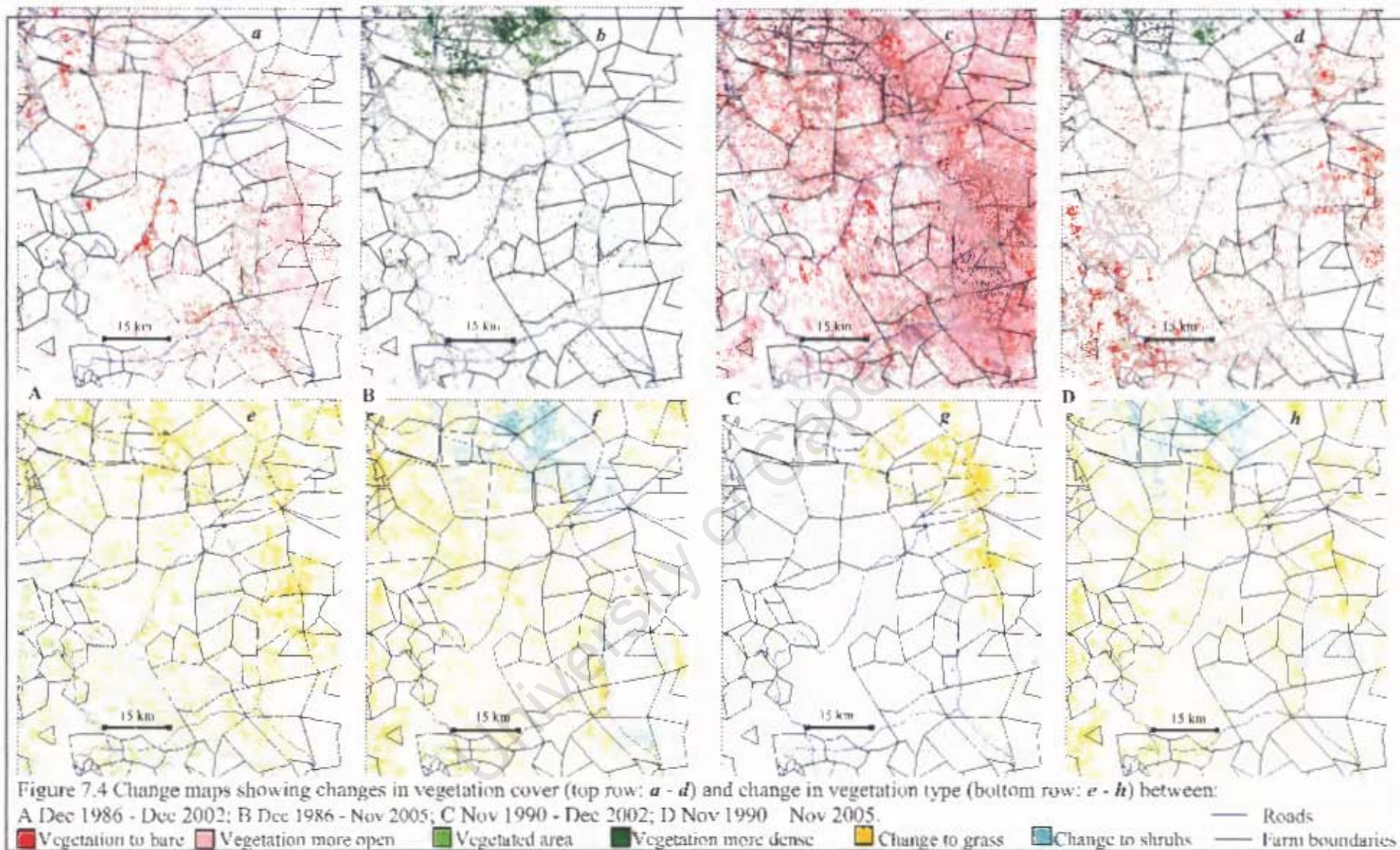
Another observation is that the changes detected from images acquired in the summer months (November, December and February) were dominated by a decrease in vegetation cover or conversion to bare or open areas, except between December 1986 and November 2005, comparing to the results from the May images (Figure 7.4 and Figure 7.5).

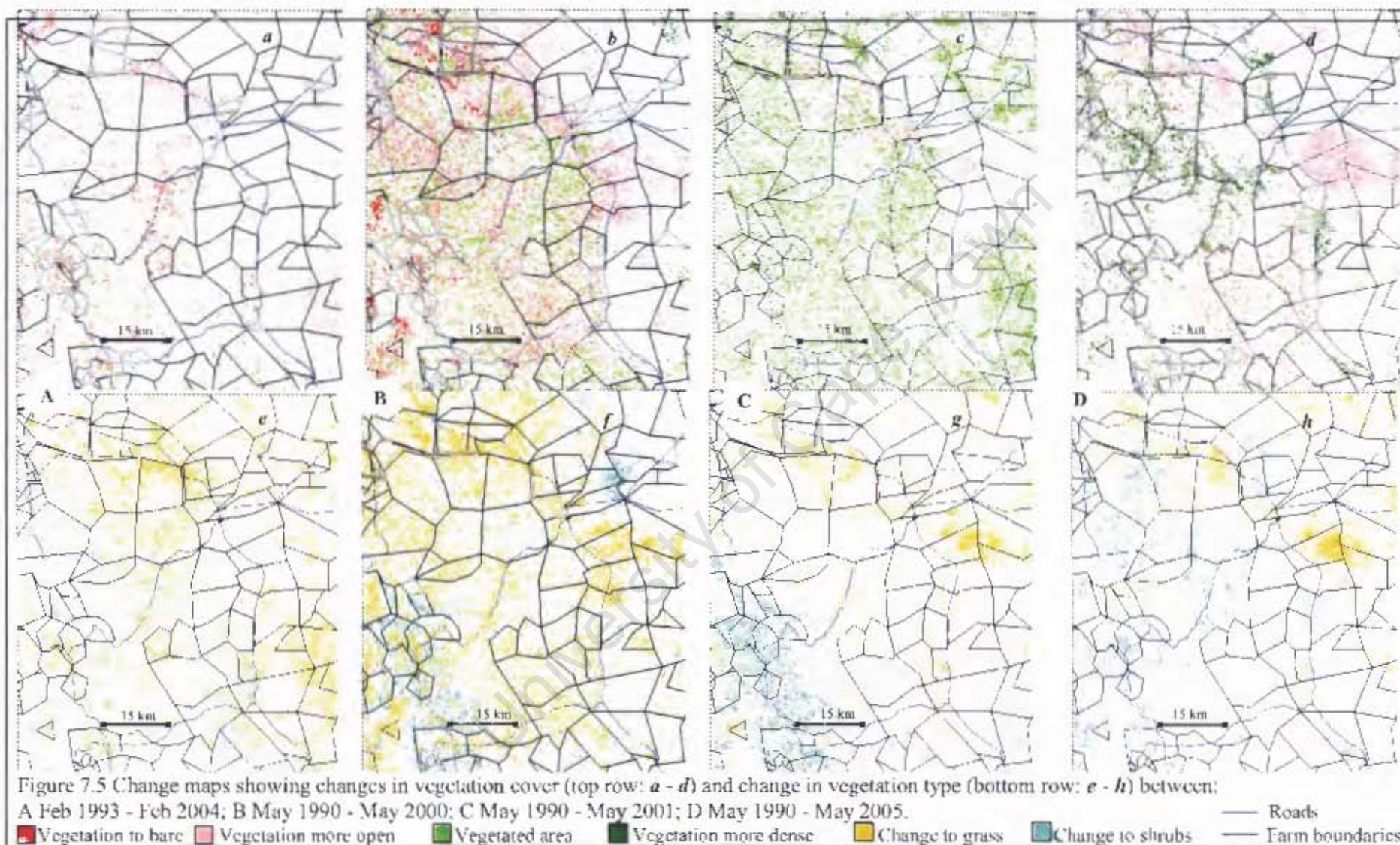
Similar to the spectral change results that are related to change in vegetation cover, the spectral changes related to shift between grass and shrub vegetation classes (the bottom rows (images *e* - *h* in both figures) also revealed variations in the type of change that occurred.

When comparing the change results from both approaches (top and bottom rows in both figures), there is a tendency for areas that have shows a decrease in vegetation cover towards an increase in grass vegetation. Those areas which showed an increase in vegetation cover, on the other hand appear to be more closely related to an increase in shrub vegetation. This pattern is also evident in the subsets presented in the next section (Figure 7.6 to Figure 7.9).

Table 7.3 A summary of the dominant direction of spectral changes related to vegetation cover. Total annual rainfall and total rainfall in the three months prior to image acquisition (in brackets) are given, as averages between the three sites: De Riet, Vaalputs and Goegap Nature Reserve.

Image date pair	Average annual rainfall and rainfall 3 months prior to image acquisition (in brackets) (mm) from De Riet, Vaalputs and Goegap gauges.		Area (%) of the total detected changes represented by each change class				Dominant change classes
	Date 1	Date 2	Conversion to bare	Vegetation recovery	Vegetation increase	Vegetation decrease	
Long term							
Dec 1986 - Dec 2002	117 (15)	114 (15)	43	< 1	1	55	Vegetation decrease, conversion to bare
Dec 1986 - Nov 2005	117 (15)	171 (60)	20	5	74	1	Vegetation increase
Nov 1990 - Dec 2002	122 (6)	114 (15)	20	< 1	< 1	80	Vegetation decrease
May 1990 – May 2000	122 (53)	136 (40)	24	33	3	40	Vegetation decrease, vegetation recovery
May 1990 – May 2001	122 (53)	162 (64)	1	84	3	11	Vegetation recovery
May 1990 – May 2005	122 (53)	171 (42)	13	12	30	44	Vegetation decrease, vegetation increase
Nov 1990 - Nov 2005	122 (6)	171 (60)	88	< 1	11	1	Conversion to bare
Feb 1993 - Feb 2004	153 (8)	100 (25)	44	14	< 1	42	Conversion to bare, vegetation decrease
Short term							
May 1990 – Nov 1990	122 (53)	122 (6)	6	4	1	89	Vegetation decrease
May 2000 – May 2001	136 (40)	162 (64)	2	64	3	30	Vegetation recovery
Feb 2004 - Nov 2005	100 (25)	171 (60)	80	< 1	19	1	Conversion to bare, vegetation increase
May 2005 – Nov 2005	171 (42)	171 (60)	38	54	< 1	8	Vegetation recovery, conversion to bare





7.3.2 Selected change subsets

Whereas there were variations in the spatial and temporal distribution of vegetation change in both approaches, there were certain localised areas of change that seem to show consistent directional changes over the monitoring period (Figure 7.6 - Figure 7.9). The subsets presented in this section are derived from change maps representing the November/December months and the May month, to highlight local changes that occurred at selected areas along the ecotone.

South eastern part of Goegap Nature Reserve

In Figure 7.6, the changes detected between December 1986 and December 2002 (image *a*) were predominantly related to a conversion to bare areas, whereas between December 1986 and November 2005 (image *b*), the changes were predominantly related to an increase in vegetation cover. The red rings both in the top and the bottom images highlight certain areas where the changes are characterised by fluctuations between the images. The orange rings in the bottom images *e* - *h* of Figure 7.6 highlight an area which shows consistent sign of increase in grass vegetation.

Dabeep farm area

In the top images *a* - *d* in Figure 7.7, the areas around Dabeep farm were predominantly marked by changes related to vegetation decrease, except between December 1986 and November 2005 (compare the orange rings vs a red one). Similarly in the bottom images *e* - *h*, spectral changes related to an increase in grass dominates the changes, except between December 1986 and November 2005 where areas of increase in shrub cover were also prominent particularly to the north east of the subset area. The orange rings highlight an area with directional change between the images. Also notable from this figure is the possible influence of land use on the detected changes, particularly the images C and D both in the top row and in the bottom row, which are characterised by a visible contrast in the detected change information on either side of the road.

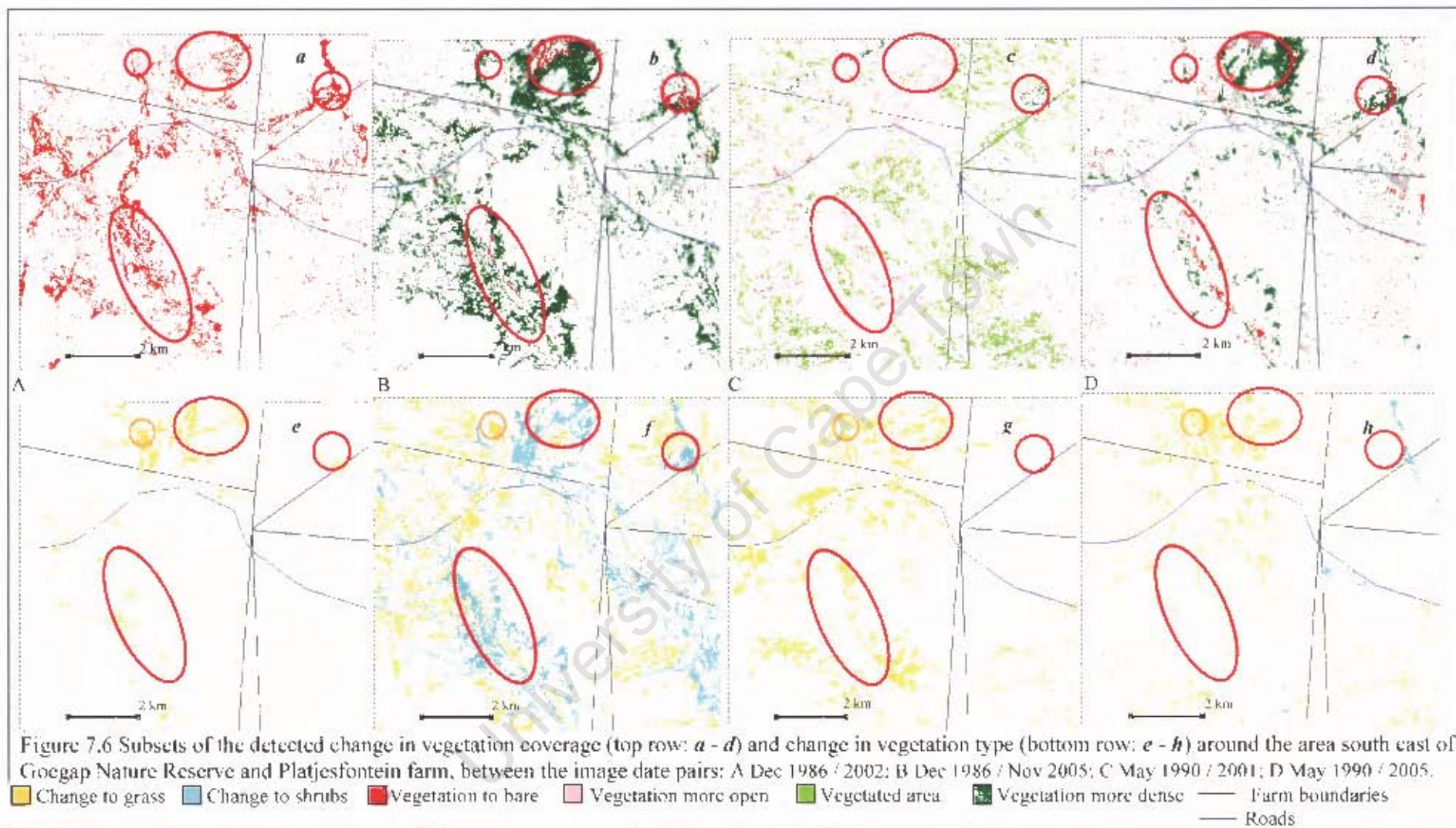
Gamoep area

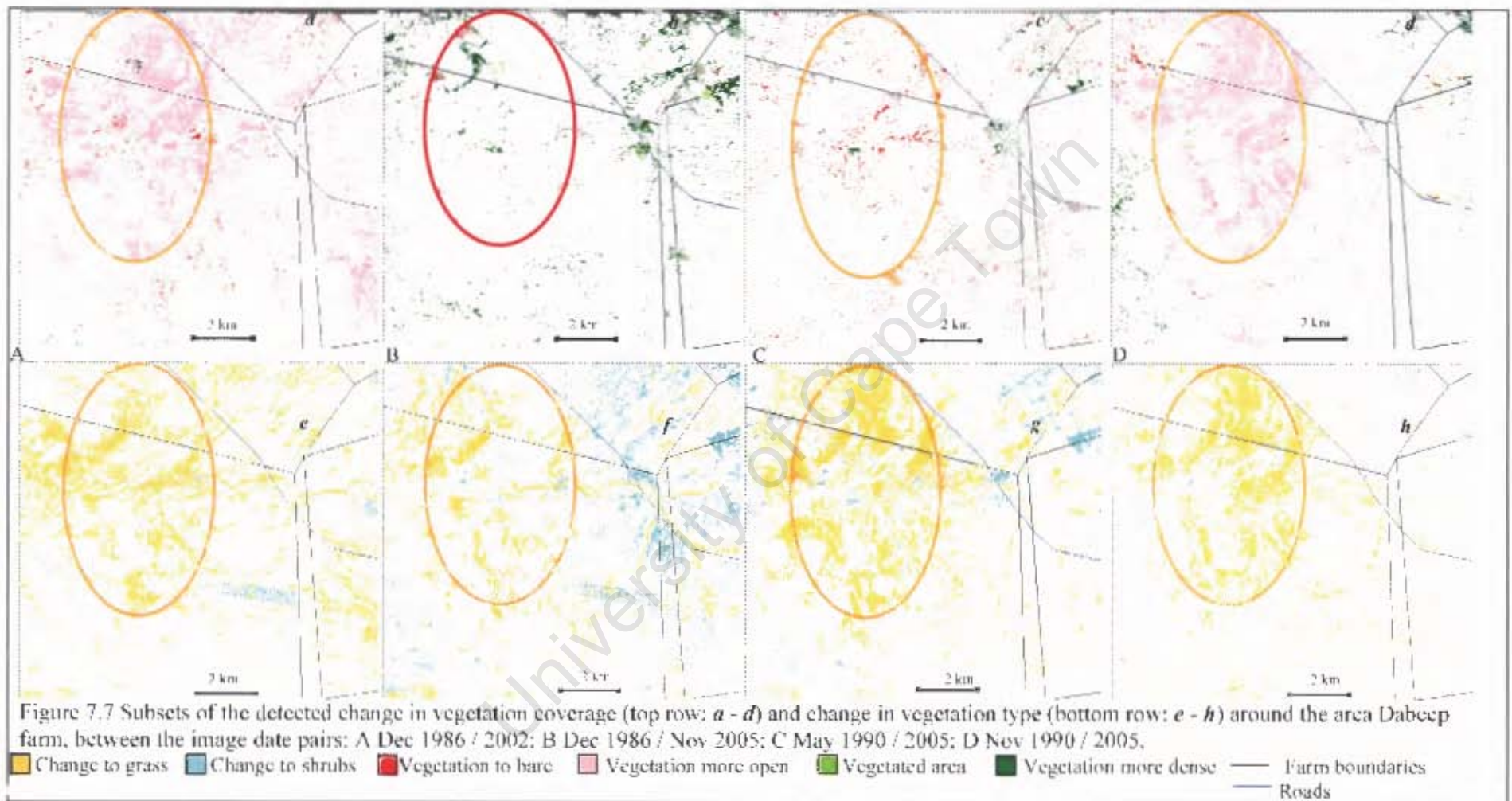
Around the Gamoep area, highlighted areas show consistent spectral changes related to a reduction in vegetation cover and an increase in grass vegetation (Figure 7.8). This area also shows evidence of the potential influence of land use on the detected changes, as indicated by regular change structures, evident in the third and the fourth pairs (C and D) in both spectral change types.

Vaalputs area

The change subsets at Vaalputs represent the typical fluctuations in the direction of change both in terms of spectral changes related to vegetation cover and shift in vegetation types (Figure 7.9). Detected areas of change show fluctuation between vegetation decrease, vegetation increase or no detected change and between increase in grass and increase in shrubs or no change.

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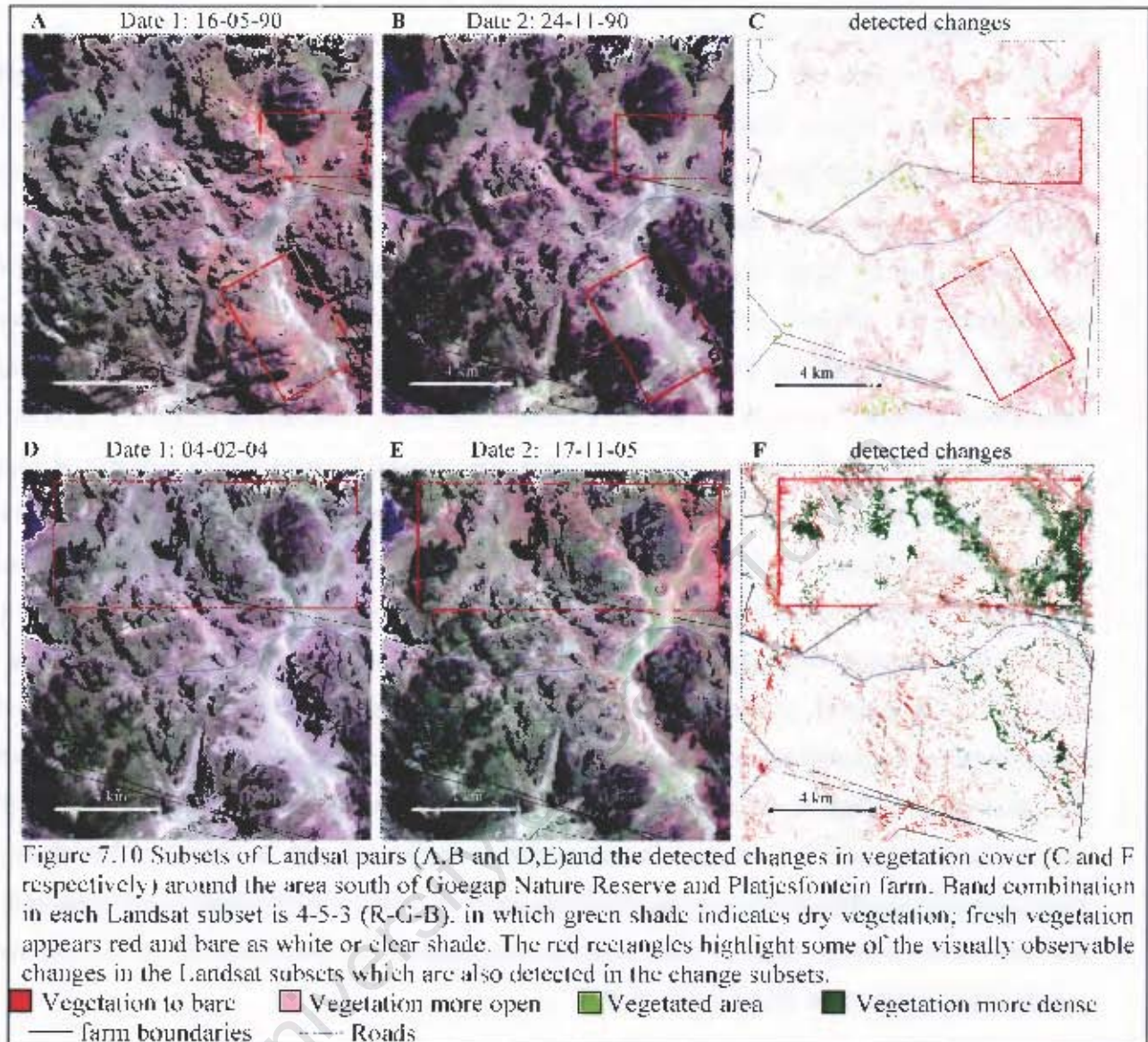




7.4 Discussion

7.4.1 Evaluation of the methods

The method developed by Vogel 2006 for land cover change detection in savannas was applied in an arid Karoo system without modification of spectral thresholds. Source of errors to the detected change results may come from the standard problems encountered in change detection studies such as registration error, atmospheric discrepancy and other environmental differences between the dates of image acquisition in the image pairs compared. A visual comparison of the results with the original images indicates that the method has mainly correctly detected vegetation modification as illustrated in the examples below using a six month time frame comparison (Figure 7.10 A to C), and a 21 month time frame comparison (Figure 7.10 D to F), for a subset of the north eastern part of the study area around Goegap Nature Reserve. A visual comparison of the images A and B indicates a typical general decrease in vegetation cover, where relatively dense vegetation (red shaded areas) has turned to sparse vegetation (greenish grey shade; band combination in both images is R-G-B 4-5-3). The spectral change result (C) reflects these changes correctly. In the second comparison (images D to F) the reverse is true, as indicated by a general increase in vegetation cover, which was correctly detected from the change detection classification. In contrast, in Figure 7.10 F, the patterns of elongated red shaped change areas are likely to be a result of mis-registration along the mountain slopes, rather than real spectral changes. Even though images were co-registered with an RMS of less than 0.5 pixel, lower geometric accuracy in mountainous areas may lead to difficulties in the correction of parallax errors in single images. This local mis-registration has introduced errors as commonly reported in the literature (Rogan et al. 2002).



The challenge in the classification-dependent approach that aimed at detecting spectral changes related to shift between grass and shrub vegetation was the lack of thresholds to train the classification of change images into appropriate change classes. Thus, how much a change in spectral information should translate into a change class from one type of vegetation to another was done arbitrarily via unsupervised classification. While the conservative nature of the classified changes prevented errors or overestimation of change area, only the most intense changes were considered as change classes, and more subtle changes were therefore compromised. The resulting change maps thus provide only the direction of spectral changes but do not explicitly provide information on the level of vegetation shift. Areas of continuous

increase in grass vegetation between the change images were confirmed to be grass in the current status, using the vegetation map of the area.

Some of the results suggest a decrease in vegetation cover with a change to grass, whereas changes related to an increase in vegetation cover were primarily associated with a change to shrub vegetation. This may be influenced by the different morphologies of the two growth forms. Grasses (which along the ecotone are dominated by *Stipagrostis brevifolia*) grow upright and have small spiky leaves. In addition, these grasslands are characterised as having a large portion of accumulated dry biomass. This results in less green surface material being exposed to the sensor, as compared to the shrubs. These differences in spectral properties need to be investigated in more detail in the field.

7.4.2 Detected changes

One of the main findings from the analysis was that changes detected over much of the area seemed to be temporal and not directional as indicated by a fluctuation in the direction of change between the years. During the period of observation, most of the detected areas of change were characterised by an alteration in vegetation cover, as well as by a shift in vegetation type which varied between the years. Only small areas showed changes that appeared to be directional. This suggests that, over the period of 20 years, the vegetation has been relatively stable in terms of directional change, but was marked by vegetation fluctuations both in the grass dominated eastern part and the shrub dominated western part of the study area. This pattern is commonly reported in land cover change studies, especially in arid and semi-arid environments where vegetation cover is highly dependent upon precipitation (Stephenson 1990; Chavez and Mackinnon 1994; Bradley and Mustard 2005). Up to 76% of the detected change in the annual dynamics of the vegetation index data could be explained by rainfall variability in a study across sub-Saharan Africa (Vanacker et al. 2005). Similarly, Vogel (in prep) has found that only 0.002% of the study area was affected by irreversible vegetation loss over the period of 20 years in central Namibia whereas most of the detected changes were regarded as reversible or short term. Vogel (in prep) related temporal changes to phenological modifications due to the high variability in precipitation in the region, and to short term land use effects at the time when the respective satellite images were taken.

Most of the fluctuations in the direction of detected change in the current study resulted from the high inter-annual rainfall variability in the area. Inter-annual differences in rainfall patterns is indicated to have detectable impacts on the spatial patterns of land cover change (Lambin 1996). The coefficient of variation of rainfall at three sites along the study area: De

Riet, Vaalputs and Goegap for which rainfall data is available for the period of the observation is 41%, 53% and 33% respectively. However, as the rainfall pattern also varies at different sites along the ecotone, comparing rainfall did not always reflect the observed changes (compare Table 7.3). A general increase in rainfall between December 1986 and November 2005 might have caused the observed dominant increase in vegetation cover, but compare with a dominant conversion to bare ground detected between November 1990 and November 2005 when the rainfall was much higher for the second date in Figure 7.4 D. Such discrepancy may be related to atmospheric correction and calibration, which is sometimes not inadequate as missing temporal shifts of calibration constants for the Landsat 5 data. The influence of seasonal and inter-annual climatic variability on land cover change is commonly addressed by analysing the relationship between vegetation indices and climatic patterns (Serneels et al. 2001; Weiss, Marsh and Pfirman 2001; Weiss et al. 2004; Vanacker et al. 2005). Using the normalised difference vegetation index (NDVI) derived from NOAA-AVHRR data for Namaqualand area (which covers the current study area), Fox et al., (2005) have reported a significant correlation with precipitation variables.

In addition to the influence of rainfall variability on the detected change results, local changes in land use management may also explain certain areas of the detected changes, particularly when the changes have a defined structure or regular shapes (see Figure 7.7, Figure 7.8 and Figure 7.9). A sharp boundary between change areas is characteristic of land use impacts, and has been used to distinguish patches of change areas that are due to anthropogenic impacts, from the natural vegetation conversion which is a more gradual process, and creates fuzzy boundaries between the change classes (Hutchinson et al. 2000; Serneels et al. 2001; Vogel et al. in prep). Different land use management practices may also be the reason for fence-line contrasts observed in the imagery, which appear to have a long history in the region. Land is used primarily for livestock grazing, but past differences in grazing management may have created camps (paddocks) of different grazing impacts which could create distinct patches in the detected change areas. The impacts of heavy grazing in Namaqualand is characterised by the reduction in vegetation cover (Todd and Hoffman 1999), or shift in vegetation composition such as the loss of perennial shrub cover at the expense of the annual component as well as the replacement of palatable species by unpalatable species (Todd and Hoffman 1999; Riginos and Hoffman 2003; Anderson and Hoffman 2007). The part of Goegap Nature Reserve considered for this study, and at Vaalputs study site, livestock grazing has been replaced with indigenous antelope species since 1990 and 1983 respectively. The effect of this change in land use on the detected change results was not visible at the scale of observation. The accurate interpretation of the influence of

land use on some of the observed changes, however, requires detailed data on both the historic and the current land use patterns at different sites along the ecotone.

It was interesting to note that the areas that showed consistency in the direction of change between the images were primarily those which reflected a decrease in vegetation as well as those which reflected a shift from shrub to grass vegetation, as highlighted in section 7.3.2 (Figure 7.6 - Figure 7.9). Whereas the original state of the vegetation could not be confirmed, these patches of change were compared to the distribution map of grass and shrubs produced in the previous chapter and were confirmed as grass in the present state. Evidence of increasing grass cover is of importance for vegetation change scenarios at the ecotone which suggest that succulent species in Namaqualand are at risk from a future decrease in winter rainfall in the area (Midgley and Thuiller 2007). This may be due to the shallow rooted nature of most succulent species especially the mesembs, and an increased competition from grass (Chapter 5). This supports Esler and Rundel (1999) who have also proposed that increased summer rainfall will lead to a rapid increase in grass cover and thus an increased competitive pressure. However, as indicated for by fluctuation in the direction of the detected changes in the current study, changes occur predominantly as a result of rainfall-driven fluctuations in phenology rather than the actual vegetation change.

This investigation has indicated the ability for utilising remote sensing for detecting and monitoring vegetation changes along the ecotone, and has set the baseline for future vegetation monitoring in the area. A remote sensing method based on differencing the second principal components of the multivariate Principal Component Analyses was specifically developed in this study to detect spectral changes related to shift in grassland and shrubland vegetation types. With appropriate digital manipulations of earlier Landsat data (MSS), potential exists to combine these data with more recent data to increase the time scale of observations. Considering longer period of observation (e.g. by using older (MSS) imagery) will also enable one to note when some of the changes visible as fence-line contrasts have occurred. Despite advances in the detection of land cover change however, the interpretation of the observed land cover change in terms of climatic, ecological and anthropogenic processes is still a complex issue (Vanacker et al. 2005). Thus, it still remains to be investigated whether the observed changes in grass and in shrubs have responded primarily to climate or land use, as this is the critical information needed to predict how the vegetation might respond to the anticipated climate changes.

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8. Synthesis and conclusions

This thesis has contributed towards an ecological understanding of the functioning and the dynamics of ecotone vegetation. Specifically, the research was aimed at:

1) investigating the factors influencing the distribution of species at the ecotone, and 2) investigating the current and past distribution patterns of the vegetation that characterises the ecotone. The nature of the questions addressed called for investigations that run across different spatial and temporal scales, and this was one of the main strengths of the project. A combination of detailed community level investigations (both observational and experimental), and a variety of remotely sensed data and techniques were thus applied to capture processes and patterns at different scales.

The objective of this chapter is to give a synthesis of the main findings that emerged from various investigations, and discuss the implications with a special focus on the dynamics of the ecotone vegetation. First, I review the investigations concerning the distribution patterns of grass and shrubs in relation to soils and competition between plants, and discuss the implications of the results. In the second section, I consider the spatio-temporal dimension of the distribution of grasses and shrubs, as addressed by remote sensing technology, and point out the strengths and limitations of this approach. Finally, I summarise the main conclusions of this research and point towards new lines of research that will contribute to an improved understanding of the ecotone vegetation.

8.1 The influence of soils and competition on vegetation distribution

Three studies were undertaken to investigate the abiotic and biotic factors influencing the distribution of the vegetation. The first study was a description of soil properties along community gradients of grasslands and succulent shrublands (Chapter 3). Multivariate ordinations and statistical techniques have revealed that variation in the underlying physical and chemical soil properties explained between 8% - 14% of the variation in the vegetation, and thus contribute little to the observed vegetation patterns. Soil depth and sand content showed significant but weak correlations with the two most abundant species, *Stipagrostis brevifolia* (positive correlations) and *Ruschia robusta* (negative correlations). Furthermore, *S. brevifolia* was negatively, but weakly correlated with organic matter and phosphorus, whereas *R. robusta* was weakly positively correlated with silt content. Soil depth, soil texture and organic content are among the commonly reported soil variables that affect local vegetation patterns by influencing local soil moisture and nutrient regimes in arid environments where water is limiting (Bliss and Cox 1964; Bowers and Lowe 1986; Abd El-Ghani 1998, 2000; Abd El-Ghani and Amer 2003;

Buxbaum and Vanderbilt 2007). The distribution of C₄ grass in Namaqualand has been described as being associated with distinct soil patches, particularly deeper and sandy soils, a notion probably derived from studies that looked at the widely distributed *Stipagrostis ciliata* (Lloyd 1989; Carrick 2001). In the area near Vanrhynsdorp in the main winter rainfall part of Namaqualand, Carrick (2001) found that the soils of the *S. ciliata* community were very similar in texture to those dominated by the mesembs, and proposed that the infertile nature of the grass-dominated soils prevents the mesembs from colonising grass-dominated communities. The wider distribution of *S. ciliata*, which is also reported on deeper aeolian sand in Bushmanland (Lloyd 1989) suggests that it is able to grow over a range of environments. Significant, though very weak, positive correlations between *S. brevifolia* cover and soil depth and sand content reported in this thesis indicate the affinity of grass towards deeper, sandy soils, in contrast with *R. robusta* which was negatively correlated with both soil variables. The positive (albeit weak) correlation of *R. robusta* with organic matter supports Carrick's (2001) suggestion that mesembs are favoured by more fertile soils. However, at less than 14% coefficients of determination between vegetation and soil variables, and lack of trends in the ordination, the current investigation indicates that soil preferences are less important in patterning these communities at the ecotone, and provides clarity on earlier made generalisations about the distribution of grass in the area. The abiotic environment such as soil moisture has also been indicated as unimportant in influencing the distribution of the Succulent Karoo species at the ecotone between the Succulent Karoo and the Fynbos biomes, and it is suggested that plant interactions are important in the absence of fire (Lechmere-Oertel and Cowling 2001; Agenbag et al. 2004).

The second and third studies in this thesis have addressed the role of competition in influencing the distribution of grass and shrub communities at the ecotone. In the second study (Chapter 4), a reciprocal seedling transplant experiment was undertaken to investigate the effects of soils and root competition in *S. brevifolia* and *R. robusta* communities on the establishment of seedlings of each species. The results suggested that the influence of soil is insignificant particularly on *R. robusta* seedlings. The importance of inter-specific competition was demonstrated in the same experiment, where the influence of root competition from the established grass vegetation prevented the establishment of *R. robusta* seedlings. Conclusions about the influence of soil or competition on the establishment of *S. brevifolia* could not be determined experimentally, as all the seedlings died early on in the experiment irrespective of treatment or soil type. Regarding the establishment of *R. robusta* which could be monitored for the duration of the experiment, observations support conclusions from Chapter 3, that soil preferences are less important, and demonstrate the importance of plant competition in

influencing the distribution of grass and succulent shrub communities at the ecotone. On the other hand, the co-existence of shrubs and grasses in the ecotone may be a consequence of a trade-off between colonization (shrubs' strategy) and competition (grasses' strategy). Whereas this suggests that competitive exclusion may be driving these communities, it does not explain the presence of communities where both grasses and shrubs co-dominate as frequently observed at the ecotone.

In the third study (Chapter 5), I considered communities in which both grass and shrubs co-occur. The objective was to investigate the competitive interactions between adult individuals of the dominant species, using a nearest neighbour analysis technique. The rooting depths of the most abundant species were also compared to explain the observed competitive relationships. Results from the nearest neighbour analysis provided evidence of competitive interactions between the grass *S. brevifolia* and a shrub *R. robusta* (the two most abundant species in communities where the two growth forms co-occur), at all four sites investigated along the ecotone. Furthermore, *S. brevifolia* had stronger competitive effects on *R. robusta* than vice versa, in these communities. There was no evidence of competitive interactions between *S. brevifolia* and *Leipoldtia pauciflora*, another leaf succulent shrub that co-occurred with *S. brevifolia* at one site.

The above studies have indicated the role of competition in the ecotonal communities. Competition in arid and semi-arid environments was initially considered relatively unimportant in structuring arid environments (e.g. Grime 1974, 1977), but more recently, below-ground competition in particular has received considerable attention (e.g. Tilman 1990; Goldberg and Novoplansky 1997). Cowling and Hilton-Taylor (1999), and Esler et al., (1999) held a similar view that competition between plants had a negligible influence on the vegetation of the Succulent Karoo biome, despite evidence to the contrary (Cunliffe et al. 1990; Yeaton and Esler 1990; Esler and Cowling 1993; Yeaton et al. 1993). The results from my investigations support recent views on the importance of competition in structuring Succulent Karoo communities (e.g. Lechmere-Oertel and Cowling 2001; Carrick 2003). The segregated communities of grass and shrubs could be explained by competitive exclusion as indicated in the case of *R. robusta* where the establishment of the seedlings in *S. brevifolia* community was competitively limited. In mixed grass/shrub communities in the study area, competitive relationships may not be strong enough to cause competitive exclusion of the less competitive species, facilitating co-existence between the species. Accordingly, species may co-exist or they may segregate into different communities, which is largely moderated by competition coefficients among them (Hardin 1960; Brown 1971; Rosenzweig 1981; Scholes and Archer 1997; Gordon 2000). With the occurrence

of disjunct communities which seem to be competitively moderated however, one does not exclude alternative explanations such as the poor seed dispersal distances for Namaqualand's perennial species, and particularly the mesembs (Esler 1999) which may also contribute to the vegetation patterns.

The distribution of the root systems between the grass and the succulent shrubs were compared to explain the observed patterns in competition relationships. A clear separation in the rooting depth between *S. brevifolia* and *Leipoldtia pauciflora*, explains the observed lack of competitive interactions between the two species. The root system of *L. pauciflora* is predominantly fine, and concentrated in the top 10 cm of the soil, whereas most of the root mass of *S. brevifolia* occurred between 10 and 40 cm, and the two species can co-exist through the vertical separation in the root systems. Co-dominance between *L. pauciflora* and *S. brevifolia*, however, is confined to the north eastern part of the study area, where the rainfall is typical of the winter rainfall Succulent Karoo biome to which the mesembs are well adapted (Cowling et al. 1994; Carrick 2001). Most of the root system of *R. robusta* shrubs is confined to the top 20 cm, but unlike many other mesembs (Esler et al. 1999; Carrick 2001), *R. robusta* displays differential rooting depth, with a taproot at Kougoedvlakte and no taproot near Goegap Nature Reserve as reported in this thesis. Shallow roots and succulent leaf tissues are suggested as the two morphological adaptations to take advantage of the high incidence of small winter rainfall events in Namaqualand which usually only penetrate the top few centimeters of the soil (Von Willert et al. 1992; Cowling et al. 1994; Milton et al. 1997; Esler and Rundel 1999; Carrick 2001). With a small proportion of *R. robusta* root mass extending beneath 20 cm soil layer in a study at Paulshoek in Namaqualand, Carrick (2003) described this as unusually deep among the mesembs. The morphological plasticity of *R. robusta* roots is probably an evolutionary adaptation that contributed to the wider distribution at the ecotone, where rainfall is less seasonal and less predictable relative to the main Succulent Karoo biome. Evidence of inter-specific competitive interaction between the grass *S. brevifolia* and *R. robusta* is explained by the degree of partial overlap in the vertical root distribution between these species. Stronger competitive impacts from *S. brevifolia* on *R. robusta* may be explained by the fact that in relation to *R. robusta*, which has only about 6% of the root mass beneath 20 cm deep, the root system of *S. brevifolia* has a deeper vertical area where most of the root mass occurs. As each species dominates in a different layer, the net competition by *S. brevifolia* on *R. robusta* in the communities where they co-occur, is minimised.

The stronger competitive effect of *S. brevifolia* on *R. robusta* at all four sites investigated is important for the dynamics of the ecotone vegetation. The observed competitive results might

be an indication of a reduction in water availability in the upper soil layer, where most of the root mass for *R. robusta* is concentrated. A more thorough analysis of water relations between grass and succulent shrubs in the study area is however required, but from the observed patterns in rooting depths, it is inferred that the stronger competition from grass reflects a reduced soil water available to *R. robusta* individuals. These views are in line with Esler and Rundel (1999) who suggest that an increased summer rainfall could lead to a rapid increase in grass cover and thus an increased competitive pressure. Rainfall trend over the past 50 years in Namaqualand indicates a decrease in winter rainfall, and an increase in summer rainfall (MacKellar et al. 2007), which is consistent with the predicted future climate change in the area (Rutherford et al. 1999; Hannah et al. 2002). The dynamics in the distribution of grasses relative to shrubs at the ecotone is a subject of urgency especially under the perceived climate change shifts in the area. A small competitive difference is apparently sufficient to cause a rapid extermination of the less competitive species (Hardin 1960). The spatio-temporal dimension of the distribution of grass and shrubs is covered in the next section.

The explanation for the relationships between grass and the succulent shrubs observed in this thesis is contrary to that which is commonly reported. Competition based models such as the two-layer hypothesis to explain co-existence between grass and woody plants in the savanna propose that grasses with shallow roots depend on water in the top layer of the soil, whereas shrubs have deeper root system and thus access water in the deeper layers of the soil (Walter 1971; Walker and Noy-Meir 1982; Knoop and Walker 1985; Sala et al. 1989; Snyman 2005). The ecological relationship between the shallow rooted succulent shrubs and the relatively deeper rooted grass at an arid ecotone investigated in this study can be explained by the two-layer hypothesis in a similar but reversed manner, to that proposed for grass shrubs/trees in the savanna. My findings thus demonstrate the possibility of two different water obtaining strategies, where the succulent shrubs seem to be playing the typical “grass” role described in most models of resource/water partitioning between grass and shrubs/trees, and vice versa. This is a contribution to arid ecology in general, and specifically to community ecology in the Karoo where the possibility of co-existence between the succulent shrubs and grass has been largely overlooked or misinterpreted. Although untested, others simply propose that succulent shrubs and grasses compete for water in the same horizontal plane (Midgley and van der Heyden 1999). Similarly, Desmet (2007) contends that the mesembs and grasses never co-dominate in plant communities, as both functional groups share a similar, shallow root structure.

8.2 The spatio-temporal distribution

Remote sensing technology is regarded as a valuable tool for evaluating dynamics at broad scales as it provides data through time and over large spatial areas (Schmidt and Karnieli 2000; Kerr and Ostrovsky 2003; Turner et al. 2003). Investigations were undertaken using remote sensing technology to 1) detect the current spatial distribution (Chapters 6), and 2) to detect the changes in the vegetation at the ecotone over the last 20 years (Chapter 7).

Computer assisted classifications of recent satellite imagery resulted in the production of a detailed map, depicting the spatial distribution of grass and shrub vegetation. Vegetation maps are important tools for local vegetation studies and monitoring but also as references for local improvement of existing national vegetation maps. The strength of the produced map lies in the detection and the mapping of grass vegetation patches embedded in the matrix of Namaqualand shrublands in the western part of the study area, which have not been mapped before, and the high classification accuracy at which the map was produced. The challenge in the classification, however, was in the delineation of mixed grass/shrub communities and in determining the relative abundance of each growth form in the mixed communities. Mixed vegetation areas have great potential for deriving the critical information required in developing and monitoring the direction of vegetation change and thus it is of great necessity to improve the delineation of these areas. Further investigations are underway to test the potential of other remote sensing systems, such as radar imaging, which might hold promise for improving vegetation mapping in the area. This thesis, however, succeeded in establishing the spectral properties of grass and shrubs which can be useful for future vegetation mapping in the area, but also which were used as described below, to develop the necessary change detection method for the area.

A remote sensing method, based on differencing the second principal components of the multivariate Principal Component Analyses was specifically developed in this study to detect changes in grass and shrub vegetation. This was based on the basic remote sensing logic that when different vegetation types can be spectrally distinguished, then the spectral properties used in a classification scheme to map such vegetation could be applied to multivariate datasets to detect the direction of change in the vegetation. The method that I used to detect shifts from one vegetation type to another is somewhat limited by the lack of reference data. Therefore, only information on the direction of change was provided and not explicit information on the relative extent of grass and shrub conversion. Continued site-specific research and surveys on the ecotonal communities is needed to provide ground information for the improvement of local change detection techniques. Nevertheless, for the period of observation, and according to the applied techniques in the analysis of vegetation change, most of the detected areas of change

were characterised by alterations in vegetation cover, as well as in the direction of vegetation shift, and only a small area showed signs of directional vegetation change. Inter-annual vegetation fluctuations that dominated the detected change areas indicate that the vegetation has been relatively stable over the last 20 years. Where directional change was detected it was either related to a decrease in general vegetation cover or to an increase in grass cover. Evidence of increasing grassiness is of significance at the ecotone, especially in terms of future climate change predictions, and given the observed competitive relationships between grass and succulent shrubs at this climatic ecotone. The skeletons of dead shrubs, as was frequently observed in the investigated communities, might be telling a story of past changes and future trends in grass and shrubs dynamics, and requires further investigation. The next step in this investigation lies in improving the results by lengthening the period of observation, and more importantly in the interpretation of the observed vegetation change in terms of climatic, ecological and anthropogenic parameters.

8.3 Main conclusions and future directions

The current investigations have contributed locally to an understanding of the ecotone, and the specific techniques required in monitoring the vegetation change. Moreover, specific investigations contributed significantly to their respective ecological fields.

The main conclusions that are pertinent to the objectives of the thesis are: 1) that competition plays a significant role in structuring grass and succulent shrub communities characterising the ecotone, whereas the influence of soils appears to be less important, and 2) that the vegetation seems to be relatively stable, but it is characterised by inter-annual fluctuations as obtained from remote sensing analysis. Evidence of an increase in grass vegetation was observed, which may be related to change in climatic patterns at the expense of the succulent shrubs, and an increased competition from grass on the succulent shrub form. These views support Dunnett and Grime (1999) who have proposed that inter-specific competition modulates the impacts of climate change. There was no evidence of the Succulent Karoo invasion eastward into the arid grassland as proposed by Acocks (1975). His view was based on the assumption that the grass component in the flora was being selectively grazed by domestic animals. However, he also noted that the movement has been slow because the Succulent Karoo plants are not adapted to the summer rainfall regime that characterises the Nama-Karoo biome.

In order to meet the global challenge of understanding possible ecosystem responses to the impacts of climate change, the presented investigations have established a base-line for further investigations as outlined in specific chapters. The detection of land cover change using

remote sensing techniques is a relatively advanced science, but the interpretation of the observed change, in terms of climatic, ecological and anthropogenic processes remains a complex issue (Vanacker et al. 2005). Land use clearly has a visible impact on the environment as seen in the many fence-line contrasts which can be observed both in the field and from maps derived from remotely sensed data. Gathering further data such as detailed land use patterns, rainfall and soil type is important. Together with GIS and other statistical tools this information may help explain vegetation changes in the region in relation to these factors.

University of Cape Town

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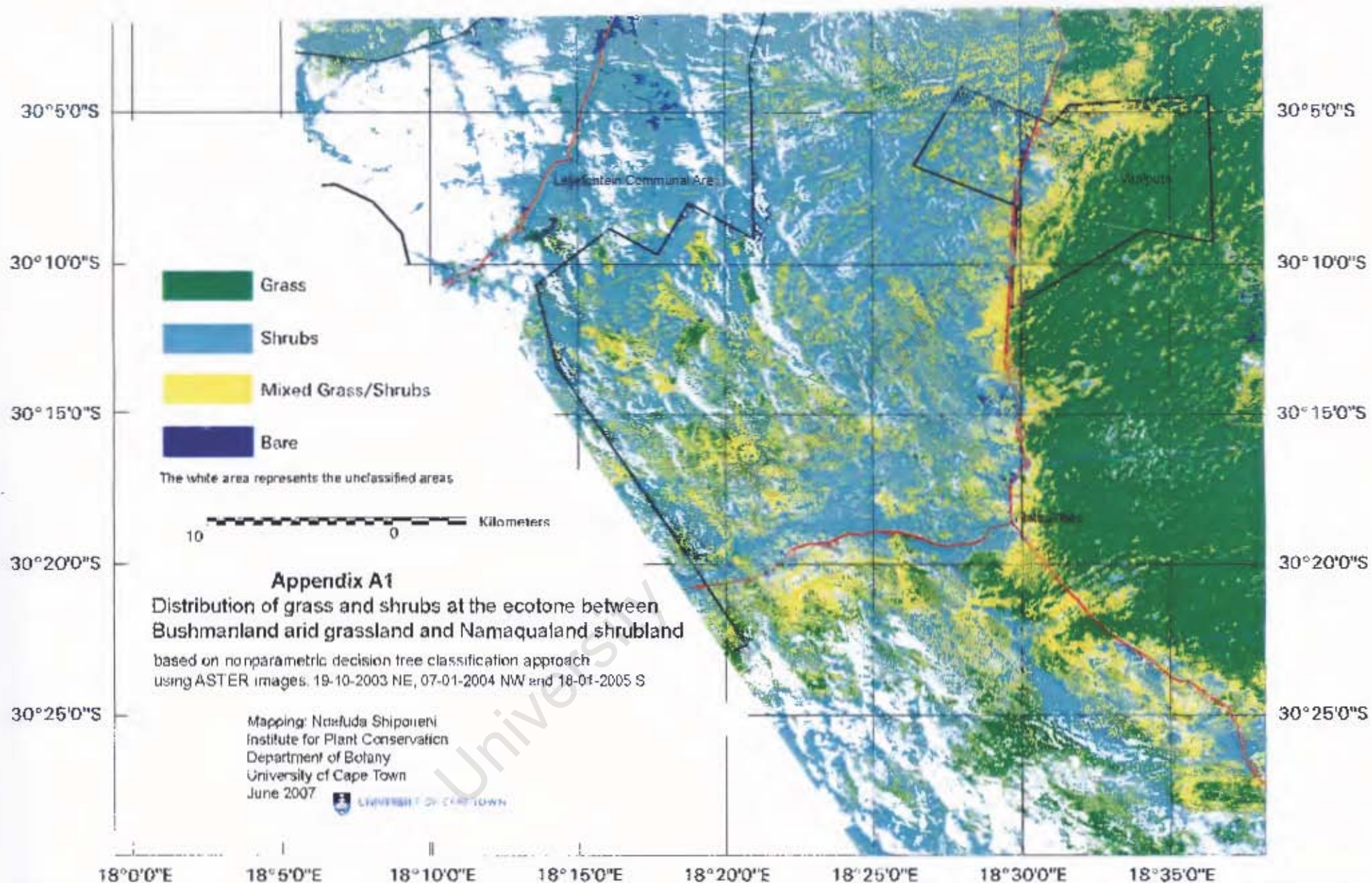
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University of Cape Town

Appendices

Appendix A0 Soil physical and chemical characteristics of the study area presented as mean at each site.

	Boesman plaat	Burdens puts	De Riet	Goegap A	Goegap B	Kougoed vlakte A	Kougoed vlakte B	Vaalputs
Soil depth (cm)	51	52	48	86	76	45	36	33
Total sand (%)	88	90	89	88	90	90	89	94
Silt (%)	1.0	0.7	1.5	1.1	0.6	0.9	0.6	0.7
Clay (%)	N/A	7.26	4.80	4.96	6.51	6.87	7.79	12.47
pH (in CaCl ₂)	1.92	2.22	1.59	2.10	0.92	1.13	1.71	1.76
Calcium (cmo kg ⁻¹)	1.99	1.9391	1.14	0.55	0.63	1.23	1.93	2.06
Magnesium (cmo kg ⁻¹)	28.9	28.3	44.1	21.5	17.8	31.9	28.9	32.8
Phosphorus (mg kg ⁻¹)	189	190	121	82	85	155	183	290
Potassium (mg kg ⁻¹)	39.4	80.7	35.1	34.3	24.9	29.9	37.1	18.6
Sodium (mg kg ⁻¹)	6.44	7.74	6.49	6.70	6.70	6.97	7.36	7.49
Conductivity (Msm)	3	2	3	4	4	3	3	5
Organic matter (%)	3	10	3	5	5	6	3	1



18°0'0"E 18°5'0"E 18°10'0"E 18°15'0"E 18°20'0"E 18°25'0"E 18°30'0"E 18°35'0"E

