

A functional analysis of the response of the Southern
Kalahari dune vegetation to land-use intensity

by

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ABSTRACT

Natural and anthropogenic environmental variables pressures exert fitness pressures on our flora and vegetation and necessitate an understanding of the mechanisms of plant responses to those pressures. Overgrazing and desertification are examples of the stressors that affect plant community composition, on both large and small scales. In order to investigate the plant community response to these stressors it has been shown that it is more practical and informative to group plant species according to their functional characteristics into functional types than attempting to predict plant response solely based on previous range distribution data. The present study involved a survey of the dunefield vegetation of several privately owned farms as well as a communal farm in the southern Kalahari. The farms were subjectively chosen to represent a gradient from underutilized to overutilized. Plant community surveys were conducted on the farms and the dominant plant species were sampled and researched for selected functional traits to explore possible relationships between traits and grazing pressure. Ordination techniques were used to identify plant functional grazing response types. The identification of plant functional types through easy measurable traits will be a great aid in modelling and long-term environmental monitoring approaches. Of the three dunefield habitats, the dune street habitat was identified as the most vulnerable to overgrazing. A reduction in cumulative cover and an increase in bare surface cover indicated increased grazing pressure in the dune crest habitat. In the dune streets shrub cover and annual grass cover increased when veld was overgrazed. Functional analysis of 112 Kalahari plant species for a set of 47 plant traits showed that species clustering were strongly related to vegetative characteristics. The emerging clusters were strongly associated with major life forms, which comprised phanerophytes of different size classes, geophytes and herbaceous perennials, as well as herbaceous annuals. These clusters were identifiable even with the inclusion of reproductive traits. Selected vegetative traits are good indicators of plant response to land-use intensity since these traits lend competitive advantages to plant persistence under utilisation pressure. Plant height, spinescence, specific leaf area, leaf dry matter content, leaf sclerophylly and stem density were found to be examples of such traits. Phanerophyte and chamaephyte dominated functional groups were mostly associated with lower range condition and hemicryptophyte dominated groups with higher range condition, whereas herbaceous therophyte dominated groups did not show any specific association.



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Chapter 1

Introduction

1.1 Background

Global climate change, desertification, food security and biodiversity protection are examples of socio-environmental issues that are currently very much “in vogue”. These popularized concerns are, however, far from being transient, fashionable, “green conscious” preservationists’ buzz-words. Immediate, real world concerns over the sustainable use of land for food supply, eco-tourism and biodiversity conservation begs long-term focus on these concerns and necessitates investigations into the patterns and processes of natural vegetation. Currently only 6.2% of the land area of South Africa is under formal protection and 80% of all the land is under private ownership (Mucina & Rutherford, 2006). Private landowners therefore have a very important role to play in approaching biodiversity conservation. Different land-use practices could influence plant diversity and distribution and demand investigation. Implicitly, the mere floristic description of the vegetation of natural areas will be insufficient if long-term sustainable use and preservation is envisaged. There are currently several global, multi-national projects involved in the study and monitoring of biodiversity responses to natural and/or human-induced environmental change for example the International Long-Term Ecological Research (ILTER) programme, Environmental Long-Term Observatory for Southern Africa (ELTOSA) and the South African Environmental Observation Network (SAEON) as well as the Biodiversity Transect Analysis in Africa (BIOTA) that partially funded this study.

This study formed part of phase II of the BIOTA project that was funded by the German Federal Ministry of Education and Research (BMBF). This endeavour spanned several countries and included the BIOTA East Africa, BIOTA West Africa and BIOTA Southern Africa regional projects. In the BIOTA project the effects of climate change and anthropogenic influences on biodiversity were investigated through surveys and experimentation. The goal was to understand the biotic and abiotic processes involved in biodiversity change to improve the prediction of future scenarios and provide tools for role players to improve the management of their local environments. BIOTA was a multi-disciplinary project that involved disciplines as diverse as botany, zoology, geology, remote sensing, modeling and social ecology. This study fell under the botanical arm and focuses on the functional response patterns of Kalahari vegetation with respect to land-use intensity (i.e. grazing intensity).

1.2 The plant functional type concept

Plant species are not static, but rather exhibit marked changes in distribution in space and time. This ability to spread and adapt to different environments (speciation occurring in the process) may take place at a slow rate in human terms but takes place nonetheless and is essential for the survival of plant species (Anderson, 2001).

The capacity of plant species to respond to changes in their environment can be coupled to the functional traits of the plant species. Functional adaptation to changing environments is a continuous process with the possibility that some trait attributes may become redundant in time. It would be advantageous to identify plant species that have similar plant functional traits and to group these species into functional types. A clear, unified definition of a functional type is elusive. Gitay and Noble (1997) define a plant functional type as “A non-phylogenetic classification leading to a grouping of organisms that respond in a similar way to a syndrome of environmental factors”. Scholes *et al.* (1997) state that it is “a set of co-varying parameter ranges for plant attributes related to resource acquisition, growth, reproduction, dispersal and response to environmental stress”. In this study a plant functional type will be regarded as:

“a set of trait states that represent a unified response to changes in the environment or have similar effects on the environment.”

Here it is important to distinguish between functional response types and functional effect types. Functional response types are groups of species that react similarly to environmental change (e.g. resource availability, disturbance) whereas functional effect types are plant groups that have similar effects on the environment and its ecological processes, for example fire-promoting species or nurse species (Diaz & Cabido, 2001). In this study the focus was on functional response types, and more specifically the response to grazing disturbance. Note however that the plant functional type term defined above reflects inclusion of both effect and response types for accuracy. Importantly, the functional type does not assume any taxonomic linkages between the plant species within a functional type.

The identification of plant functional types (PFTs) provides a simplified structure for studying plant survival strategies. Local conditions have the effect of filtering for certain plant traits (Diaz *et al.*, 1999a) that will promote establishment, persistence and reproduction. If selected sets of traits are repeated in predictable patterns, of which there is evidence (Diaz *et al.*, 1999a), predictions can be made regarding the direction of change that vegetation will undergo under certain biotic and/or abiotic influences. Such simplified entities can be more easily incorporated into computer-based

simulations of plant responses to climate change, land-use regimes and other environmental flux scenarios (Boer & Stafford Smith, 2003).

It is generally accepted by most plant ecologists today that vegetation is, in essence, a dynamic system of interwoven plant strategies and processes geared towards survival and reproduction (Kent & Coker, 1994; Skarpe, 1996). The close link between plant traits and climate was already promoted by Schimper (1898, cited in Westoby & Wright, 2006) and Raunkiaer (1934, cited in Lavorel & Garnier, 2002). The coupling of form and function as a starting point to investigate plant dynamics is as logical an approach as it has been neglected. Although the seeds for the focused investigation of trait-environment linkages were sown in the late 19th and early 20th century, it is only relatively recently that the topic received renewed attention. In 1967 for example Root, albeit in the study of the blue gray gnatcatcher bird, used the term *guild*, to denote species that use a resource in a similar way or that overlap in niche requirements. It was around this time that studies on plant functional traits started to rekindle.

Since the birth of the *guild* concept many additional terms and definitions have been formulated as the scientific discipline of functional ecology evolved. Confusion arose as the application of terms differed between authors and variations on definitions developed. The main dichotomy in the sea of terminology concerned those terms that refer to structural or taxonomic features of plant species and those that refer to responses to environmental factors or resources. Overlap in the terminology used for these two aspects of plant ecology caused confusion.

The result of this ambiguity was several extensions to the *guild* concept (Gitay & Noble, 1997):

<i>Assemblage guilds:</i>	guilds based on taxonomic classification (Jaksic, 1981);
<i>Community guilds:</i>	guilds based on the use of the same resource (Jaksic, 1981);
<i>Management guilds:</i>	species respond similarly to many environmental factors that affect the environment (Verner, 1984);
<i>Functional guilds:</i>	similar to Root's (1967) definition of a guild (Szaro, 1986);
<i>Structural guilds:</i>	species that use the same resource (Szaro, 1986);
<i>Response guilds:</i>	species that respond similarly to habitat disturbance (Szaro, 1986).

Guilds could ambiguously therefore refer to groupings based either on taxonomy, similar resource use or response to disturbance. Additional terminology such as *league* and *clique* was employed in an attempt to structure the *guild* concept. *League* refers to a group of organisms that use more than one resource in a similar manner (Faber, 1991) and *clique* to organisms that have some food resource in common (Yodzis, 1982). Menge *et al.* (1986) and Gitay and Noble (1997)

suggested that the term *guild* be reserved for references to structure and similar resource use and the term *functional type* be used for similar responses to an environmental disturbance.

Morphological, anatomical and physiological traits of plant species that presently influence their ability to persist and thrive under local environmental conditions are assumed to have a functional role. Sometimes certain traits may be evolutionary relics of which the functional significance is not relevant anymore. These cases highlight the possible danger of consistently applying functionality to traits. External influences such as climate, disturbance and biotic interactions act as filters on these plant traits (Diaz *et al.*, 1999b). Taxonomic affiliation stands separate from the filtering process. It is the traits that are subjected to filtering and not taxonomic identity (Diaz *et al.*, 1999a). Although plants with close taxonomic affinities may live together in the same local environment it is not the taxonomy *per se* that determines successful habitation, but rather the traits. One could argue that it is the common correspondence in traits between closely related species that may often see them incidentally occupying broadly similar habitats.

According to Semanova and Van der Maarel (2000), plant species that have similar functionality can be assembled into functional types. However, such a grouping is broad and can include similar functioning with regard to disturbance and/or resource use. In the present study the plant functional type aspect that was investigated was the response to disturbance. This is in line with the application of the term by Gitay and Noble (1997), Gondard *et al.* (2003) and Jauffret and Lavorel (2003). Although Gitay and Noble (1997) also suggested the application of resource use under the term plant functional type, they mentioned that the context should then be specified.

The ability of a plant species to establish, persist and reproduce in any environment depends on that species' inherent functional characteristics. These heritable characteristics or traits endow the plant species with strategies that can be suitable to a specific habitat or that make it more adaptable to a variety of habitats than another species. To embark on an investigation into the various strategies of different plant species one first has to focus on a response to a single variable. This study for example focused on the linkage between grazing disturbance and grazing related plant traits. A simultaneous investigation of the relationship between specific plant traits related to e.g. fire as well as grazing could confound the effects of the two variables. It would be difficult to attribute a change observed in a plant trait score to either fire or grazing specifically.

In practice, however, such an attempt to couple a specific trait to a specific environmental response is not without shortcomings. For example, the capacity of a plant to resprout could be advantageous as both a fire response and a grazing response. Although a single trait may be involved in several of a plant's environmental responses, it is not the trait in isolation that should

be considered but rather an assembly of different traits with specific scores that define a specific adaptation (Diaz *et al.*, 1999a).

The quantification of traits is not always easy to accomplish and therefore traits can be considered as “hard” or “soft” (Weiher *et al.*, 1999; Lavorel & Garnier, 2002; Cornelissen *et al.*, 2003). Seed persistence for example could be considered an important trait for investigation but this is a “hard” trait to quantify. Instead the traits seed mass and seed size, which are “soft” traits, are used as surrogates for seed persistence because smaller seeds are buried faster and escape predation better than larger seeds (Cornelissen *et al.*, 2003).

1.3 Effects of grazing on the vegetation

Vegetation dynamics in relation to land-use (grazing) intensity in the arid savanna of South Africa and Botswana have been investigated and discussed in the context of the following themes:

- Shrub-grass layer interactions in response to grazing (Skarpe, 1990a, 1991b).
- Shrub spatial dynamics in response to grazing (Skarpe, 1991a).
- Modelling of grass-shrub layer interactions according to rainfall (Scanlon *et al.*, 2005).
- Veld condition and/or vegetation composition in relation to moisture availability (Van Rooyen *et al.*, 1984; Fourie *et al.*, 1987, Ringrose *et al.*, 2003).
- Wildlife and livestock numbers in relation to distance from watering points and/or human habitation (Bergstrom & Skarpe, 1999).
- Plant species composition in relation to distance from watering points and/or habitation (Kalikawe, 1990; Van Rooyen *et al.*, 1991; Perkins & Thomas, 1993; Van Rooyen *et al.*, 1994; Thomas *et al.*, 2000).
- Detection of vegetation change due to land-use practice and land-use intensity through remote sensing (Ringrose *et al.*, 1996; Palmer & Van Rooyen, 1998).

Due to the important and limiting effect of moisture, great variation in seasonal cover is found in the Kalahari, with early summer rain favouring perennial grass growth and late summer rain favouring shrub growth (Van Rooyen *et al.*, 1984). Species composition does not, however, exhibit similar variability. Plant community composition in relation to grazing intensity has been investigated mainly through evaluating species composition change with distance from watering points (piospheres). Uncertainty exists over whether this species turnover is attributable to seasonal moisture availability or greater grazing pressures nearer the watering points (Van Rooyen *et al.*, 1991). Artificial watering points are likely to discourage migration and lead to increased utilization of areas adjacent to the water sources.

Kalikawe (1990) identified specific herbaceous and woody species that increase or decrease with distance from watering points in the Kalahari in Botswana. Long-term monitoring of vegetation at watering points in the Kgalagadi Transfrontier Park have also shown species composition changes with distance from watering points, although this was not pronounced in the river bed and river terrace habitats (Van Rooyen *et al.*, 1991). Species were categorized according to their frequency in veld utilized to different degrees. A subsequent paper by Van Rooyen *et al.* (1994) dispatched the notion of increased veld degradation close to watering points, except for the sacrifice zone, and identified fodder availability as the most limiting resource. Perkins and Thomas (1993) stated that available grazing is the major control on livestock production, but also indicated that water is the primary limiting factor because water is required for grass production in the first instance. Thomas *et al.* (2000) identified species composition changes with distance from watering points and confirmed the presence of sacrifice zones close to these points.

1.4 Problem identification and study aims

This study is an attempt to understand the relationship between grazing intensity and the plant traits that respond to this type of disturbance. Surveys were conducted on several farms that were selected to represent a grazing gradient within the same broad habitat. The plant species occurring on these farms were recorded and analyzed for specific plant functional traits.

The objectives of the study were to answer the following key questions:

- How does plant species composition change along a land-use intensity gradient?
- How do species richness and the Shannon-Wiener index of species diversity change along a land-use intensity gradient?
- How do different plant traits respond to changes in land-use intensity?
- Do plant functional response types emerge along the land-use gradient?

This study did not follow the popular approach of studying plant community response to grazing pressure by focusing on piosphere grazing pressure zones around watering points, but rather selected a series of farms as being representative of a land-use intensity gradient. This study will explore the interaction between vegetation and/or species trait attribute changes in response to grazing pressure.

1.5 Dissertation structure

The structure of this dissertation was in a traditional format consisting of introductory chapters and successive chapters with specific themes. However, the theme orientated chapters (Chapters

4 to 6), which represent the scientific research content of the dissertation, were each structured according to scientific article format. The list of references used for all chapters was provided at the end of the thesis in a single set.

Chapter 2

The study area

2.1 Introduction

This study was conducted in the southwestern Kalahari, an area of which the floristic affinities with the phytogeographical regions within southern Africa is debated. From a phytogeographical point of view the southwestern Kalahari forms part of the Palaeotropical Floristic Kingdom, which stretches from the south of Africa northwards around the tropical rainforests and up to the edge of the Sahara desert (Van Wyk & Smit, 2001). The specific affinity of the southwestern Kalahari with the two regions that constitute the kingdom has been disputed by different authors. Some authors (Juergens, 1991) group the Kalahari with the Karoo-Namib region while others (Skarpe, 1986; Werger, 1986) see it as part of the Sudano-Zambezian region. It has also been classified as a transitional zone, *viz.* Kalahari Highveld Transitional Zone, between the Karoo-Namib and Sudano-Zambezian subregions (White, 1983).

A classification based on the physiognomic characteristics (growth form and structure) and environmental factors (availability of water, seasonality of rainfall and temperature) has been used to allocate the southwestern Kalahari to one of the biomes of southern Africa (Rutherford & Westfall 1994). Work by Acocks (1953), Steyn (1990) and Westfall and Van Staden (1996) support the classification of the southwestern Kalahari as part of the Savanna Biome. Savannas possess a continuous grass layer as well as a woody stratum, exhibit distinct seasonality in rainfall and are often subjected to fire (Low & Rebelo, 1998; Van Rooyen & Van Rooyen, 1998). The southwestern Kalahari can further be characterised as an arid savanna with microphyllous wooded grasslands and thickets, base-rich substrates and hot, dry, lowland regions (Van Rooyen & Van Rooyen, 1998). With a low annual rainfall from 150 to 450 mm, parts of the southwestern Kalahari could even be considered a desert.

The field surveys for this study were conducted in the southwestern Kalahari (Figure 2.1), an area at approximately 900 to 1 200 m above sea level (Van Rooyen, 2001).

2.2 Climate

The mean annual rainfall for Twee Rivieren is 220 mm per annum (Van Rooyen *et al.*, 1991) and 189 mm for Upington (South African Weather Service, 16 Feb 2006). Rainfall is erratic with rainfall varying from 100 mm to 700 mm per annum in the same locality (Van Rooyen & Van Rooyen, 1998). The

southern Kalahari falls within the summer rainfall region with the most rain occurring from January to April.

A rainfall gradient exists over the region from the west to the east with precipitation decreasing towards the west (Figure 2.1a). The owners of the farms Alpha and Swartpan reported mean annual rainfall of 267 mm and 212 mm respectively on their farms for the period 1999 to 2004 and 2000 to 2004 respectively. As with most desert environments temperatures can be extreme. Winter lows can reach -10°C and summer highs 45.4°C (Van Rooyen, 2001).

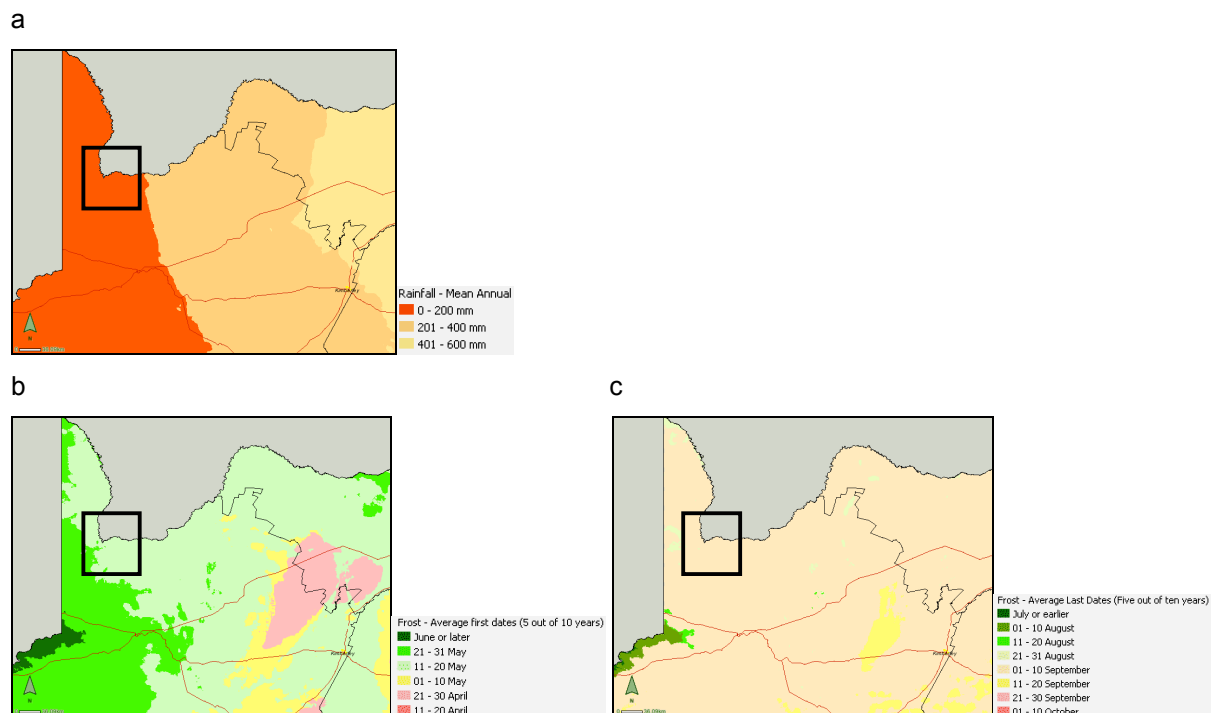


Figure 2.1 (a) Rainfall decreases across the southwestern Kalahari from east to west. (b), (c) Frost occurs in the Kalahari and in the study area these frost events occur from approximately middle May to the beginning of September (Agricultural Geo-referenced Information System, Department of Agriculture, www.agis.agric.za, 1 Des 2006).

Frost events often occur and these may stretch from approximately the middle of May to the beginning of September (Figure 2.1b, c). A Walter diagram (Walter, 1963) of monthly rainfall and temperature for the town Upington is shown in Figure 2.2. Upington lies in the transition zone between Kalahari savanna and Karoo shrubland and is ca. 200 km south of the study area.

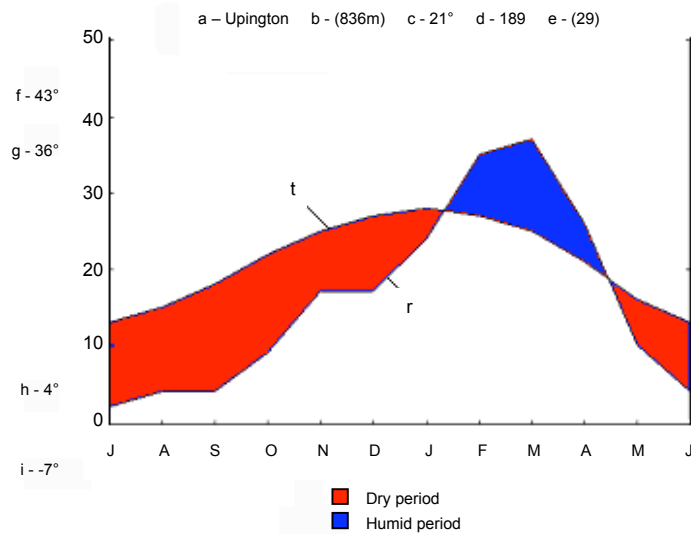


Figure 2.2 Walter diagram showing monthly rainfall and temperature at Upington (South African Weather Service, 3 December 2004), a = weather station, b = height above sea-level, c = mean annual temperature in °C, d = mean annual precipitation in mm, e = duration of observations in years, f = highest temperature recorded, g = mean daily maximum of the warmest month, h = mean daily minimum of the coldest month, i = lowest temperature recorded, t = temperature, r = rainfall. The temperature axis (Y left) is in increments of 10°C and the precipitation axis (Y right) in increments of 20 mm. The X axis is the period from July to June.

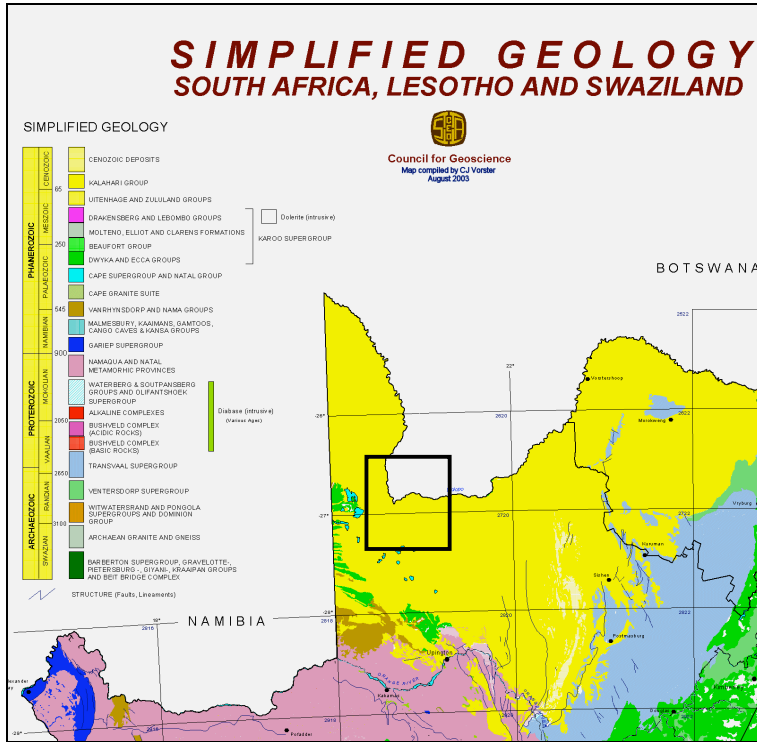
2.3 Geology and soil

Geologically the southwestern Kalahari is relatively young and consists of unconsolidated Tertiary to Recent deposits less than 60 million years old with less pronounced dune topography (Van Rooyen & Van Rooyen, 1998, Vorster, 2003). The region resides under the Kalahari Group of sedimentary rocks with underlying tillites (Figure 2.3a and b). This geological group is overlain by vast stretches of aeolian sand that form dunes running in a northwest-southeast direction (Figure 2.4a and b).

These sands can be traced back to the flexing of the interior continental crust of southern Africa due to presumed mantle plume activity during the late Cretaceous, ca. 65 million years ago (McCarthy & Rubidge, 2005). The flexing resulted in the formation of elevations and depressions, of which the Kalahari basin was such a depression. Rivers drained into the depression forming large interior lakes, never reaching the ocean and depositing large quantities of sediments. The southwestern Kalahari sands display two distinct surfaces. In the extreme west and southwest large piles of dunes run for hundreds of kilometers, but to the east of the Nossob River the landscape is flatter and the dune topography is less pronounced (Van Rooyen, 2001). Dunes range in height from 10 – 20 m above dune street level (Bullard *et al.*, 1995).



a



b

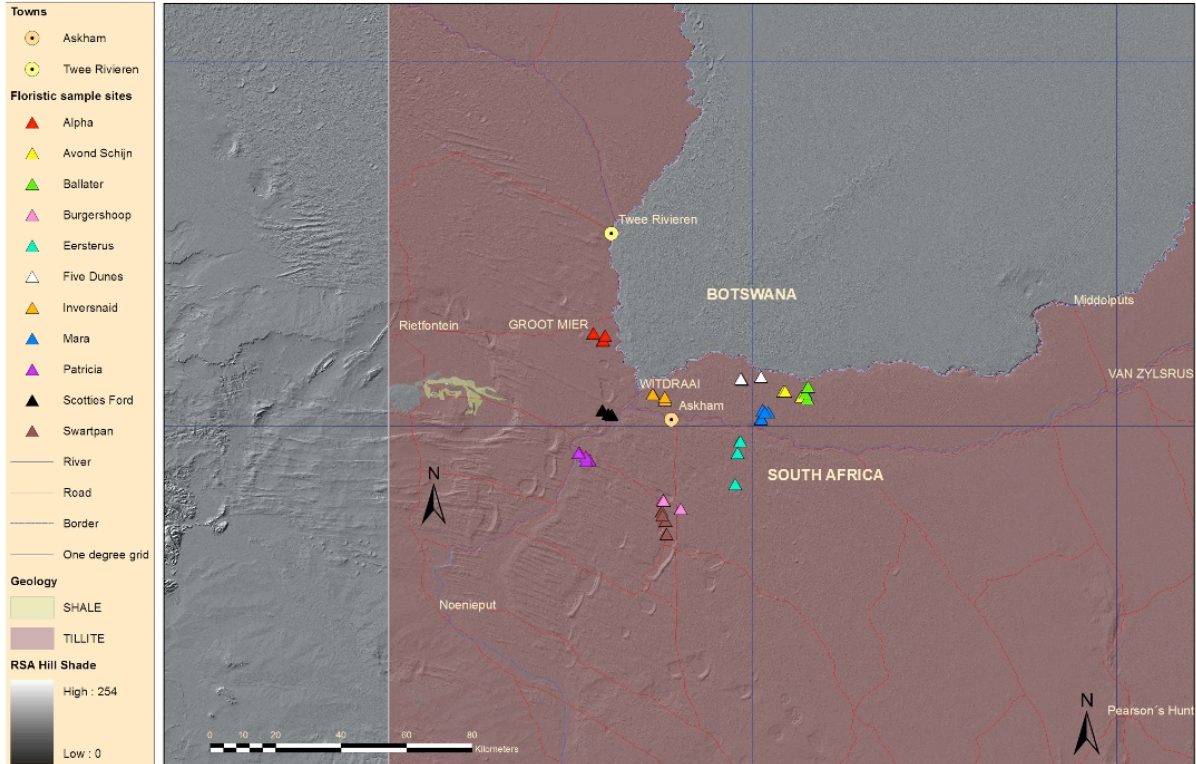
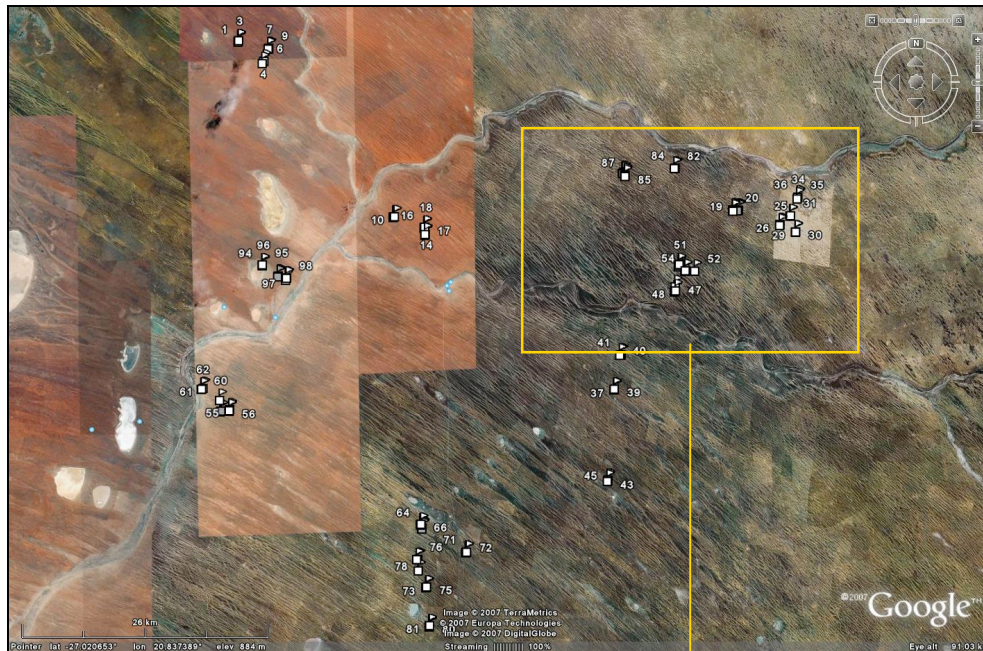


Figure 2.3 The study region consists of the Kalahari group of sedimentary rocks with underlying tillites (Vorster, 2003). Coloured triangles denote sampling sites on farms.

a



b

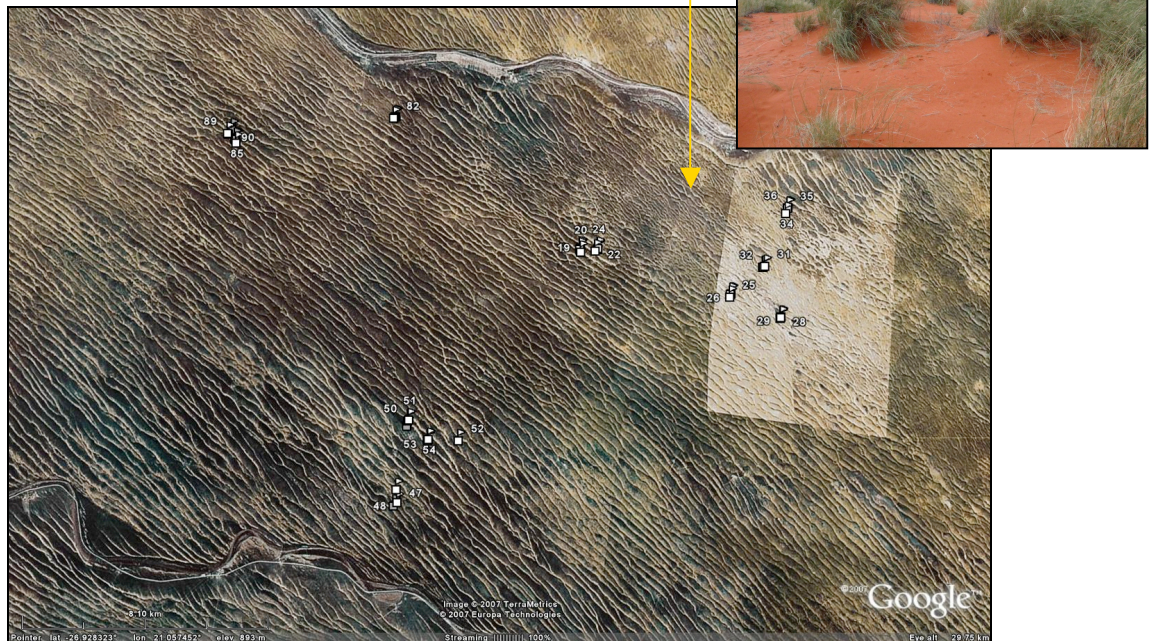
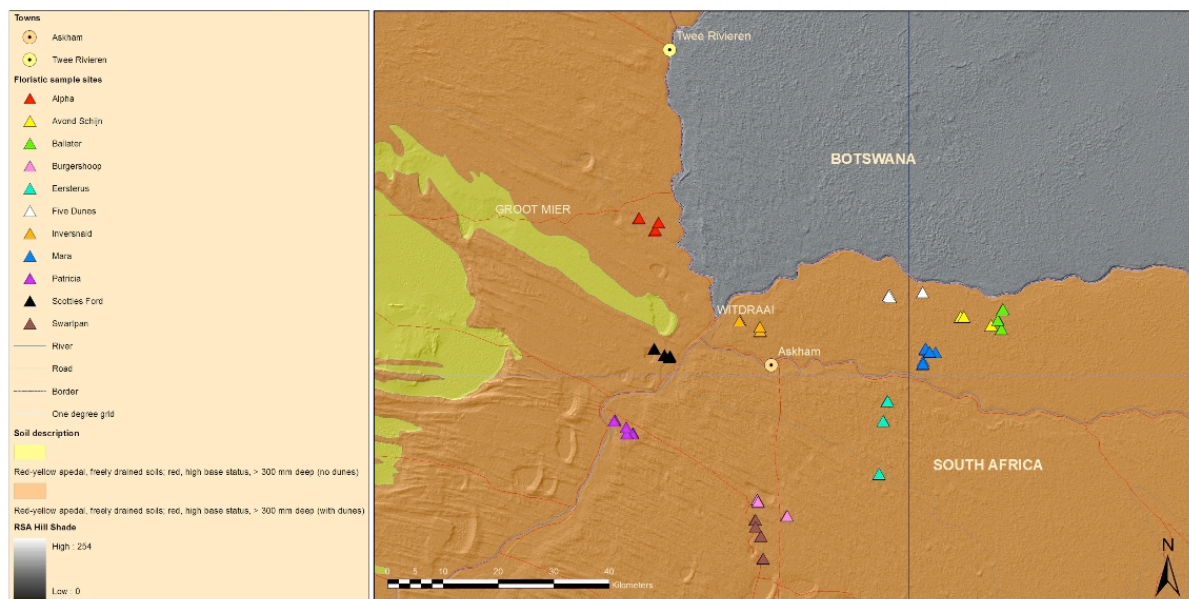


Figure 2.4 (a & b) GoogleEarth satellite images of the southern Kalahari region in which the northwest-southeast arranged dunes are visible together with light coloured pans (GoogleEarth, 6 December 2007; <http://earth.google.com>). Survey plot numbers are indicated with dune street and dune slope shown as squares and dune crest plots as triangles.

The soils of the southwestern Kalahari can be classified as the Namib form, with orthic A horizons overlying regic sand (MacVicar, 1991) that is generally deep. The red-yellow apedal soils are freely drained and structureless with the red soils having a high base status (Figure 2.5a). The soils have relatively good water retention (Figure 2.5b) and display the inverse texture effect (Noy-Meir, 1973). The soils are generally infertile (Buckley *et al.*, 1987b; Skarpe, 1991a; Van Rooyen & Van Rooyen, 1998) with the soil fertility seeming to decrease from dune crest to dune street (Buckley *et al.*, 1987a).

a



b

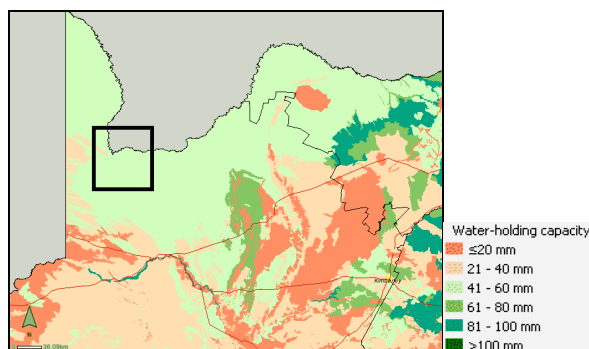


Figure 2.5 Characteristics of southwestern Kalahari soils, (a) soil classes and generalized soil patterns and (b) water-holding capacity (Agricultural Geo-referenced Information System, Department of Agriculture; www.agis.agric.za, 1 Des 2006). Coloured triangles denote relevé sites on farms.

The relatively homogenous edaphic conditions found in the dunefield savanna of the southern Kalahari makes this area a suitable location for an investigation into plant response to grazing because co-varying environmental factors (such as edaphic properties) that may mask plant response to grazing influences are limited in such an edaphically homogenous area.

2.4 Vegetation

The southern Kalahari is located in the Kalahari Highveld Transitional Zone (White, 1983) that divides the Karoo-Namib Regional Centre of Endemism and the Zambebian Regional Centre of Endemism (Van Wyk & Smith, 2001). All the farms included in the survey are located within the Shrubby Kalahari Dune Bushveld (Low & Rebelo, 1998). According to the new vegetation classification of South Africa (Mucina & Rutherford, 2006) most of the farms included in this study fall within the *Gordonia* Duneveld except for the farms Inversnaid and part of Scotties Ford which fall under the Aoub Duneveld (Figures 2.6 & 2.7).

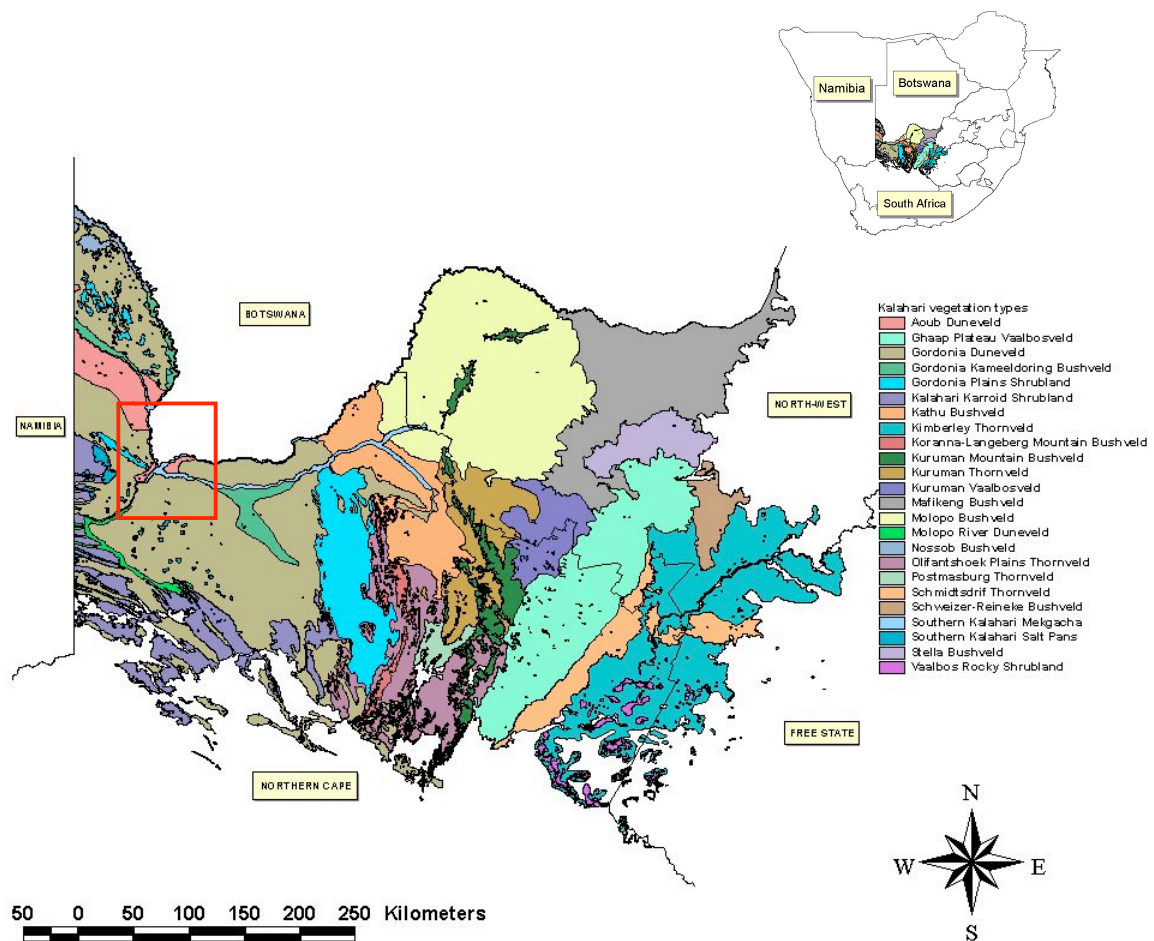


Figure 2.6 Vegetation types of the southern Kalahari that occur in South Africa (Mucina *et al.*, 2005). The study area (red block) consists primarily of the *Gordonia* Duneveld vegetation type.

With its classification as an arid savanna or as a semi-desert the southwestern Kalahari has a lower grazing (carrying) capacity than the moister savannas and grasslands to the east. Figure 2.8 shows that grazing capacity has a strong relationship to the east-west annual rainfall gradient (compare

Figure 2.1a). It should be noted that this grazing capacity has a specific agricultural context, i.e. livestock, and does not consider wildlife resource use and associated wildlife stocking density calculations (grazer and browser units) as advocated by Bothma *et al.* (2004)



Figure 2.7 A map that shows the location of 11 farms included in this study relative to vegetation types of the southern Kalahari as well as the location of the relevés on each of the farms.

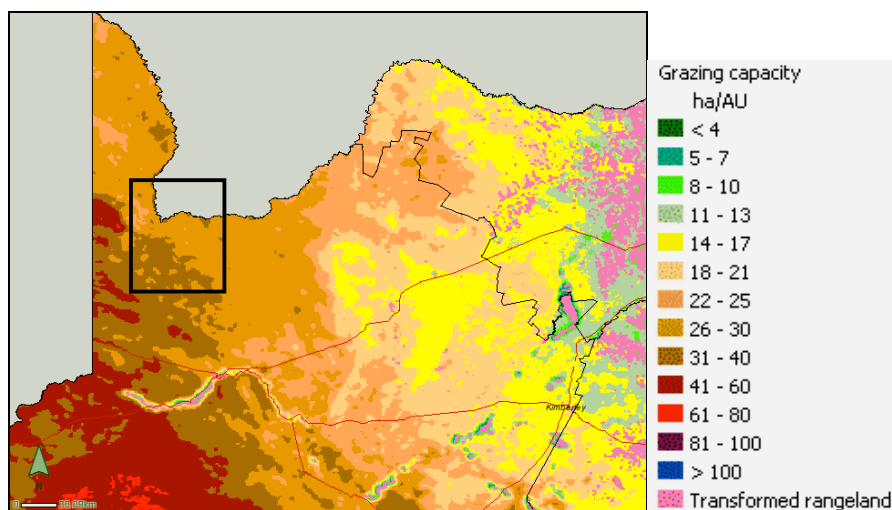


Figure 2.8 The grazing capacity (AU = large animal unit) across the southwestern Kalahari coincides with the northwest-southeast annual rainfall gradient, with grazing capacity decreasing towards the northwest (Agricultural Geo-referenced Information System, Department of Agriculture, 1 Des 2006).

Distinct habitat types can be distinguished within the southwestern Kalahari dunefield vegetation. These are dune crests, dune slopes, dune streets (valleys), pans, rivers and calcrete cliffs. In his syntaxonomical survey of the Kalahari dunefield vegetation, Lubbinge (1999) identified several plant communities of the southern Kalahari. The plant communities present on the farms included in the current study are listed in Table 2.1. Grassland is a prominent feature of the Kalahari with approximately 13% of the species of the Kgalagadi Transfrontier Park being grasses (Van Rooyen & Bezuidenhout, 1997).

Table 2.1 Plant communities that are found on the farms included in this study in the southwestern Kalahari according to Lubbinge (1999)

	Inversnaid	Scotties Ford	Alpha	Avonds Schijn	Ballater	Burgershoop	Eersterus	Five Dunes	Mara	Patricia	Swartpan
Sub-associations											
<i>Acacia haematoxylon-Stipagrostetum amabilis-Requienietosum sphaerosperma</i>			X	X	X	X	X	X	X	X	X
<i>Acacia haematoxylon-Stipagrostetum amabilis-Hermannietosum tomentosae</i>			X	X	X	X	X	X	X	X	X
<i>Stipagrostio amabilis-Acacietaum melliferae-Eragrostitosum trichophorae</i>	X	X									
<i>Stipagrostio amabilis-Acacietaum melliferae-Acacietaosum eriolobae</i>	X	X									
Association											
<i>Centropodio glaucae-Stipagrostetum amabilis</i>	X	X									
<i>Harpagophyto procumbentis-Rhigosetum trichotomii</i>	X	X									
<i>Plexipus garipensis (Chascanum pumilum)-Centropodia glauca-Acacia haematoxylon</i> dune streets (without syntaxonomical status)			X	X	X	X	X	X	X	X	X
<i>Eragrostis lehmanniana-Aristida meridionalis-Acacia haematoxylon</i> dune streets and plains (without syntaxonomical status)			X	X	X	X	X	X	X	X	X
<i>Acacietaum melliferae- Acacietaum eriolobae</i>	X	X									
<i>Stipagrostio uniplumis-Acacietaum melliferae</i>	X	X	X	X	X	X	X	X	X	X	X
Alliance											
<i>Rhigoso trichotomii-Stipagrostetum obtusae</i>			X	X	X	X	X	X	X	X	X
<i>Schmidtio kalihariensis-Acacietaum eriolobae</i>	X	X									

2.5 Survey sites and site selection

The starting objective for the field surveys was to select a group of farms on similar geological formations, with similar soil types, subjected to similar climatic conditions and located within the same vegetation type but with varying degrees of utilization (grazing intensity). This would help limit the effect of co-varying environmental factors that would mask species response to grazing. Farms were selected on the basis of perceived degradation state due to overgrazing in order to establish a series of farms that form a grazing gradient from overgrazed to undergrazed veld. The farm selection was done with the aid of Mr Seppie Esterhuizen, an agricultural extension officer of the Northern Cape Department of Agriculture, with extensive knowledge of the veld condition of the farms as well as their management histories.

In total eleven farms were selected for the survey. Ten of the farms are privately owned and commercially operated for livestock farming, mostly with sheep. One farm, Scotties Ford, is communal land and has only relatively recently (1999) become the property of the local Khomani San community. Subsistence farming with mostly goats is practiced on Scotties Ford. All of the farms have artificial watering points distributed throughout except for Scotties Ford.

Based on the opinion of the agricultural extension officer the farms could subjectively be grouped into the following broad condition states:

Good to very good condition:	Burgershoop Swartpan Eersterus Five Dunes
Above average to below average condition:	Alpha Scotties Ford Inversnaid Patricia
Poor to very poor condition:	Avonds Schijn Mara Ballater

The locations of the farms within the study area are shown in Figure 2.7. Some background information, a brief description of the farms based on first hand information from the owners, unless otherwise stated, and a photographic record of the condition on each farm (Figures 2.9 – 2.19) are provided below. A summary of stocking densities at the time of the study is provided in Table 2.2 for farms where animal numbers were disclosed by land owners. This data was obtained directly from the

farmers either in person or through postal communication. Numbers of small species of wildlife, such as duiker should be considered approximations.

2.5.1 Farm background information

Burgershoop

Cattle farming is the main focus on this 9 000 ha farm although sheep and wildlife are also kept. The farm is divided into camps and livestock are rotated between camps. The farmer has a tertiary agricultural qualification and has been farming in the Kalahari for 18 years. Only private hunting is allowed. A fire occurred in the 2000/2001 season but that particular area was avoided in the survey. The farm does not border on any river. Animal numbers on the farm were not disclosed.

Swartpan

An 8 000 ha farm that is divided into 33 camps. The owner used to be an agricultural extension officer and has a tertiary agricultural qualification. The farm has been the current owners' property for eight years and the camps are "managed". Hunting is allowed. A fire affected part of the farm in November 2000, but this site was avoided in the survey. The farm does not border on any river.

Five Dunes

This farm of 6 000 ha, is divided into camps and rotational grazing is applied. The current owner bought the farm 25 years ago from his parents, who were the previous landowners. The main focus is on sheep farming although some goats and wildlife are kept in limited numbers. The farmer emphasized that animals are never allowed to roam freely on the farm, even during periods of severe drought. *Prosopis glandulosa*, an alien invasive species, is actively controlled by cutting as well as by chemical treatment. The ephemeral Molopo River borders the farm to the north.

Eersterus

Approximately 1 000 sheep ewes are sustained on this 6 200 ha farm and this is also the main type of livestock on the farm. Wildlife is limited but gemsbok, springbok, red hartebeest and gnu occur in small numbers. Hunting is allowed, but with friends and family only. The farm is divided in ca. 30 camps and the camp gates are left open during periods of grazing/forage shortage. The farmer states that a strip of ca. 4 km along the northern boundary of the farm was previously intensively exploited by the first settlers. The elderly farmer was born on the farm and his parents arrived on the farm in 1933. There was a fire in a northern section of the farm in ca. 2002. The ephemeral Kuruman River borders the farm to the north.

Table 2.2 Size in hectares and stocking densities at the time of the study of the 11 farms included in this study in the southwestern Kalahari. Stocking densities were supplied by farmers. Large animal unit (LAU) equivalents are according to Bothma & Du Toit (2010).

	LSU equivalent (LAU/animal)	Burgershoop	Swartpan	Five Dunes	Eersterus	Alpha	Scotties Ford	Inversnaid	Patricia	Avonds Schijn	Mara	Ballater
Farm size (ha)		9000	8000	5435	6200	3500	7400	8000	10000	5400	6862	6000
Livestock numbers												
Sheep	0.15	<i>n/a</i>	1300	1113	1130	0	<i>n/a</i>	<i>n/a</i>	1700	1140	1480	5000
Goat	0.17	<i>n/a</i>	0	0	21	0	<i>n/a</i>	<i>n/a</i>	0	92	0	0
Cattle	1.21	<i>n/a</i>	60	0	42	0	<i>n/a</i>	<i>n/a</i>	0	0	0	0
Wildlife numbers												
Springbok	0.15	<i>n/a</i>	300	400	120	300	<i>n/a</i>	<i>n/a</i>	0	150	80	0
Gemsbok	0.56	<i>n/a</i>	0	30	60	130	<i>n/a</i>	<i>n/a</i>	150	24	13	0
Hartebeest	0.37	<i>n/a</i>	0	5	15	10	<i>n/a</i>	<i>n/a</i>	0	4	0	0
Ostrich	0.25	<i>n/a</i>	0	0	5	31	<i>n/a</i>	<i>n/a</i>	0	10	20	0
Eland	1.02	<i>n/a</i>	0	3	9	0	<i>n/a</i>	<i>n/a</i>	0	9	0	0
Duiker	0.09	<i>n/a</i>	0	40	40	0	<i>n/a</i>	<i>n/a</i>	0	0	2	0
Steenbok	0.06	<i>n/a</i>	0	0	0	1	<i>n/a</i>	<i>n/a</i>	0	0	0	0
Impala	0.17	<i>n/a</i>	0	0	0	0	<i>n/a</i>	<i>n/a</i>	0	6	0	0
Blue wildebeest	0.50	<i>n/a</i>	0	0	0	10	<i>n/a</i>	<i>n/a</i>	0	8	0	0
Stocking density (ha/LAU)	<i>n/a</i>	25.59	21.55	20.63	26.06	<i>n/a</i>	<i>n/a</i>	29.50	22.43	27.84	8.0	

Alpha

This 3 500 ha farm is run as the Kalahari Trails Nature Reserve by a retired professor in zoology. Before 1997 it was a cattle farm, but since it was bought in 1997 by the current owner, the farm has been converted to an exclusively wildlife farm. All camp fences have been taken down and the reserve is now a single management unit. At the time of the study, the reserve supported ca. 300 springbok, 130 gemsbok, 31 ostrich, 10 red hartebeest, 10 gnu and some other small antelope species. No sport hunting is allowed, only intermittent hunting for the purpose of controlling animal numbers. A “large number” of ostriches were removed in February 2005 (not accounted for in Table 3.1) and shortly after the survey period some gemsbok and springbok were removed. The ephemeral Nossob River borders the farm to the east.

Scotties Ford

This property belongs to the Khomani San community. In 1999, this land of 38 000 ha was handed over to the Khomani San community after a successful land claim. The farm Scotties Ford (Lentlandspan) is one of the farms that formed part of the land claim settlement. The other farms are Erin, Uitkoms, Miershooppan, Bosdoring and Andriesvale. The main focus on the farm is subsistence farming with sheep, goats and cattle but on a small scale. The farm has not been stocked with wildlife. Animal numbers are unknown. Very little water is available on the farm and the main watering point is at a pan. Wood is intensively harvested from the farm and is sold to local businesses and commercial farms. The local Khomani San Council is responsible for the management of the farm. The ephemeral Molopo River borders the farm to the southeast.

Inversnaid

The current owner was a senior employee of the South African National Parks with extensive ecological knowledge of the local environment and has been the proprietor for 35 years. The 8 000 ha farm is divided into camps and supports wildlife as well as livestock (giraffe were observed). Animal numbers on the farm were not disclosed. An old main road to Kuruman used to run through the farm. The ephemeral Molopo River borders the farm to the northwest.

Patricia

This is a 10 000 ha farm that the current owner inherited from her parents. It has been family property for 50 years. Initially the primary industry was cattle ranching but this has been changed to sheep farming (ca. 1 700 ewes). The farm is subdivided into camps. A few cows are also kept as well as wildlife, including springbok and gemsbok (ca. 150). Commercial hunting is allowed. The stocking densities indicated are almost certainly an underestimate due to the commercial hunting aspect on the property and undisclosed wildlife numbers. A fire affected parts of the farm in 2002. Woodcutting is allowed on the farm. Most of the *Acacia erioloba* trees in the ephemeral Molopo River that borders the farm on the northwestern side have been killed due to unforeseen effects in controlling *Prosopis glandulosa*.

Avonds Schijn

On this 5 400 ha farm the main focus is sheep farming, although commercial hunting is also allowed. The current farmer took over ownership of the farm from his parents. The farm is divided into camps. Approximately 70 gemsbok were removed in the 2003/2004 season (accounted for in Table 3.1). The ephemeral Molopo River borders the farm to the north.

Mara

Mara is a family farm of 6 800 ha with camps dividing the farm. According to the farmer the present overgrazed state was due to milk cows being kept some years back. There is a noticeable decrease in veld condition towards the north of the farm (personal observation). It is assumed that the present

indicated stocking density is much lower than it was in the past. The farm is bordered by the ephemeral Kuruman River to the south of the farm.

Ballater

The parents of the owner of this farm were farmers but the current owner used to be school principal and did not have much farming expertise. The farm was acquired 15 years ago and is divided into camps. Hunting is allowed, although probably not commercially since the poor condition of the veld prohibits large numbers of wildlife. Gemsbok, springbok, red hartebeest and some small antelope species occur in unknown numbers. There used to be ca. 5 000 sheep on the farm but this number was reduced to ca. 1 000 at the beginning of 2004. The ephemeral Molopo River borders the farm to the north.

2.5.2 Brief description of farm range condition

Figure 2.9 to Figure 2.19 provide background information on the general veld condition of each farm included in the study. The category in which the farm was subjectively grouped with the aid of the agricultural extension officer is indicated in the top right corner. The following information is supplied for each farm:

1. Degraded land: The maps are based on the national land cover database and show different categories of land degradation. The maps were compiled from the South African National Department of Agriculture's Agricultural Geo-referenced Information System, under the Natural Resource Atlas (www.agis.agric.za). The following comment is made on the website with regard to this index: "The nature of degraded land, barren rock and erosion scars is such that they cannot be effectively shown at national scales. Considering that the general minimum mapping unit size of entries in the Land Cover database is 25 ha, the occurrences that are shown are major and are to be considered with great concern." Farms in a poor to very poor condition show clear signs of land degradation.
2. Normalized Difference Vegetation Index (NDVI): NDVI is based on mathematical calculations applied to satellite data, in this instance the NOAA-AVHRR satellite series (advanced very high-resolution radiometer instruments). The resolution is 1.1 X 1.1 km. The maps shown are composite images of annual maximum NDVI values, averaged over 17 years. The periods of highest vegetation activity are therefore shown. These maps were also obtained from the South African National Department of Agriculture's Agricultural Geo-referenced Information System, under the Natural Resource Atlas (www.agis.agric.za). The farms that have subjectively been identified as being in a poor condition have lower NDVI values.
3. EarthSat images for each of the farms from Landsat 7: Images show dune topography, pans and riverine areas. Imagery was also obtained from the South African National Department of Agriculture's Agricultural Geo-referenced Information System, under the Natural Resource Atlas

(www.agis.agric.za). The farm Ballater (Figure 2.19) shows a startling lack of dune topography compared with neighbouring farms due to the flattening of dunes denuded of vegetation for prolonged periods.

4. Photographs taken at the location of sampling sites at the time of the surveys in each of the three dunefield habitats. As veld condition decreased, perennial grass cover also decreased, while annual grass cover and shrub cover increased.

Burgershoop

Good to very good condition

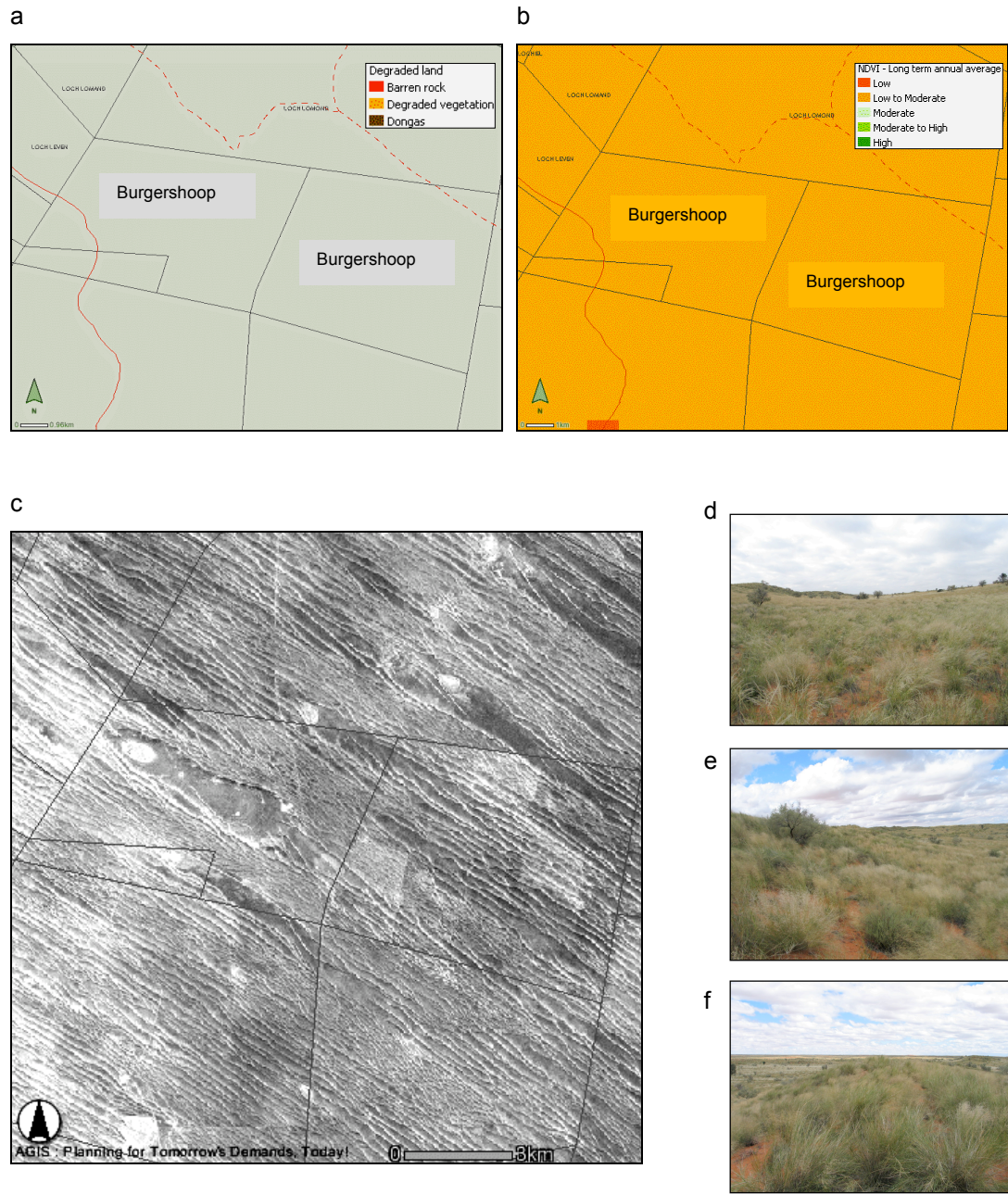


Figure 2.9 (a) Land degradation index, (b) annual Normalized Difference Vegetation Index (NDVI), (c) EarthSat image (Agricultural Geo-referenced Information System, Department of Agriculture), (d) dune street habitat, (e) dune slope habitat and (f) dune crest habitat for the farm Burgershoop.

Swartpan

Good to very good condition

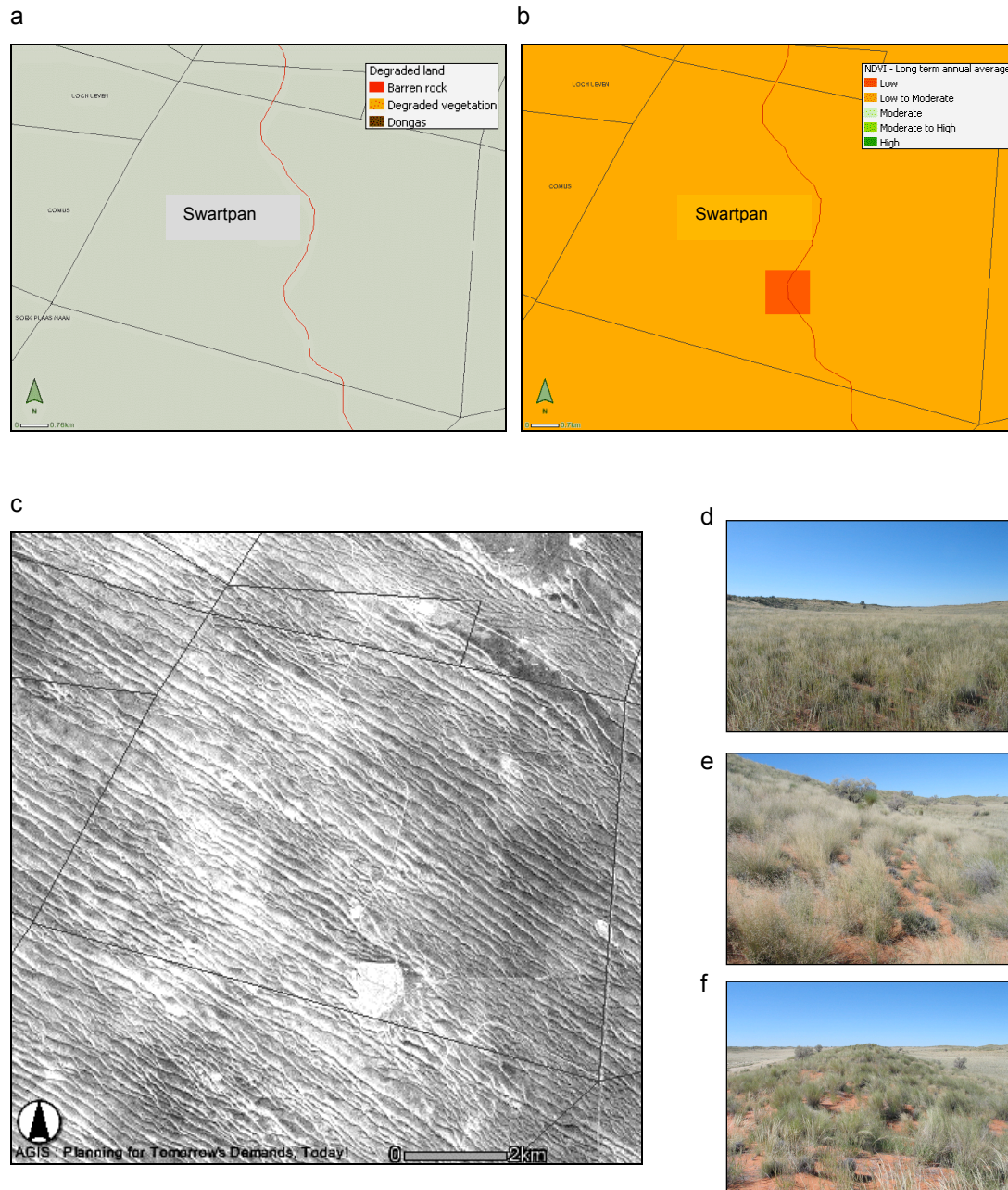


Figure 2.10 (a) Land degradation index, (b) annual Normalized Difference Vegetation Index (NDVI), (c) EarthSat image (Agricultural Geo-referenced Information System, Department of Agriculture), (d) dune street habitat, (e) dune slope habitat and (f) dune crest habitat for the farm Swartpan.

Five Dunes

Good to very good condition

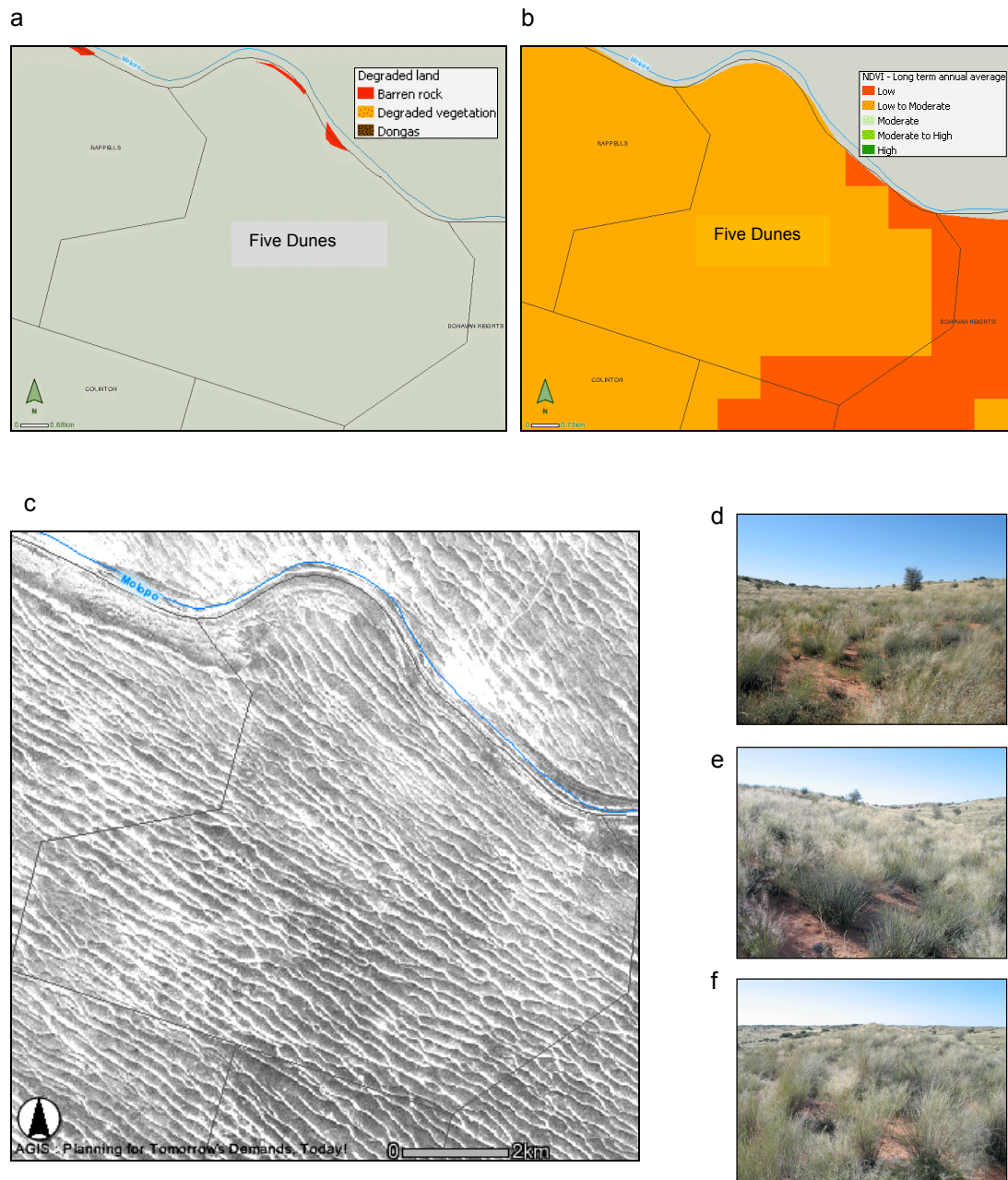


Figure 2.11 (a) Land degradation index, (b) annual Normalized Difference Vegetation Index (NDVI), (c) EarthSat image (Agricultural Geo-referenced Information System, Department of Agriculture), (d) dune street habitat, (e) dune slope habitat and (f) dune crest habitat for the farm Five Dunes.

Eersterus

Good to very good condition

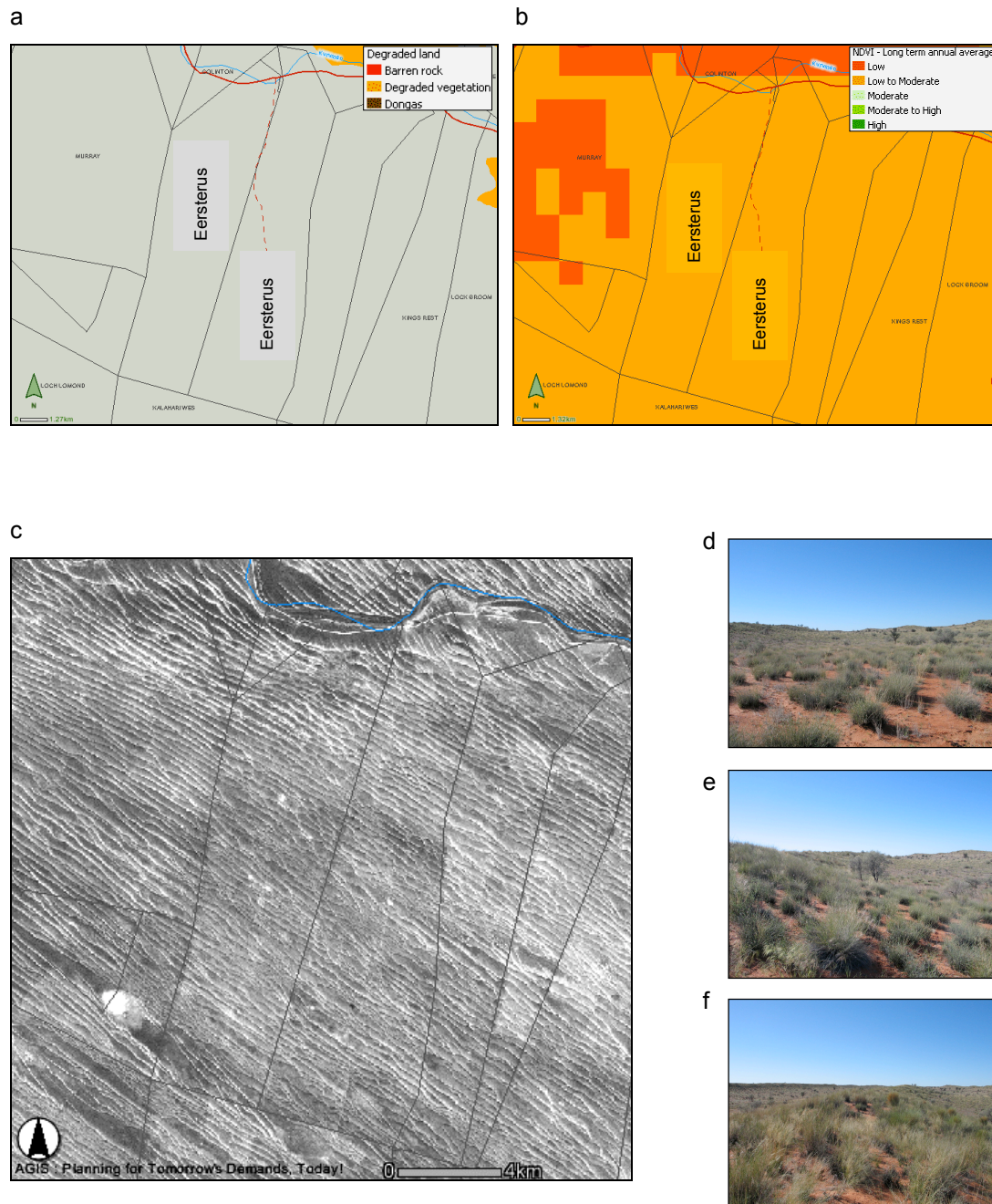


Figure 2.12 (a) Land degradation index, (b) annual Normalized Difference Vegetation Index (NDVI), (c) EarthSat image (Agricultural Geo-referenced Information System, Department of Agriculture), (d) dune street habitat, (e) dune slope habitat and (f) dune crest habitat for the farm Eersterus.

Alpha

Above average to below average condition

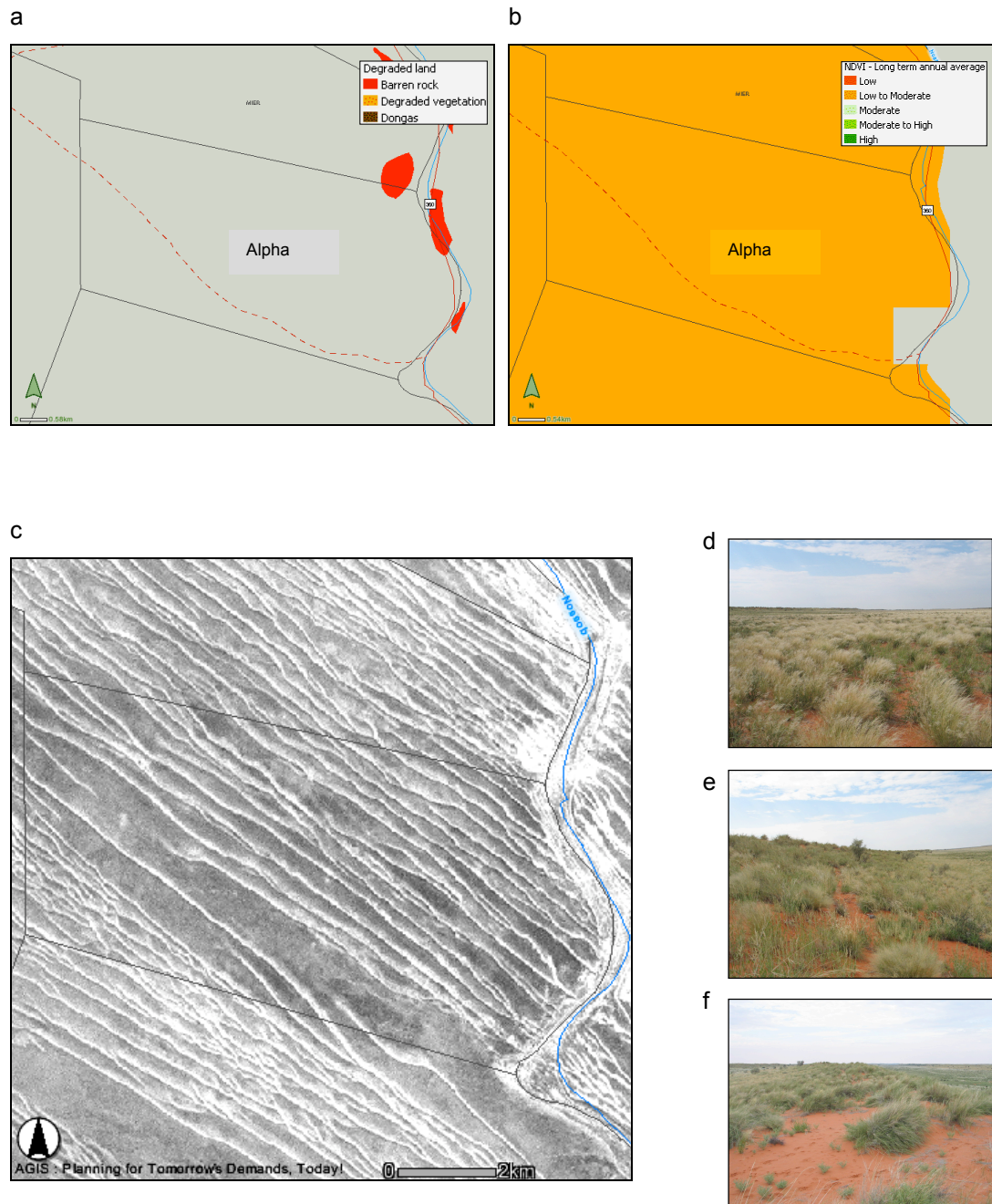


Figure 2.13 (a) Land degradation index, (b) annual Normalized Difference Vegetation Index (NDVI), (c) EarthSat image (Agricultural Geo-referenced Information System, Department of Agriculture), (d) dune street habitat, (e) dune slope habitat and (f) dune crest habitat for the farm Alpha.

Scotties Ford

Above average to below average condition

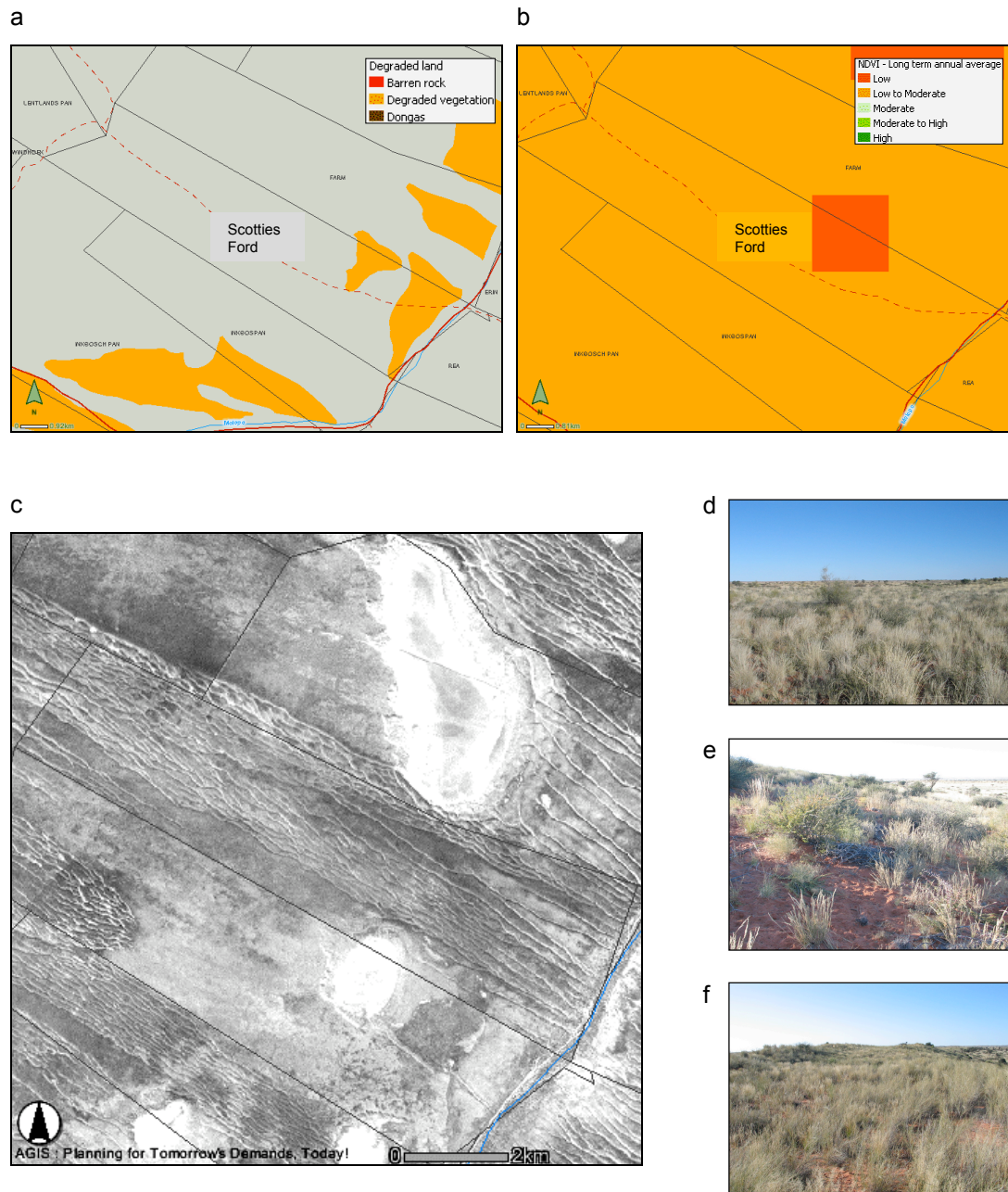


Figure 2.14 (a) Land degradation index, (b) annual Normalized Difference Vegetation Index (NDVI), (c) EarthSat image (Agricultural Geo-referenced Information System, Department of Agriculture), (d) dune street habitat, (e) dune slope habitat and (f) dune crest habitat for the farm Scotties Ford.

Inversnaid

Above average to below average condition

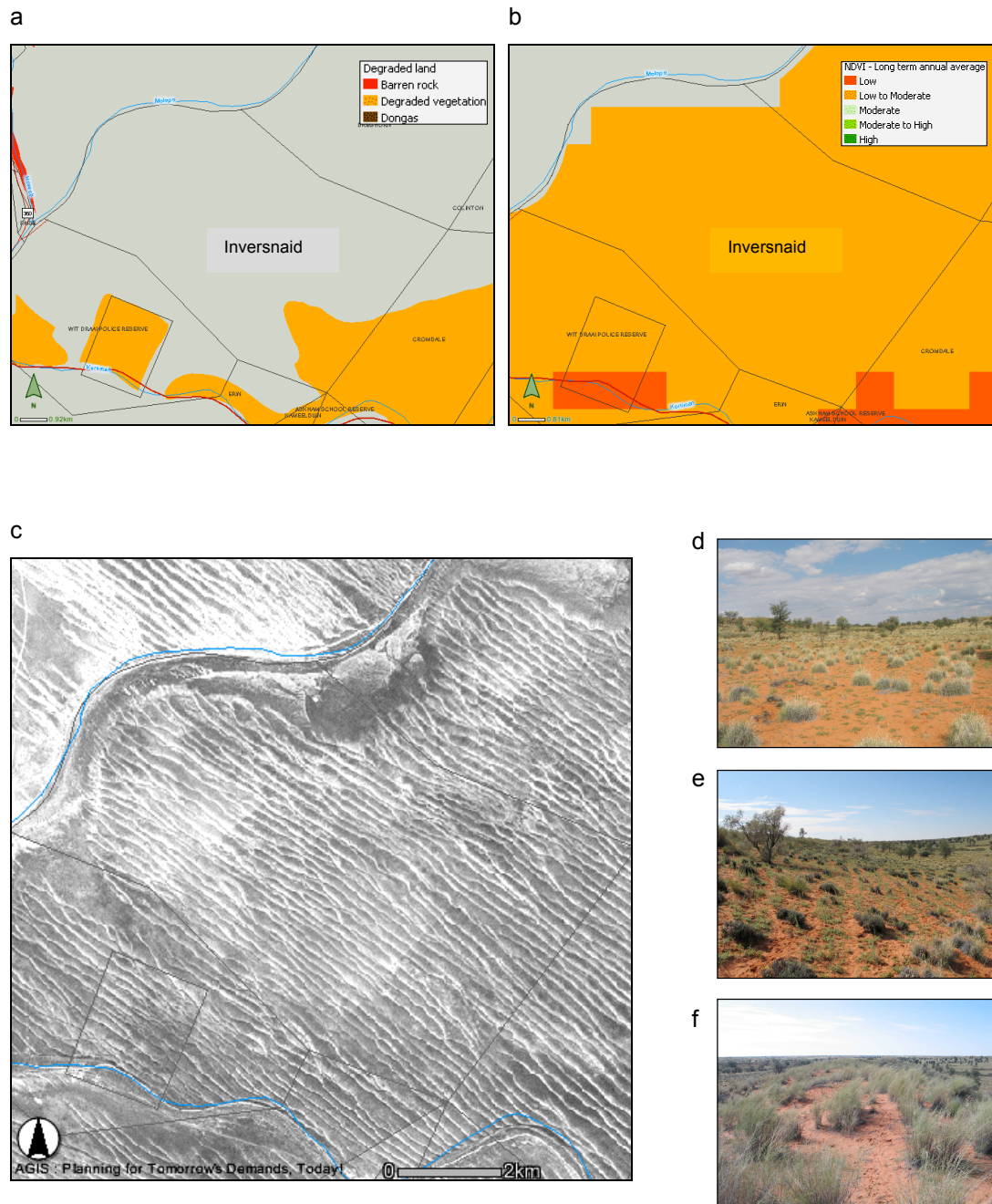


Figure 2.15 (a) Land degradation index, (b) annual Normalized Difference Vegetation Index (NDVI), (c) EarthSat image (Agricultural Geo-referenced Information System, Department of Agriculture), (d) dune street habitat, (e) dune slope habitat and (f) dune crest habitat for the farm Inversnaid.

Patricia

Above average to below average condition

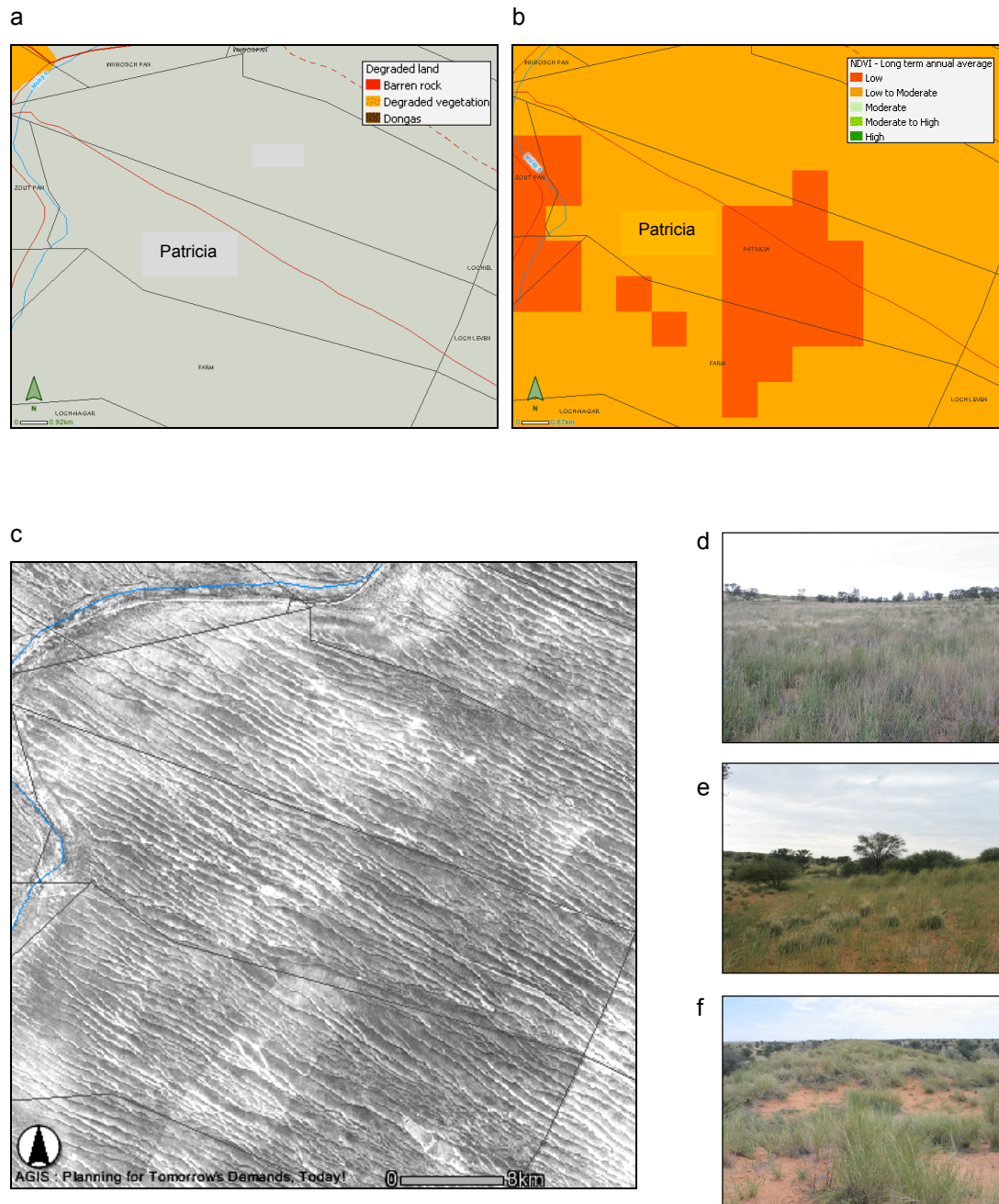


Figure 2.16 (a) Land degradation index, (b) annual Normalized Difference Vegetation Index (NDVI), (c) EarthSat image (Agricultural Geo-referenced Information System, Department of Agriculture), (d) dune street habitat, (e) dune slope habitat and (f) dune crest habitat for the farm Patricia.

Avonds Schijn

Poor to very poor condition

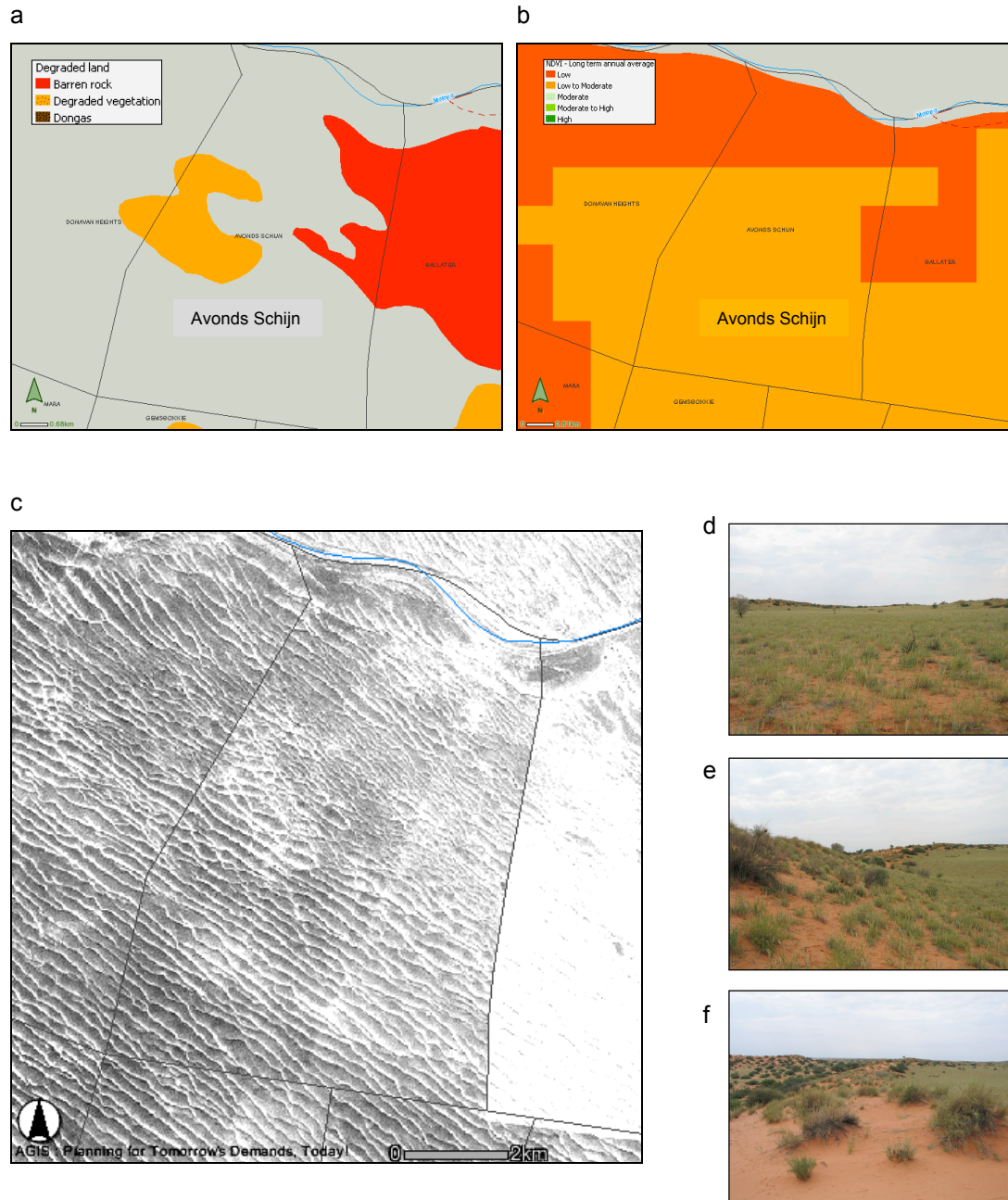


Figure 2.17 (a) Land degradation index, (b) annual Normalized Difference Vegetation Index (NDVI), (c) EarthSat image (Agricultural Geo-referenced Information System, Department of Agriculture), (d) dune street habitat, (e) dune slope habitat and (f) dune crest habitat for the farm Avonds Schijn.

Mara

Poor to very poor condition

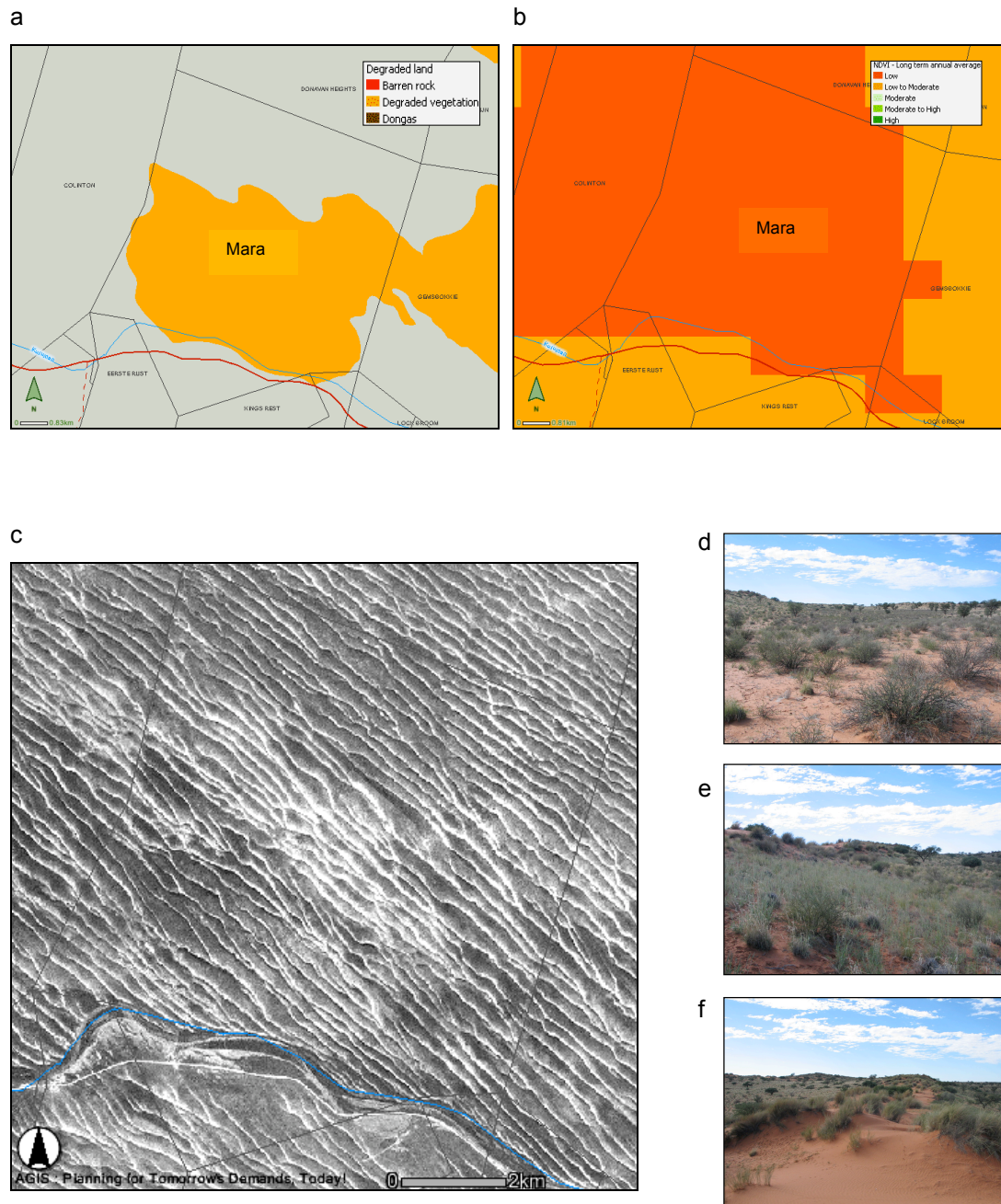


Figure 2.18 (a) Land degradation index, (b) annual Normalized Difference Vegetation Index (NDVI), (c) EarthSat image (Agricultural Geo-referenced Information System, Department of Agriculture), (d) dune street habitat, (e) dune slope habitat and (f) dune crest habitat for the farm Mara.

Ballater

Poor to very poor condition

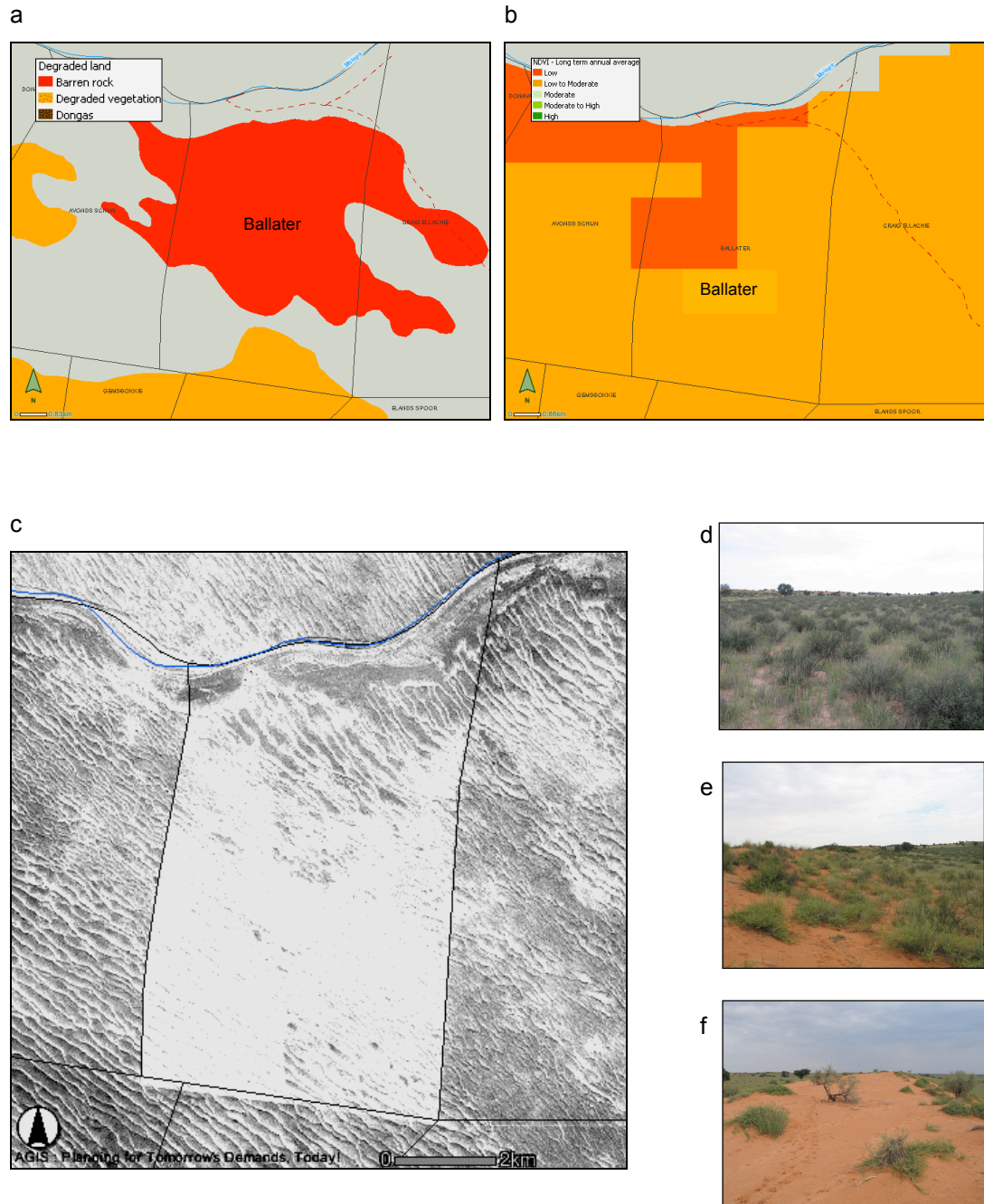


Figure 2.19 (a) Land degradation index, (b) annual Normalized Difference Vegetation Index (NDVI), (c) EarthSat image (Agricultural Geo-referenced Information System, Department of Agriculture), (d) dune street habitat, (e) dune slope habitat and (f) dune crest habitat for the farm Ballater.

Chapter 3

Materials and methods

3.1 Survey procedure

Only dunefield habitats were considered for inclusion in this study. That means sampling was confined to the dune street, dune slope and dune crest habitats (Figure 3.1), but calcrete cliffs, rivers and pans were excluded. In most cases the sampling sites were at least 1 km from the closest watering point in order to limit any possible anomalies in vegetation composition due to localized intense grazing or trampling. Homesteads were often erected close to seasonal rivers and livestock were kept in the vicinity of this potential water source. No sampling was therefore done within *ca.* 3 kilometers of the rivers.

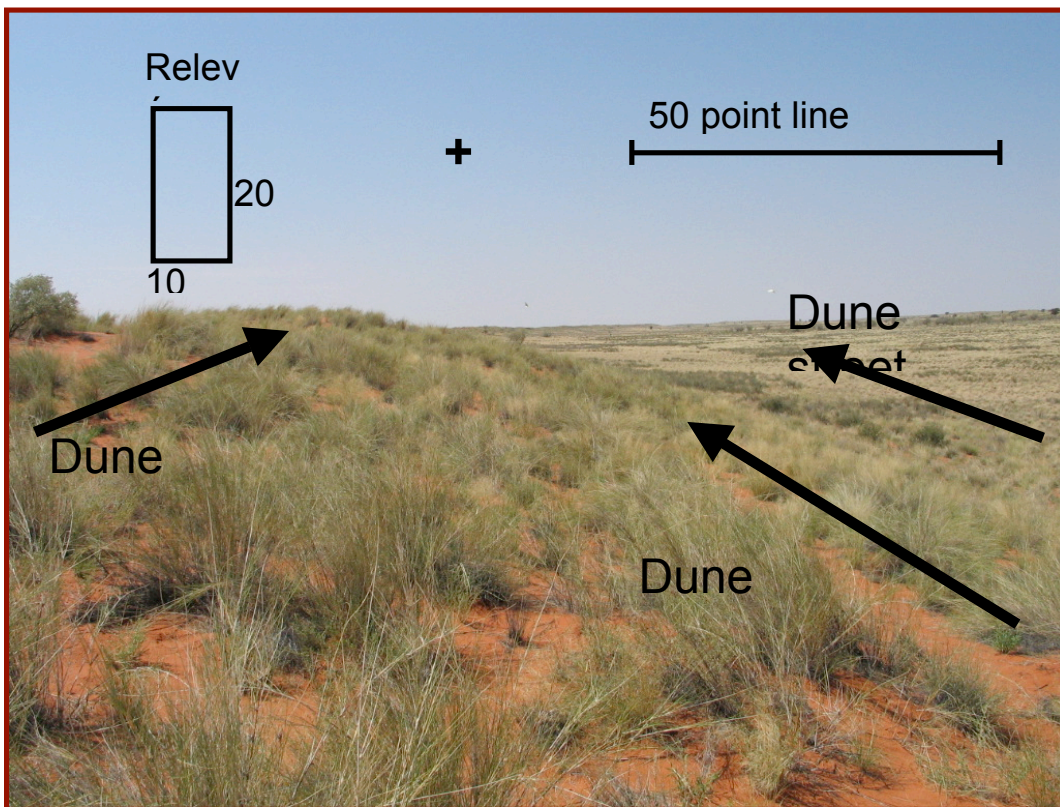


Figure 3.1 Diagram illustrating the survey layout for each of the study sites. One 10 m x 20 m plot and one 50 point line transect were used for each of the dune crest, dune slope and dune street habitats. This method was repeated on two more localities on each of the farms, therefore in total, there are 9 sample sites per farm.

Three sites were identified on each of the farms for sampling, with one sample taken at each of these sites of the dune street, dune slope and dune crest habitats. In some instances, specifically on the farm Ballater, the dunes have been denuded of vegetation to such a degree and for such a period of time that the dunes have been flattened and also lowered a great deal, which made it difficult to delimit the dune slope habitat. Thus, in total there were nine samples for each farm. On each of the nine sampling sites a 10 m x 20 m Braun-Blanquet type survey was conducted as well as a 50-point (75 m) line transect. The line transect was a wheel-point survey (Mentis, 1981) with the closest annual and perennial plant species recorded at 1.5 m intervals. The wheel-point survey was not conducted to determine basal cover.

The cover-abundance of each species within the plot was estimated according to the following scale:

r	≤1% cover; comprising of one individual only;
+	≤1% cover; comprising of more than one individual;
1	>1 – 5% cover;
2a	>5 – 15% cover;
2b	>15 – 25% cover;
3	>25 – 50% cover;
4	>50 – 75% cover and
5	>75 – 100% cover

At each sampling site the following environmental data were also recorded (see the field survey sheets in Appendix A for categories):

- Aspect
- Distance from nearest watering point
- Fire evidence
- Slope
- Soil type
- Bush encroachment
- Grazing intensity/evidence
- Browsing intensity/evidence
- Trampling
- Wood cutting

3.2 Data analysis

The following data analyses were performed:

- Composite vegetation cover was calculated for each of the relevés. This cover is calculated by summing the mid-values of the Braun-Blanquet scores for each of the species.
- Composite vegetation cover was calculated for different life forms and growth forms.
- Shannon-Wiener index of species diversity (Zar, 1984) was calculated for each of the habitat types on each of the farms as well as for the farm as a whole.
- Species richness was calculated for each of the habitat types on each of the farms as well as for the farm as a whole.
- Floristic data were subjected to a correspondence analysis in the software program CANOCO 4.5 (Wageningen, The Netherlands).

Detailed descriptions of the analysis procedures can be found in Chapter 4.

3.3 Functional analysis

3.3.1 Trait selection

The results from a number of papers were tabulated (Table 3.2) to search for traits that have been shown to exhibit either a negative or a positive response to grazing disturbance and at times land-use (e.g. tilling, cutting) (Fernandez-Gimenez & Allan-Diaz, 1999; Hadar *et al.*, 1999; Lavorel *et al.*, 1999; Landsberg *et al.*, 1999; Diaz *et al.*, 2001; Kahmen *et al.*, 2002; Jauffret & Lavorel, 2003; Veski *et al.*, 2004).

The traits in Table 3.2 changed either negatively or positively in response to grazing. Not all of the traits listed in Table 3.2 were included in the study. Plasticity of aboveground cover density, taxonomy (monocot/dicot), leaf width, plasticity under grazing and regrowth potential under grazing were not selected. However, several additional traits were included which were thought to be important to a grazing response. The traits investigated are listed below and traits in italics are those listed in Table 3.2 with their synonyms or proxies listed in brackets following each trait.

- **Morphological traits:** *plant height*, *canopy diameter (lateral spread/canopy structure)*, canopy density, *Raunkier life form*, *life span (life history/dormancy)*, *shoot architecture (growth form/habit/canopy structure/lateral spread)*, stem density, stem spinescence, leaf spinescence, *leaf area*, *specific leaf area*, *leaf dry matter content (leaf mass)*, leaf colour, leaf

angle, adaxial leaf hairiness, abaxial leaf hairiness, *leaf consistency (leaf toughness)*, leaf longevity, leaf type, leaf shape, leaf margin.

- **Regenerative traits:** organs shed, *clonality (runners)*, response to fire, *germination phenology (seasonality of germination)*, growth phenology, *flowering phenology (timing of flowering)*, fruiting phenology, pollination mode, plant and flower gender, *inflorescence prominence (inflorescence position)*, inflorescence type, flower shape, flower colour, number of seed per fruit, *seed mass class*, *fruit type (seed dispersal aids)*, *diaspore morphology (seed dispersal aids)*, *telechory (main dispersal agent)*, antitelechory, *fecundity*, *seed dormancy*, seed bank type.
- **Physiological traits:** trophic type, photosynthetic pathway, *leaf/stem surface exudates (leaf coating)*, carbohydrate storage.
- **Other:** Family, *palatability to livestock*, sociability, ecological status.

The family that a species belongs to was noted, but not included in the final analysis to emphasize trait linkages and not pre-empt taxonomic associations. Detailed descriptions of the trait categories can be seen in Appendix C.

An element of practicality limited the trait pool selection because it is preferable to use traits that are easily quantified or referenced. It is also preferable to include traits that have direct relevance to plant disturbance response such as photosynthetic rate and competitive ability. Due to the difficulty, costs and time consuming nature of measuring or quantifying such traits it is necessary to use surrogate traits such as specific leaf area (for photosynthetic rate) or plant height (for competitive ability) (McIntyre *et al.*, 1999a).

A selection of 112 common Kalahari plant species was investigated for the functional analysis. The species represent a wide spectrum of the growth forms and life forms found in the Kalahari. The sampling guidelines as found in Cornelissen *et al.* (2003) were followed. Field based analyses were performed for some of the 112 species for the following traits: plant height, canopy width, leaf area, specific leaf area (SLA), leaf dry matter content and seed mass.

For species for which no field based analyses were performed, traits were scored according to literature and herbarium specimen information (H.G.W.J. Schweickerdt Herbarium, PRE, University of Pretoria). All of the remaining traits not mentioned above for the plant species were also investigated through literature searches and herbarium specimens.

Table 3.2 Summary of traits that show a response to either grazing or land-use such as tilling or cutting

Reference	Fernandez-Gimenez & Allen-Diaz (1999)	Hadar <i>et al.</i> (1999)	Landsberg <i>et al.</i> (1999)	Lavorel <i>et al.</i> (1999)	Diaz <i>et al.</i> (2001)	Kahmen <i>et al.</i> (2002)	Jauffret & Lavorel (2003)	Vesk <i>et al.</i> (2004)
Habitat investigated	Mongolian rangeland: desert steppe, steppe and mountain-steppe	Mediterranean woody vegetation	Arid Australian rangeland	Mediterranean grassland	Grassland of Australia and Israel	Calcareous grassland of Germany	Dwarf shrubs of dry Tunisia	Pooled data from 5 studies in dry Australian shrublands and woodlands
Plant height		√	√	√	√		√	
Life form	√	√	√					
Life history								√
Life history + plant height					√			
Habit				√				
Growth form						√		√
Canopy structure				√				
Runners (stolons/rhizomes)						√		
Lateral spread				√				
Plasticity of above-ground cover density				√				
Taxonomy (monocot/dicot)					√			
Dormancy				√				
Leaf width			√					
Leaf mass					√			
Leaf area			√		√			
Specific leaf area					√			√
Leaf toughness					√			
Leaf coating			√					
Plasticity under grazing			√					
Re-growth potential under grazing			√					
Seed mass				√		√		
Fecundity			√					
Seed dispersal aids			√					
Seed dormancy				√				
Seasonality of germination			√			√		
Main dispersal agent				√				
Palatability	√						√	
Timing of flowering		√						
Inflorescence position				√				

3.3.2 *Field based analysis methodology*

Six individuals for each species were sampled. As far as possible, only plants that were healthy, had not been grazed and that were “representative” of the species were selected. Sampling was conducted in the mornings until approximately 11:00 in order to reduce the influence of moisture loss from the leaves through transpiration. Plant height and canopy width were measured by using a tape measure and a measuring rod. Plants with a height of less than 1.5 m were measured with the measuring tape and plants with a height of more than 1.5 m with a 5 m measuring rod marked at 0.5 m intervals. Two canopy width measurements were taken at right angles to each other and the mean calculated. Plant parts were harvested after the plant height and canopy width measurements had been taken and immediately placed in Zip-lock plastic bags. The bags were put into a portable cooler with ice blocks for temporary cold storage. Where possible, whole branches were cut and not individual leaves and the individual leaves removed later for leaf measurements.

At base camp the bags containing the samples were removed individually for analysis. Ten leaves per plant specimen were removed, cleaned, excess moisture removed and then weighed with a Precisa XB 160M balance (Precisa Gravimetrics A.G., Dietekom, Switzerland). The leaves were then arranged on a white board and covered with a transparent Perspex cover to spread the leaves flat on the board. A photograph was taken of the leaves together with a ruler as calibration reference (Figure 3.2a) with either a Nikon COOLPIX 950 or Canon Powershot digital camera. The leaves were then removed and placed into paper bags to air dry and were kept in this manner until further drying at the University of Pretoria. This was done by placing the bags with the leaves in a drying oven for 48 hours at 60°C. After removal from the drying oven each sample was weighed.

The photographs of the leaves were edited with Adobe Photoshop Elements version 2.0 (Figure 3.2b). This was necessary to remove grime and grit from the images as well as shadows around the leaves that could affect measurement. Leaf area measurements were conducted with the program Image Tool for Windows version 3.00 (Copyright 1995-2002, The University of Texas Health Science Center in San Antonio).

Seeds were collected in the field and weighed at the University of Pretoria on a Mettler AJ 100 balance (American Instrument Exchange, Toledo, U.S.A.) with four decimals of a gram capability. The seeds were not dried artificially. Seeds were weighed in batches that ranged from 10 to 100 seeds per batch depending on the size of the seed and then a mean seed mass calculated. Additional seed mass data were supplied by Anne Kraemer (University of Regensburg) for

Dicoma capensis, *Eragrostis trichophora*, *Plinthus sericeus* and *Sericorema remotiflora* and by Martijn Kos (University of Regensburg) for *Boscia albitrunca*.

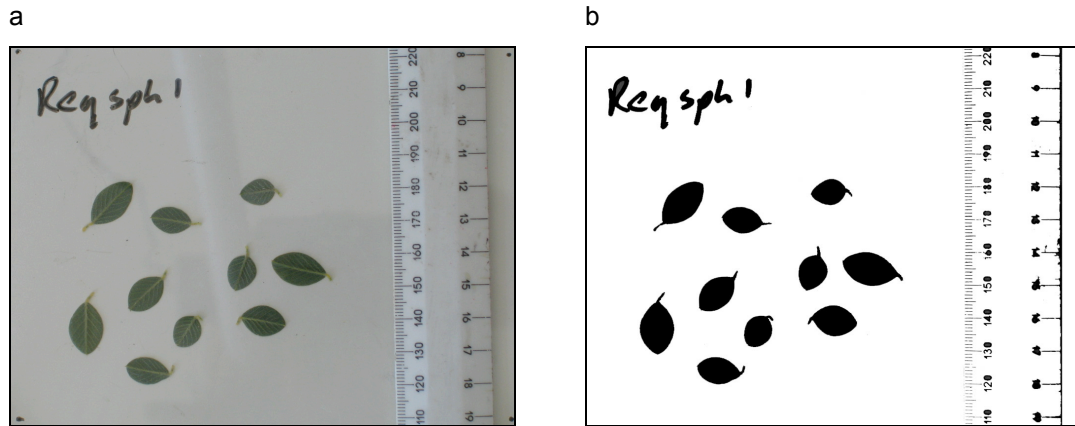


Figure 3.13 Examples of photographs of the leaves of *Requieria sphaerosperma*, (a) before editing, (b) after editing with Adobe Photoshop Elements version 2.0.

3.3.3 Data analysis

Species trait data were analyzed by performing multivariate analyses (Principal coordinates analysis) with the program Syntax (Podani, 2000) on selected species or trait sets. Product-Moment correlation matrices were constructed with the statistical program STATISTICA version 8.0 (Copyright 1984-2007, StatSoft Inc, U.S.A.). A more comprehensive description of analytical procedures is provided in Chapter 5.

Chapter 4

Changes in floristic and life form composition in dunefield vegetation along a grazing gradient on private and communal land in the southern Kalahari

Abstract

The southern Kalahari is an arid region characterised by unreliable rainfall and fodder shortages. Artificial water provision has increased the impact that livestock ranching has on the dunefield vegetation. An analysis was conducted on the floristic data of 10 commercial and one communal farm that differed in their history of land-use intensity. A range condition analysis showed that the farms represented a grazing gradient with farms representative of poor, intermediate and good range condition. Canonical correspondence analyses were conducted of floristic and environmental variables to determine range condition relationships with environmental parameters. Of the three dunefield habitats, the dune street habitat was identified as the most vulnerable to overgrazing followed by the dune slope and dune crest habitats. A reduction in cumulative cover and an increase in bare surface cover indicated increased grazing pressure in the dune crest habitat. In the dune streets shrub cover and annual grass cover increased when veld was overgrazed. Species richness was marginally significantly correlated with the range condition gradient in the dune crest ($p=0.050$) and dune street ($p=0.042$) habitats. Shannon-Wiener diversity correlated significantly with range condition in the dune slope ($p=0.35$) and dune street ($p=0.016$) habitats as well as all habitats cumulatively ($p=0.035$).

4.1 Introduction

The Kalahari is an arid region (see Chapter 2, Figure 2.3). Due to the lack of surface water and large traveling distances, European settlement in the region started only relatively recently. The first title deeds for farms in the southern Kalahari for European settlers were issued in 1893, and by 1926 farms had been established along the dry riverbeds and some pans (Leistner, 1967). The low livestock production capacity of the region was reported by several investigators (Leistner, 1967). Since the establishment of boreholes, however, the lack of water as prime deterrent for livestock production has to some degree been overcome, resulting in an increase in human and livestock populations (Bergstrom & Skarpe, 1999).

The Savanna Biome encompasses 32.5% of the terrestrial surface area of South Africa, Lesotho and Swaziland and the Kalahari Duneveld Bioregion subdivision comprises approximately 10.6% of the Savanna Biome (Mucina *et al.*, 2005). This study centered mostly on the Gordonia Duneveld vegetation unit of the Kalahari Duneveld Bioregion, and 14.2% of this unit is currently protected through the Kgalagadi Transfrontier Park to the north of the study area. In spite of the relatively infertile soils and the low, unpredictable annual rainfall large tracts of land are used for animal production. These production systems range from subsistence livestock farming to commercial operations that focus on small livestock (predominantly sheep) to wildlife ranching. Almost all livestock farms, communal and privately-owned, also have a complement of wildlife (see Chapter 3).

The susceptibility of the vegetation of the Kalahari to overgrazing can be attributed to the low production capacity (biomass production) and slow recovery potential of the system due to low nutrient levels and low annual rainfall (Fourie *et al.*, 1987; Perkins & Thomas, 1993). The occurrence of periods of abundant grazing during periods of good rainfall are often accompanied by a concomitant increase in livestock and wildlife numbers. Increases in livestock or wildlife numbers cause a reduction in the abundance of palatable plant species because these species are preferentially grazed and are effectively outcompeted by less palatable annual and perennial species (Leistner, 1967; Fourie *et al.*, 1987; Skarpe, 1991b; Van Rooyen *et al.*, 1991). Less palatable species that become common include perennial herbs such as *Hermannia tomentosa* and annuals such as *Acrotome inflata* as well as less desirable grass species such as *Aristida meridionalis*. Under intense utilization the common but mostly unpalatable annual Kalahari grass *Schmidtia kalahariensis* also increases in dominance (Thomas *et al.* 2000; Du Toit, 2001, 2002), with an overall decrease in vegetation cover (Skarpe, 1991b). In the Kalahari Thornveld it has been observed that after the removal of encroaching shrubs there is a sudden eruption into subclimax grass species (e.g. *Eragrostis lehmanniana*) and climax grass species (e.g.

Stipagrostis ciliata and *S. obtusa*) (Du Toit, 2002). This observation has been interpreted that Kalahari succession lacks a definite pioneer stage (Du Toit, 2002). However, such a rapid recovery may depend on the presence of an intact seed bank, the length of the period of the encroached state or management history, the severity of grazing following clearing and the specific dune veld habitat.

Overgrazing has been shown to be associated with an increase in the shrubby component (Leistner, 1967; Skarpe, 1990a, 1990b, 1991a, 1991b, Perkins & Thomas, 1993; Jeltsch *et al.*, 1996, 1997; Thomas *et al.*, 2000; Weber *et al.*, 2000; Du Toit, 2002). The removal of grasses through intensive grazing leads to increased soil moisture in the deeper soil layers, a stratum reserved for shrubs and trees (Skarpe, 1991a, 1991b, 1992). In combination with a reduction in the flammable biomass load which aids fewer and less intensive shrub suppressing fire events, this leads to shrubs dominating the grass layer (Skarpe, 1991a) with bush encroachment as outcome.

Some species such as *Acacia mellifera*, *Rhigozum trichotomum*, *Acacia hebeclada*, *Dichrostachys cinerea*, *Prosopis glandulosa* and *Grewia flava* are regularly associated with bush encroachment whereas certain palatable shrubs or small trees such as *Boscia albitrunca* and *Lycium* species may decrease with overgrazing (Kalikawe, 1990; Skarpe 1990b; Skarpe *et al.*, 2007). Skarpe (1990a) showed that palatable species such as *B. albitrunca* and *G. flava* may initially increase under increased utilization pressure but will drastically decrease as the utilization pressure increases. Heavily grazed areas also have a larger proportion of bare ground than areas under lower utilization (Skarpe, 1991b). It has been postulated that the encroaching *Acacia* species such as *A. mellifera* are more proliferate than the non-encroaching species because they have a shallower root system (Leistner, 1967) with access to nitrogen fixing *Rhizobium* in the topsoil (Skarpe, 1990b).

Attributing the grass-woody layer interaction mainly to soil moisture and root niche separation has however recently been refuted by observations that include woody encroachment in the absence of overgrazing (Anderson, 1856 quoted in Wiegand *et al.*, 2006), the independence of *P. glandulosa* recruitment from herbaceous biomass (Brown & Archer, 1999), the greater germination sensitivity of *A. mellifera* to rainfall rather than grazing (Kraaij & Ward, 2006) and observations of encroachment on soils too shallow for root separation (Wiegand *et al.*, 2005). It has also been hypothesized that increases in global CO₂ levels impart performance superiority to shrubs over grasses through (a) favouring of C₃ metabolism (shrubs) over C₄ metabolism (grass) species, (b) reduced transpiration of grasses causing better moisture infiltration into lower soil strata, (c) greater shrub growth rates leading to faster escape from the grass layer and (d)

investment of shrubs in defense mechanisms such as tannins which grasses do not have (Bond & Midgley, 2000; Ward & Young, 2002; Wiegand *et al.*, 2006). Shrub defense mechanisms may however not be directly linked with global CO₂ levels, but rather exist as passive, inherent traits of the growth form group.

Scholes and Walker (1993) ascribes savanna structure to two primary determinants, water supply and nutrient cycling and two secondary determinants, fire and herbivory. Woody species' germination is dependent on sufficient and sustained rainfall events with subsequent high soil moisture content, as well as available open savanna (no canopy suppression by grasses, trees or shrubs) for reduced competition (Wiegand *et al.*, 2006). The patchiness of rainfall in the savannas leads to patchy incidence of woody encroachment. The regular spatial separation and size class distribution of woody plants of a species in an encroached site has been proposed by the honeycomb rippling model of Wiegand *et al.* (2006) which relies on concentric, iterative seedling competition and death together with regular ratios between canopy and root extent of approximately 1:10. The regularity of woody plant spacing increases and becomes less clustered as shrubs grow (Meyer *et al.*, 2008). This model proposes woody plant encroachment as a natural recruitment process that does not require fire or overgrazing and in which three states may be observed in savannas: (a) woody plant encroachment, (b) mature stands of woody plants and (c) grassy stands.

In tree population dynamics recruitment (seedling emergence and growth) can be a bottleneck due to environmental and competition factors ("Demographic bottleneck model" in Sankaran *et al.*, 2004). High soil moisture affects tree recruitment by positively influencing grass biomass (fuel load) and negatively influencing grass flammability (Wiegand *et al.*, 2006), while grazing influences the bottleneck by reducing grass biomass and competition from grasses and altering the fire regime (Augustine & McNaughton, 2004; Wiegand *et al.*, 2006). Fire and grazing can therefore be viewed as "buffers" of savannas keeping them in a state of disequilibrium and away from extreme states (Jeltsch *et al.*, 2000). In a large scale view of African savannas, mean annual precipitation has been shown to be strongly linked with degree of woody cover and areas with less than ~650 mm rainfall per annum are climatically driven, with moisture as the primary determinant of woody cover extent (Sankaran *et al.*, 2005). In areas with less than ~350 mm per annum (e.g. the Kalahari) woody cover is low and herbivory and grazing disturbance is not deemed as regulatory agents of woody cover, although Kalahari sands which are generally relatively nutrient poor, may support high woody cover due to good moisture infiltration and good water holding capacity (Sankaran *et al.*, 2005). This good water holding capacity together with erratic rainfall in which rainfall of 700 mm per annum is possible in the southern Kalahari (Van

Rooyen & Van Rooyen, 1998) and herbivore species composition (Skarpe *et al.*, 2007) may lead to a greater influence on woody cover by grazing or fire.

The intention in selecting the specific study sites for this survey was not to produce a representative description of the regional vegetation and the various savanna states. The underlying motive was to produce a degradation gradient, ranging from farms in a poor, overgrazed condition to farms that are sustainably utilized and in good condition. The objectives of this part of the study were the following:

- Analyse and compare the floristic and life form composition along the degradation gradient.
- Analyse and compare life from cover, cumulative vegetation cover and cover of selected species along the degradation gradient.
- Analyse and compare the species richness and the Shannon-Wiener index of diversity along the degradation gradient.

4.2 Materials and methods

Three representative sites were subjectively selected on each farm and vegetation surveys were conducted in the dune crest, dune slope and dune street habitat types at each site. Both Braun-Blanquet and line transect surveys were conducted in each habitat type. A complete description of the survey outlay is provided in Chapter 3.

4.2.1 Range condition

The range condition for each farm was calculated by following the method of Bothma *et al.* (2004). The method involves calculating the frequencies of the grass and forb species of the line transects on each farm. The line transects provided a 450 point total for each farm and were based on the absolute nearest grass or forb species recorded at each sampling point. Species were classified according to their ecological status in order to obtain an estimate of the relative range (veld) condition of each farm. Two sources were used to determine the ecological status of Kalahari grass species, Van Oudtshoorn (2004) and Van Rooyen *et al.* (1991). Table 4.1 provides an explanation of the two different classification systems used by the authors.

The classification of Van Rooyen *et al.* (1991) is mostly based on Kalahari grass species, but also includes a selection of other growth forms such as forbs, shrubs and trees. The Van Oudtshoorn (2004) classification refers to grasses and includes most grass species of South Africa. Some species with wide distribution ranges are known to react differently to grazing pressure in different

regions. The system of Van Rooyen *et al.* (1991) considers more factors in the ecological assessment, such as productivity and resprouting ability. The final ecological status selected is based on a combination of the two sources together with personal experience. The categories assigned to grass species recorded in the line transect surveys on the farms are shown in Table 4.2.

The categories assigned to forb species (Table 4.3) were based on general species information and personal experience, since none of these species were evaluated in Van Rooyen *et al.* (1991). In the absence of information on palatability, nutrient content and production capacity, all the forb species were assigned an ecological status of Category 5. To determine a range condition score for each farm the percentage contribution of each category in the line transect was calculated. The percentages were then weighted by scores assigned to each category in the following manner:

Category 1:	10
Category 2:	7
Category 3:	5
Category 4:	4
Category 5:	1

The highest possible range condition score is 1000, if all point observations were species of Category 1 (score of 10).

Table 4.1 Two different classification systems used to assess the ecological status of Kalahari grass species (Van Rooyen *et al.*, 1991; Van Oudtshoorn, 2004)

Van Oudtshoorn (2004)	Ecological status	Ecological status	Bothma <i>et al.</i> (2004)
Description	Ecological status	Ecological status	Description
Abundant in good veld. Decrease when veld is overgrazed or undergrazed. Palatable, climax grass species.	Decreaser	Category 1	Valuable and palatable tufted or stoloniferous grass species with a high productivity and high grazing value.
Abundant in underutilized veld. Unpalatable, robust climax grass species.	Increaser 1	Category 2	Tufted, perennial grass species with an intermediate productivity and moderate grazing value.
Abundant in overgrazed veld. Pioneer and subclimax grass species.	Increaser 2	Category 3	Tufted, tall, perennial grass species with a high productivity but a low grazing value.
		Category 4	Unpalatable, annual and perennial, tufted and stoloniferous grass species with an intermediate productivity and low grazing value.
Common in overgrazed veld. Unpalatable, densely tufted climax grass species. Outcompete palatable grass species.	Increaser 3	Category 5 (Encroacher species)	Unpalatable, annual grass and forb species with a low productivity and low grazing value.

Table 4.2 Ecological status assigned to Kalahari grass species according to Van Oudtshoorn (2004) and Van Rooyen *et al.* (1991) and the ecological status selected for this study

Grass species	Van Oudtshoorn (2004)	Van Rooyen <i>et al.</i> (1991)	Ecological status selected
<i>Aristida adscensionis</i>	Increaser 2	Category 1	Category 3
<i>Aristida meridionalis</i>	Increaser 3	Category 1	Category 3
<i>Centropodia glauca</i>	Decreaser	Category 2	Category 1
<i>Eragrostis lehmanniana</i>	Increaser 2	Category 2	Category 2
<i>Eragrostis trichophora</i>	Increaser 2	Status not given	Category 3
<i>Schmidtia kalahariensis</i>	Increaser 2	Category 4	Category 4
<i>Stipagrostis amabilis</i>	Status not given	Category 3	Category 2 [†]
<i>Stipagrostis ciliata</i>	Decreaser	Category 1	Category 1
<i>Stipagrostis obtusa</i>	Decreaser	Category 1	Category 1
<i>Stipagrostis uniplumis</i>	Increaser 2	Category 1	Category 3

[†] Personal communication: N. Van Rooyen (University of Pretoria, Pretoria)

4.2.2 Ordinations of vegetation and habitat variables

A correspondence analysis (CA) with CANOCO 4.5 (Microcomputer Power, Ithaca, New York) of the floristic data was performed to investigate the relationships between species composition of different farms and of different habitats. A canonical correspondence analysis (CCA) was performed on the floristic and environmental data for each of the dune crest, dune slope and dune street habitats. The aim was to investigate whether the degradation gradient was evident from the ordination and which factors characterized the gradient. The ordination results were compared with the range condition assessment to investigate whether the two analyses produced similar trends.

In the ordination graphs black arrows, representing habitat variables, denote the direction of the change and the length of the arrow denotes the degree of change of the variable. The angle between variables indicates the association between the variables. Small angles between variables (arrows point in the same direction) correspond to a positive relationship, right angles to no relationship and large angles (approaching 180°, pointing in opposite directions) to negative relationships.

4.2.3 Cumulative total vegetation cover and cumulative life form / growth form cover

Cumulative vegetation cover was calculated by summing the Braun-Blanquet scores for species in a relevé. The value used in these calculations was the midpoint of a Braun-Blanquet category range. For example, if a species scored within the range 6–15% cover in a relevé, the value used in determining cumulative cover for the relevé was 10.5%. It should be noted that cumulative

vegetation cover is not equivalent to total vegetation cover because of the overlap that may occur between the canopies of plants in a relevé.

The cumulative cover for the following life form / growth form categories was calculated: tree, shrub, dwarf shrub, perennial grass, annual grass, perennial herb and annual herb. The percentage bare surface area was compared with life form / growth form cumulative cover.

4.2.4 Species richness and species diversity using the Shannon-Wiener index of diversity

Mean species richness was calculated for each habitat type on a farm. For example, the mean species richness for the dune crest habitat on a farm was calculated by taking the mean of the species richness values for each of the three dune crest relevés on a farm. The species richness and species diversity were compared across the grazing gradient.

The Shannon-Wiener index of diversity combines species richness with abundance to provide an index that offsets the fact that some areas may be species rich, but that most of the species are rare. In this instance Shannon-Wiener species diversity was calculated by cover (Krebs, 1999):

$$H' = -\sum_{i=1}^s p_i \ln p_i$$

where, s = the number of species
 p_i = the cover of the i th species expressed as a proportion of total cover
 ln = log base_e

4.2.5 Statistical analysis

The relationships between the range condition score and species richness, Shannon-Wiener diversity, cumulative cover, on-site grazing and utilization indicators, life/growth form cover and bare surface cover were analyzed in STATISTICA (StatSoft, Inc., Tulsa, U.S.A.) by means of a Pearson's Product-Moment correlation matrix.

4.3 Results

4.3.1 Range condition

The range condition for each farm was calculated first in order to provide a quantitative measure of the capacity of the vegetation to support livestock or wildlife. This objective measure could then

serve as baseline for further investigations. The range condition scores corresponded well with the initial subjective condition assessment as described in Chapter 3 (Figure 4.1). The higher the range condition score, the better the range condition. The grazing gradient in Figure 4.1 therefore runs from left to right on the X-axis. The highest possible score is 1000.

4.3.2 Ordinations of vegetation and habitat variables

The correspondence analysis (CA) of the floristic data showed that the dune crest relevés formed a distinct cluster, separate from the dune slope and dune street relevés (Figure 4.2). The dune slope and dune street relevés, however, showed some overlap. Species characteristic for specific habitats, especially the dune crest habitat, could also be identified (Figure 4.2), e.g. *Stipagrostis amabilis* (Sti ama) in the dune crest habitat or *Centropodia glauca* (Cen gla) in the dune slope habitat.

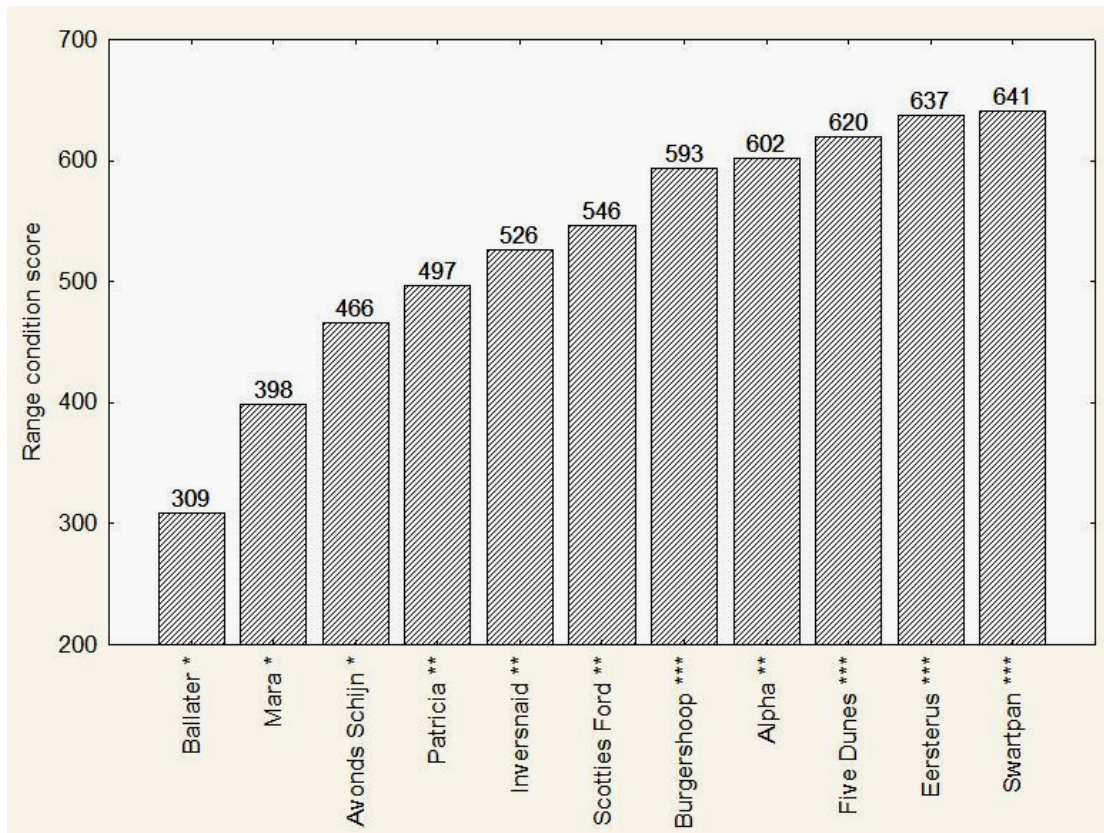
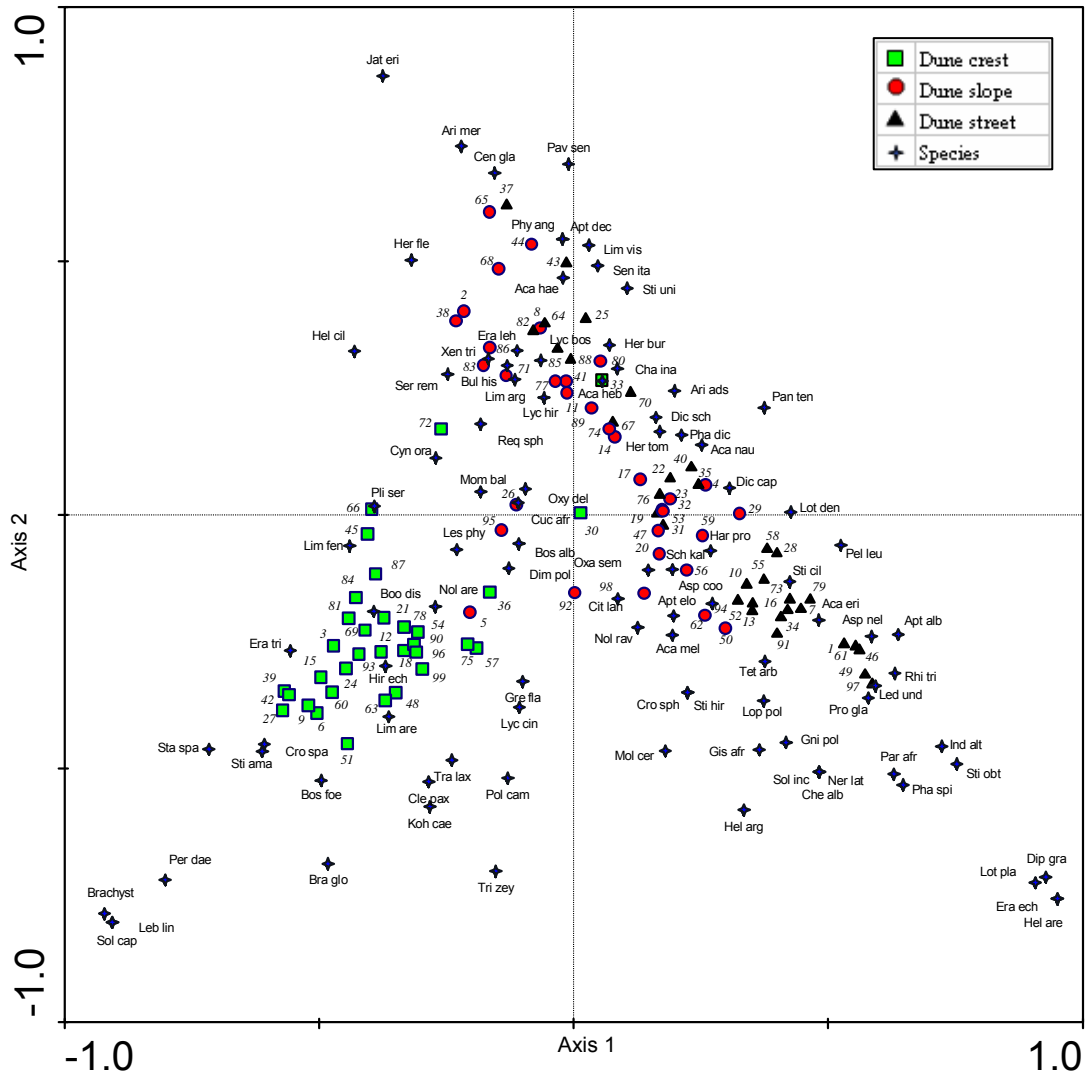


Figure 4.1 The range condition scores for 11 farms in the southwestern Kalahari. The grazing gradient runs from left to right on the X-axis with a high score indicating a good range condition and a low score indicating a poor range condition. The asterisks denote an *a priori* subjective assessment of range condition with *** = range in a good to very good condition, ** = range in a moderate condition and * = range in a poor to very poor condition.

Figure 4.3 shows the distribution of the relevés of the five farms with the highest range condition scores on the same CA ordination. The dune crest relevés again formed a very distinct grouping as in Figure 4.2. Dune slope relevés aggregated at the top of the ordination plane whereas dune street relevés were spread from the top to the bottom-right corner of the ordination plane.

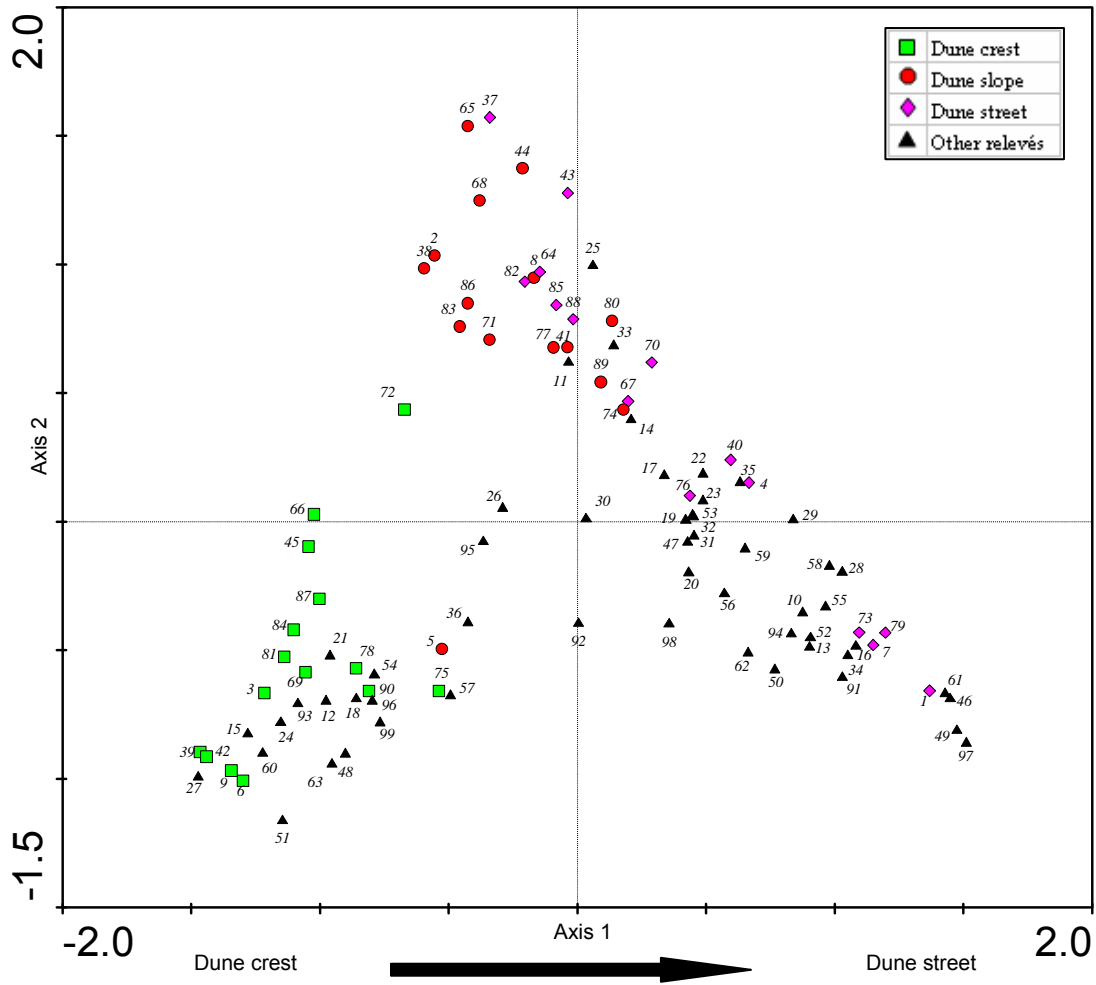
In Figure 4.4 the six farms with the lowest range condition scores are highlighted. Dune crest relevés again formed a distinct grouping, albeit with three outliers among the dune slope and dune street domains. The dune slope and dune street relevés were distributed from the center to the bottom-right of the ordination plane. Dune street relevés were mostly grouped further to the bottom-right of the ordination plane than dune slope relevés.

Some of the habitat/plant community variables were correlated with the range condition score in specific habitats only (Table 4.4) (e.g. annual grass cumulative cover in the dune street habitat) whereas other variables were significantly correlated across all habitat types (e.g. grazing evidence and perennial grass cumulative cover). No result is given for the variable 'slope' in the dune street habitat because no variation was observed in this parameter in the dune street habitat.



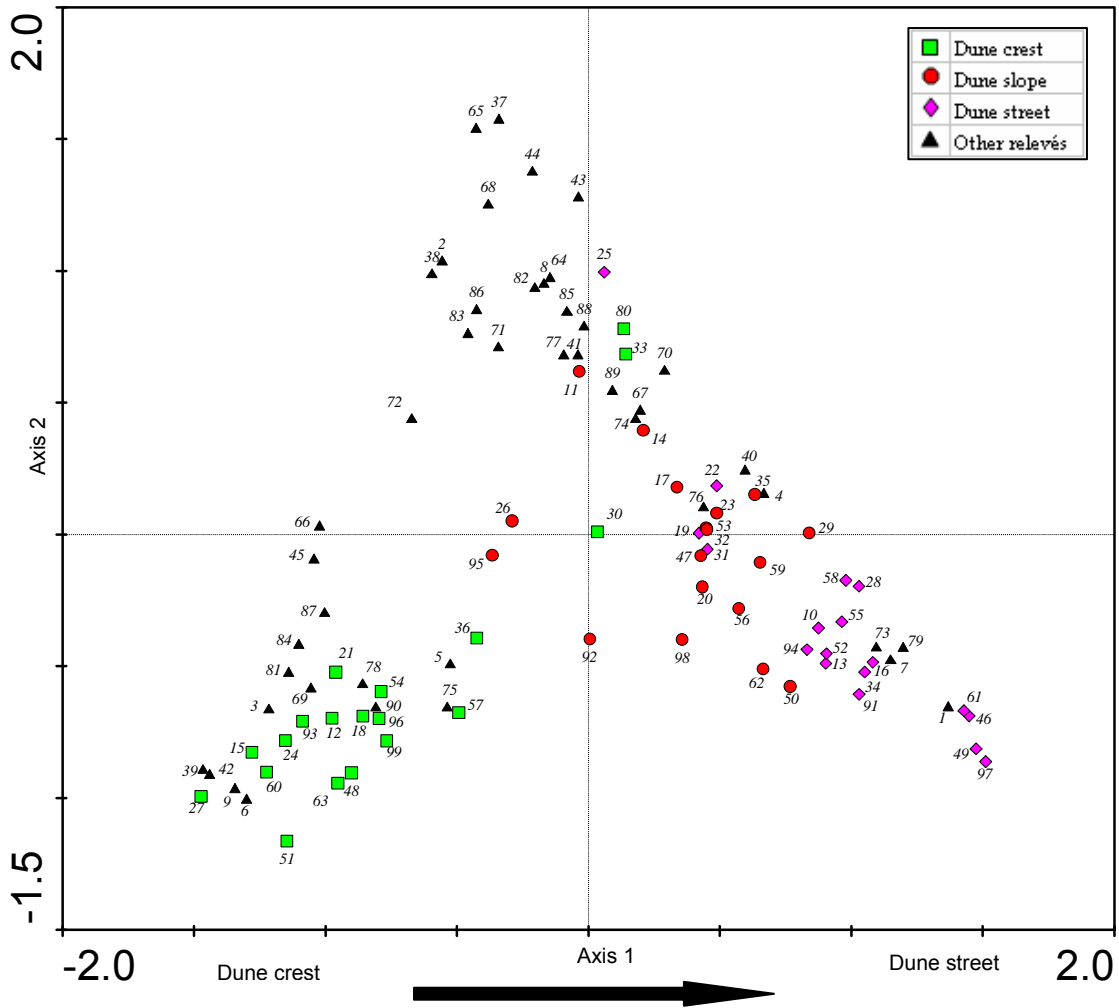
Axes	1	2	3	4	Total inertia
Eigenvalues:	0.617	0.442	0.363	0.302	4.223
Cumulative percentage variance of species data	14.6	25.1	33.7	40.8	
Sum of all eigenvalues					4.223

Figure 4.2 Correspondence analysis (CA) of Braun-Blanquet floristic data of 11 farms in the southwestern Kalahari showing the distribution of dune crest, dune slope and dune street relevés in the ordination plane as well as the association of species with the relevés. See appendix A for an explanation of species abbreviations and relevé numbers.



Axes	1	2	3	4	Total inertia
Eigenvalues:	0.617	0.442	0.363	0.302	4.223
Cumulative percentage variance of species data	14.6	25.1	33.7	40.8	
Sum of all eigenvalues					4.223

Figure 4.3 Correspondence analysis (CA) of Braun-Blanquet floristic data of all farms, with the five farms with the highest range condition scores highlighted.

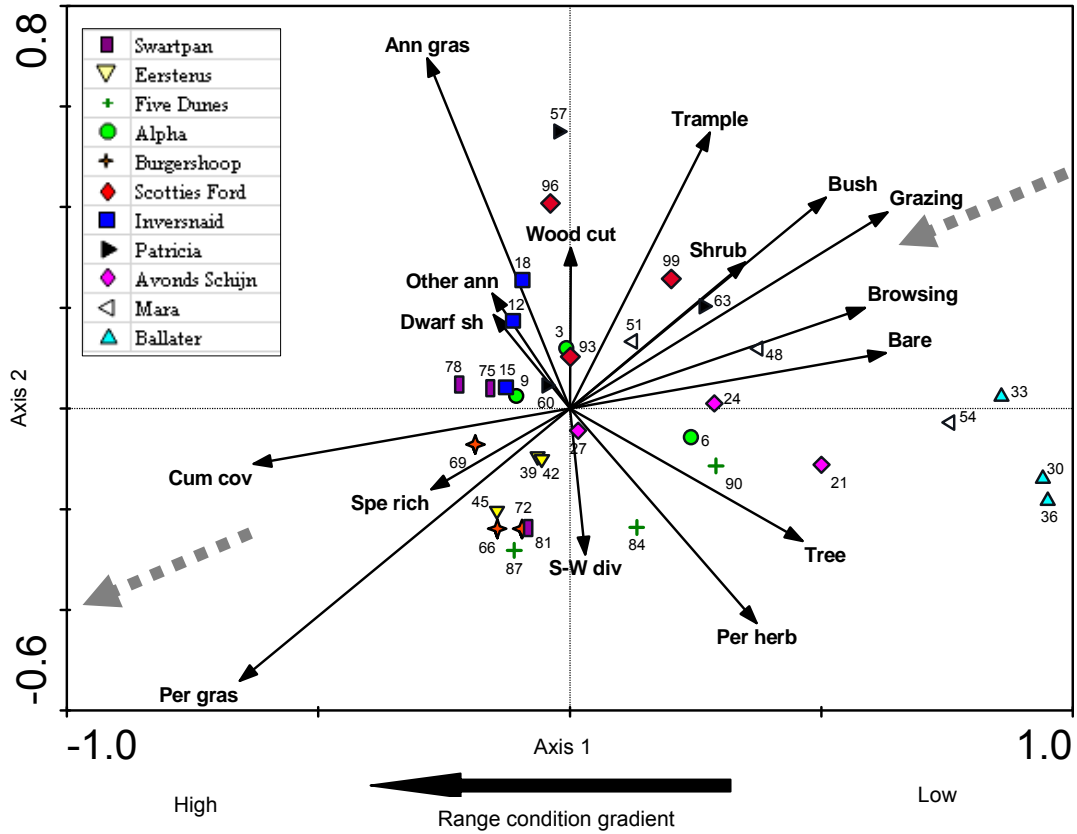


Axes	1	2	3	4	Total inertia
Eigenvalues:	0.617	0.442	0.363	0.302	4.223
Cumulative percentage variance of species data	14.6	25.1	33.7	40.8	
Sum of all eigenvalues					4.223

Figure 4.4 Correspondence analysis (CA) of Braun-Blanquet floristic data of all farms, with the six farms with the lowest range condition scores highlighted.

Table 4.4 Pearson's Product-Moment correlation (r) table between range condition score and various plant community parameters. Entries in red denote significance at the 95% level of significance. Details of the categories of habitat variables are shown in the field form sample listed in Appendix C

		Farm as a whole	Dune street	Dune slope	Dune crest
Mean species richness	r	0.3440	0.6196	0.3313	0.6030
	p	0.300	0.042	0.320	0.050
Mean S-W species diversity	r	0.6165	0.7002	0.6381	0.2356
	p	0.043	0.016	0.035	0.485
Mean cumulative cover (%)	r	0.6873	-0.0294	0.6202	0.8908
	p	0.019	0.932	0.042	.000
Slope	r	0.1655	0	0.2461	0.0436
	p	0.627	0	0.466	0.899
Bush encroachment	r	-0.7137	-0.6564	-0.6368	-0.6274
	p	0.014	0.028	0.035	0.039
Grazing evidence	r	-0.8762	-0.8555	-0.7031	-0.9237
	p	0.000	0.001	0.016	0.000
Browsing evidence	r	-0.9091	-0.8867	-0.8443	-0.7728
	p	0.000	0.000	0.001	0.005
Wood cutting evidence	r	0.1708	0.1372	0.2005	0.1708
	p	0.616	0.687	0.555	0.616
Trampling evidence	r	-0.5185	-0.4061	-0.5434	-0.5711
	p	0.102	0.215	0.084	0.067
Perennial grass cumulative cover (%)	r	0.9169	0.8751	0.8383	0.9367
	p	0.000	0.000	0.001	0.000
Perennial herb cumulative cover (%)	r	-0.5341	-0.5211	-0.5498	-0.2801
	p	0.091	0.100	0.080	0.404
Dwarf shrub cumulative cover (%)	r	0.1815	0.1021	0.2130	0.1593
	p	0.593	0.765	0.529	0.640
Shrub cumulative cover (%)	r	-0.6628	-0.7021	-0.4082	-0.0892
	p	0.026	0.016	0.213	0.794
Tree cumulative cover (%)	r	-0.1615	-0.2042	0.1452	-0.4599
	p	0.635	0.547	0.670	0.155
Annual grass cumulative cover (%)	r	-0.4992	-0.7547	-0.4530	0.3200
	p	0.118	0.007	0.162	0.337
Other annual cumulative cover (%)	r	0.4538	0.3288	0.3113	0.4300
	p	0.161	0.324	0.351	0.187
Bare surface cumulative cover (%)	r	-0.6873	0.0294	-0.6202	-0.8908
	p	0.019	0.932	0.042	0.000

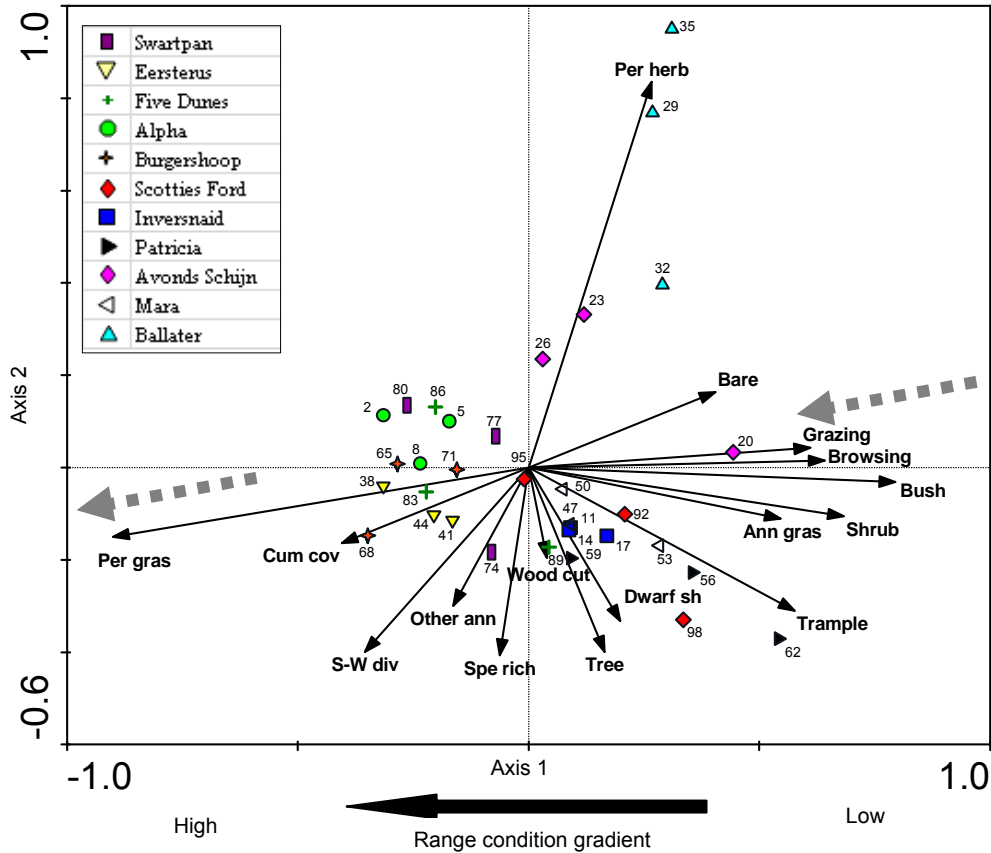


Axes	1	2	3	4	Total inertia
Eigenvalues	0.281	0.212	0.17	0.149	2.21
Species-environment correlations	0.94	0.941	0.957	0.926	
Cumulative percentage variance of species data	12.7	22.3	30	36.8	
of species-environment relation	21.3	37.3	50.2	61.4	
Sum of all eigenvalues					2.21
Sum of all canonical eigenvalues					1.323

Figure 4.5 Canonical correspondence analysis (CCA) of floristic data in conjunction with habitat variables in the dune crest habitat of 11 farms in the southwestern Kalahari. Ann gras = annual grass cumulative cover; Other ann = other annuals cumulative cover; Per gras = perennial grass cumulative cover; Per herb = perennial herb cumulative cover; Dwarf sh = dwarf shrub cumulative cover; Shrub = shrub cumulative cover; Tree = tree cumulative cover; Bare = bare soil cover; Cum cov = total cumulative cover; Slope = slope incline; Soil = soil consistency; Trample = trampling evidence; Wood cut = wood cutting evidence; Grazing = grazing evidence; Browsing = browsing evidence; Bush = bush encroachment evidence; Spe rich = species richness; S-W div = Shannon-Wiener index of species diversity.

Table 4.5 Two-way Product-Moment correlation matrix (r and p values) of habitat variables for the dune crest habitat. Entries in red denote significance at the 95% level of significance

		Shannon-Wiener index of diversity	Species richness	Total cumulative cover	Bush encroachment	Grazing evidence	Browsing evidence	Wood cutting evidence	Trampling evidence	Perennial grass cumulative cover	Perennial herb cumulative cover	Dwarf shrub cumulative cover	Shrub cumulative cover	Tree cumulative cover	Annual grass cumulative cover	Other annual species cumulative cover	Bare surface cumulative cover
Shannon-Wiener index of diversity	r	1.000	0.758	0.320	0.300	-0.100	0.141	0.219	0.112	0.232	0.397	0.478	0.218	0.180	0.010	0.205	0.320
	p		0.000	0.069	0.090	0.580	0.434	0.221	0.535	0.194	0.022	0.005	0.224	0.315	0.956	0.254	0.069
Species richness	r	0.758	1.000	0.584	-0.050	-0.437	-0.267	0.469	-0.106	0.533	0.284	0.515	0.088	-0.202	0.146	0.299	0.584
	p	0.000		0.000	0.783	0.011	0.134	0.006	0.559	0.001	0.109	0.002	0.626	0.259	0.418	0.091	0.000
Total cumulative cover	r	0.320	0.584	1.000	-0.339	-0.701	-0.533	0.133	-0.384	0.920	0.034	0.275	-0.096	-0.275	0.485	0.538	-1.000
	p	0.069	0.000		0.053	0.000	0.001	0.461	0.027	0.000	0.849	0.122	0.594	0.122	0.004	0.001	--
Bush encroachment	r	0.300	-0.050	-0.339	1.000	0.519	0.547	0.154	0.392	-0.472	0.169	0.221	0.478	0.227	0.015	-0.203	0.339
	p	0.090	0.783	0.053		0.002	0.001	0.393	0.024	0.006	0.348	0.217	0.005	0.204	0.933	0.258	0.053
Grazing evidence	r	-0.100	-0.437	-0.701	0.519	1.000	0.743	-0.210	0.687	-0.772	0.059	-0.054	0.139	0.354	-0.115	-0.352	0.701
	p	0.580	0.011	0.000	0.002		0.000	0.242	0.000	0.000	0.744	0.766	0.440	0.043	0.525	0.045	0.000
Browsing evidence	r	0.141	-0.267	-0.533	0.547	0.743	1.000	-0.053	0.516	-0.631	0.119	0.022	0.398	0.467	-0.179	-0.178	0.533
	p	0.434	0.134	0.001	0.001	0.000		0.768	0.002	0.000	0.508	0.902	0.022	0.006	0.318	0.321	0.001
Wood cutting evidence	r	0.219	0.469	0.133	0.154	-0.210	-0.053	1.000	-0.079	0.087	-0.026	0.349	0.123	-0.113	0.027	0.185	-0.133
	p	0.221	0.006	0.467	0.393	0.242	0.768		0.662	0.629	0.887	0.046	0.495	0.530	0.880	0.303	0.461
Trampling evidence	r	0.112	-0.106	-0.384	0.392	0.687	0.516	-0.079	1.000	-0.509	-0.154	0.194	0.241	0.154	0.099	-0.123	0.384
	p	0.535	0.559	0.027	0.024	0.000	0.002	0.662		0.003	0.391	0.279	0.176	0.392	0.582	0.497	0.027
Perennial grass cumulative cover	r	0.232	0.533	0.920	-0.472	-0.772	-0.631	0.087	-0.509	1.000	-0.014	0.168	-0.254	-0.279	0.214	0.330	-0.920
	p	0.194	0.001	0.000	0.006	0.000	0.000	0.629	0.003		0.939	0.350	0.154	0.115	0.231	0.061	0.000
Perennial herb cumulative cover	r	0.397	0.284	0.034	0.169	0.059	0.119	-0.026	-0.154	-0.014	1.000	0.084	0.083	-0.001	-0.150	-0.011	-0.034
	p	0.022	0.109	0.849	0.348	0.744	0.508	0.887	0.391	0.939		0.643	0.646	0.995	0.404	0.953	0.849
Dwarf shrub cumulative cover	r	0.478	0.515	0.275	0.221	-0.054	0.022	0.349	0.194	0.168	0.084	1.000	0.137	-0.254	0.140	0.230	-0.275
	p	0.005	0.002	0.122	0.217	0.766	0.902	0.046	0.279	0.350	0.643		0.447	0.153	0.436	0.197	0.122
Shrub cumulative cover	r	0.218	0.088	-0.096	0.478	0.139	0.398	0.123	0.241	-0.254	0.083	0.137	1.000	0.055	-0.150	0.273	0.096
	p	0.224	0.626	0.594	0.005	0.440	0.022	0.495	0.176	0.154	0.646	0.447		0.763	0.406	0.124	0.594
Tree cumulative cover	r	0.180	-0.202	-0.275	0.227	0.354	0.467	-0.113	0.154	-0.279	-0.001	-0.254	0.055	1.000	-0.254	-0.126	0.275
	p	0.315	0.259	0.122	0.204	0.043	0.006	0.530	0.392	0.115	0.995	0.153	0.763		0.155	0.483	0.122
Annual grass cumulative cover	r	0.010	0.146	0.485	0.015	-0.115	-0.179	0.027	0.099	0.214	-0.150	0.140	-0.150	-0.254	1.000	0.176	-0.485
	p	0.956	0.418	0.004	0.933	0.525	0.318	0.880	0.582	0.231	0.404	0.436	0.406	0.155		0.329	0.004
Other annual species cumulative cover	r	0.205	0.299	0.538	-0.203	-0.352	-0.178	0.185	-0.123	0.330	-0.011	0.230	0.273	-0.126	0.176	1.000	-0.538
	p	0.254	0.091	0.001	0.258	0.045	0.321	0.303	0.497	0.061	0.953	0.197	0.124	0.483	0.329		0.001
Bare surface cumulative cover	r	-0.320	-0.584	-1.000	0.339	0.701	0.533	-0.133	0.384	-0.920	-0.034	-0.275	0.096	0.275	-0.485	-0.538	1.000
	p	0.069	0.000	--	0.053	0.000	0.001	0.461	0.027	0.000	0.849	0.122	0.594	0.122	0.004	0.001	

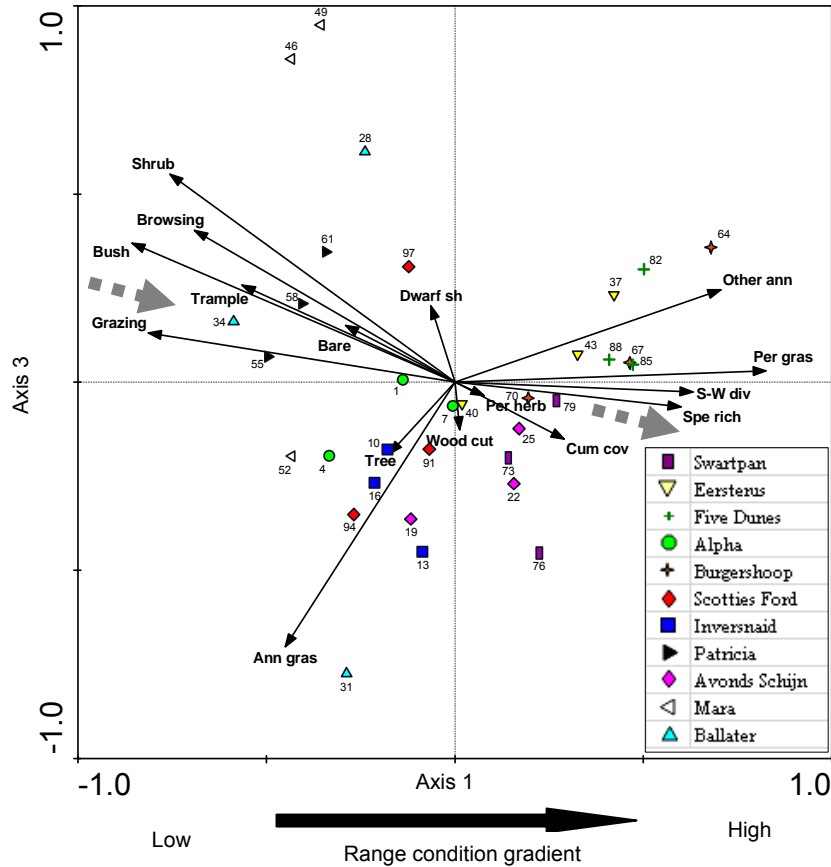


Axes	1	2	3	4	Total inertia
Eigenvalues	0.451	0.347	0.288	0.215	2.93
Species-environment correlations	0.981	0.968	0.958	0.951	
Cumulative percentage variance of species data	15.4	27.2	37.1	44.4	
of species-environment relation	22.3	39.4	53.7	64.3	
Sum of all eigenvalues					2.93
Sum of all canonical eigenvalues					2.023

Figure 4.6 Canonical correspondence analysis (CCA) of floristic data in conjunction with habitat variables in the dune slope habitat of 11 farms in the southwestern Kalahari. Ann gras = annual grass cumulative cover; Other ann = other annuals cumulative cover; Per gras = perennial grass cumulative cover; Per herb = perennial herb cumulative cover; Dwarf sh = dwarf shrub cumulative cover; Shrub = shrub cumulative cover; Tree = tree cumulative cover; Bare = bare soil cover; Cum cov = total cumulative cover; Slope = slope incline; Soil = soil consistency; Trample = trampling evidence; Wood cut = wood cutting evidence; Grazing = grazing evidence; Browsing = browsing evidence; Bush = bush encroachment evidence; Spe rich = species richness; S-W div = Shannon-Wiener index of species diversity.

Table 4.6 Two-way Product-Moment correlation matrix (r and p values) of habitat variables for the dune slope habitat. Entries in red denote significance at the 95% level

		Shannon-Wiener index of diversity	Species richness	Total cumulative cover	Bush encroachment	Grazing evidence	Browsing evidence	Wood cutting evidence	Trampling evidence	Perennial grass cumulative cover	Perennial herb cumulative cover	Dwarf shrub cumulative cover	Shrub cumulative cover	Tree cumulative cover	Annual grass cumulative cover	Other annual species cumulative cover	Bare surface cumulative cover
Shannon-Wiener index of diversity	r	1.000	0.825	0.255	-0.153	-0.574	-0.476	0.376	-0.164	0.400	-0.248	0.503	-0.126	0.074	-0.377	0.440	-0.255
	p		0.000	0.152	0.396	0.000	0.005	0.031	0.361	0.021	0.164	0.003	0.486	0.682	0.031	0.010	0.152
Species richness	r	0.825	1.000	0.109	-0.041	-0.330	-0.253	0.380	0.046	0.140	-0.140	0.601	0.009	-0.081	-0.187	0.352	-0.109
	p	0.000		0.547	0.819	0.061	0.155	0.029	0.801	0.437	0.436	0.000	0.959	0.653	0.297	0.045	0.547
Total cumulative cover	r	0.255	0.109	1.000	-0.242	-0.446	-0.403	-0.361	-0.405	0.696	-0.110	-0.007	-0.019	0.242	0.044	0.205	-1.000
	p	0.152	0.547		0.175	0.009	0.020	0.039	0.019	0.000	0.543	0.970	0.918	0.174	0.806	0.253	--
Bush encroachment	r	-0.153	-0.041	-0.242	1.000	0.331	0.494	0.055	0.329	-0.655	0.264	0.147	0.760	0.211	0.161	-0.047	0.242
	p	0.396	0.819	0.175		0.060	0.004	0.760	0.061	0.000	0.138	0.416	0.000	0.239	0.371	0.796	0.175
Grazing evidence	r	-0.574	-0.330	-0.446	0.331	1.000	0.750	-0.251	0.624	-0.653	0.028	-0.175	0.087	0.010	0.547	-0.082	0.446
	p	0.000	0.061	0.009	0.060		0.000	0.160	0.000	0.000	0.876	0.330	0.629	0.957	0.001	0.651	0.009
Browsing evidence	r	-0.476	-0.253	-0.403	0.494	0.750	1.000	-0.285	0.621	-0.593	-0.016	-0.128	0.302	0.057	0.428	-0.206	0.403
	p	0.005	0.155	0.020	0.004	0.000		0.108	0.000	0.000	0.929	0.479	0.088	0.754	0.013	0.251	0.020
Wood cutting evidence	r	0.376	0.380	-0.361	0.055	-0.251	-0.285	1.000	-0.092	-0.182	0.069	0.545	-0.067	-0.193	-0.239	0.196	0.361
	p	0.031	0.029	0.039	0.760	0.160	0.108		0.609	0.311	0.704	0.001	0.710	0.282	0.180	0.275	0.039
Trampling evidence	r	-0.164	0.046	-0.405	0.329	0.624	0.621	-0.092	1.000	-0.536	-0.289	-0.033	0.211	0.143	0.503	-0.149	0.405
	p	0.361	0.801	0.019	0.061	0.000	0.000	0.609		0.001	0.103	0.857	0.239	0.428	0.001	0.408	0.019
Perennial grass cumulative cover	r	0.400	0.140	0.696	-0.655	-0.653	-0.593	-0.182	-0.536	1.000	-0.357	-0.087	-0.417	0.054	-0.447	0.171	-0.696
	p	0.021	0.437	0.000	0.000	0.000	0.000	0.311	0.001		0.042	0.629	0.016	0.764	0.009	0.341	0.000
Perennial herb cumulative cover	r	-0.248	-0.140	-0.110	0.264	0.028	-0.016	0.069	-0.289	-0.357	1.000	0.051	0.136	-0.396	-0.101	-0.096	0.110
	p	0.164	0.436	0.543	0.138	0.876	0.929	0.704	0.103	0.042		0.777	0.449	0.022	0.578	0.595	0.543
Dwarf shrub cumulative cover	r	0.503	0.601	-0.007	0.147	-0.175	-0.128	0.545	-0.033	-0.087	0.051	1.000	0.066	-0.178	-0.086	0.324	0.007
	p	0.003	0.000	0.970	0.416	0.330	0.479	0.001	0.857	0.629	0.777		0.714	0.322	0.635	0.066	0.970
Shrub cumulative cover	r	-0.126	0.009	-0.019	0.760	0.087	0.302	-0.067	0.211	-0.417	0.136	0.066	1.000	0.148	0.088	-0.271	0.019
	p	0.486	0.959	0.918	0.000	0.629	0.088	0.710	0.239	0.016	0.449	0.714		0.412	0.627	0.127	0.918
Tree cumulative cover	r	0.074	-0.081	0.242	0.211	0.010	0.057	-0.193	0.143	0.054	-0.396	-0.178	0.148	1.000	0.056	0.194	-0.242
	p	0.682	0.653	0.174	0.239	0.957	0.754	0.282	0.428	0.764	0.022	0.322	0.412		0.757	0.279	0.174
Annual grass cumulative cover	r	-0.377	-0.187	0.044	0.161	0.547	0.428	-0.239	0.503	-0.447	-0.101	-0.086	0.088	0.056	1.000	-0.290	-0.044
	p	0.031	0.297	0.806	0.371	0.001	0.013	0.180	0.003	0.009	0.578	0.635	0.627	0.757		0.102	0.806
Other annual species cumulative cover	r	0.440	0.352	0.205	-0.047	-0.082	-0.206	0.196	-0.149	0.171	-0.096	0.324	-0.271	0.194	-0.290	1.000	-0.205
	p	0.010	0.045	0.253	0.796	0.651	0.251	0.275	0.408	0.341	0.595	0.066	0.127	0.279	0.102		0.253
Bare surface cumulative cover	r	-0.255	-0.109	-1.000	0.242	0.446	0.403	0.361	0.405	-0.696	0.110	0.007	0.019	-0.242	-0.044	-0.205	1.000
	p	0.152	0.547	--	0.175	0.009	0.020	0.039	0.019	0.000	0.543	0.970	0.918	0.174	0.806	0.253	



Axes	1	2	3	4	Total inertia
Eigenvalues	0.489	0.352	0.246	0.172	2.687
Species-environment correlations	0.95	0.927	0.97	0.94	
Cumulative percentage variance of species data	18.2	31.3	40.4	46.8	
of species-environment relation	26.6	45.9	59.2	68.6	
Sum of all eigenvalues					2.687
Sum of all canonical eigenvalues					1.835

Figure 4.7 Canonical correspondence analysis (CCA) of floristic data in conjunction with habitat variables in the dune street habitat of 11 farms in the southwestern Kalahari. Ann gras = annual grass cumulative cover; Other ann = other annuals cumulative cover; Per gras = perennial grass cumulative cover; Per herb = perennial herb cumulative cover; Dwarf sh = dwarf shrub cumulative cover; Shrub = shrub cumulative cover; Tree = tree cumulative cover; Bare = bare soil cover; Cum cov = total cumulative cover; Slope = slope incline; Soil = soil consistency; Trample = trampling evidence; Wood cut = wood cutting evidence; Grazing = grazing evidence; Browsing = browsing evidence; Bush = bush encroachment evidence; Spe rich = species richness; S-W div = Shannon-Wiener index of species diversity.

Table 4.7 Two-way Product-Moment correlation matrix (r and p values) of habitat variables for the dune street habitat. Entries in red denote significance at the 95% level

		Shannon-Wiener index of diversity	Species richness	Total cumulative cover	Bush encroachment	Grazing evidence	Browsing evidence	Wood cutting evidence	Trampling evidence	Perennial grass cumulative cover	Perennial herb cumulative cover	Dwarf shrub cumulative cover	Shrub cumulative cover	Tree cumulative cover	Annual grass cumulative cover	Other annual species cumulative cover	Bare surface cumulative cover
Shannon-Wiener index of diversity	r	1.000	0.856	0.265	-0.397	-0.636	-0.525	0.294	-0.142	0.595	-0.121	0.265	-0.452	0.178	-0.355	0.559	-0.265
	p		0.000	0.137	0.022	0.000	0.002	0.097	0.431	0.000	0.502	0.136	0.008	0.323	0.042	0.001	0.137
Species richness	r	0.856	1.000	0.114	-0.436	-0.558	-0.508	0.374	-0.181	0.460	-0.133	0.240	-0.474	0.168	-0.258	0.458	-0.114
	p	0.000		0.528	0.011	0.001	0.003	0.032	0.312	0.007	0.460	0.178	0.005	0.351	0.148	0.007	0.528
Total cumulative cover	r	0.265	0.114	1.000	-0.243	-0.225	-0.230	-0.107	-0.188	0.309	0.278	0.106	-0.082	-0.134	0.322	0.459	-1.000
	p	0.137	0.528		0.174	0.208	0.199	0.554	0.295	0.080	0.117	0.559	0.650	0.459	0.068	0.007	0.000
Bush encroachment	r	-0.397	-0.436	-0.243	1.000	0.681	0.693	-0.044	0.545	-0.638	-0.062	0.162	0.870	0.098	0.008	-0.400	0.243
	p	0.022	0.011	0.174		0.000	0.000	0.809	0.001	0.000	0.730	0.367	0.000	0.589	0.967	0.021	0.174
Grazing evidence	r	-0.636	-0.558	-0.225	0.681	1.000	0.761	-0.323	0.543	-0.850	0.096	-0.073	0.687	0.265	0.364	-0.401	0.225
	p	0.000	0.001	0.208	0.000		0.000	0.067	0.001	0.000	0.595	0.688	0.000	0.137	0.037	0.021	0.208
Browsing evidence	r	-0.525	-0.508	-0.230	0.693	0.761	1.000	-0.320	0.532	-0.627	0.197	0.123	0.692	-0.028	0.036	-0.356	0.230
	p	0.002	0.003	0.199	0.000	0.000		0.070	0.001	0.000	0.272	0.497	0.000	0.879	0.843	0.042	0.199
Wood cutting evidence	r	0.294	0.374	-0.107	-0.044	-0.323	-0.320	1.000	-0.114	0.078	-0.030	-0.050	-0.107	0.067	-0.098	-0.017	0.107
	p	0.097	0.032	0.554	0.809	0.067	0.070		0.529	0.667	0.870	0.784	0.553	0.712	0.586	0.927	0.554
Trampling evidence	r	-0.142	-0.181	-0.188	0.545	0.543	0.532	-0.114	1.000	-0.424	-0.341	0.215	0.538	0.448	0.051	-0.203	0.188
	p	0.431	0.312	0.295	0.001	0.001	0.001	0.529		0.014	0.052	0.229	0.001	0.009	0.778	0.257	0.295
Perennial grass cumulative cover	r	0.595	0.460	0.309	-0.638	-0.850	-0.627	0.078	-0.424	1.000	-0.239	0.166	-0.614	-0.298	-0.480	0.427	-0.309
	p	0.000	0.007	0.080	0.000	0.000	0.000	0.667	0.014		0.180	0.356	0.000	0.092	0.005	0.013	0.080
Perennial herb cumulative cover	r	-0.121	-0.133	0.278	-0.062	0.096	0.197	-0.030	-0.341	-0.239	1.000	-0.148	-0.029	-0.081	0.076	0.126	-0.278
	p	0.502	0.460	0.117	0.730	0.595	0.272	0.870	0.052	0.180		0.410	0.873	0.655	0.673	0.486	0.117
Dwarf shrub cumulative cover	r	0.265	0.240	0.106	0.162	-0.073	0.123	-0.050	0.215	0.166	-0.148	1.000	0.055	-0.023	-0.206	0.027	-0.106
	p	0.136	0.178	0.559	0.367	0.688	0.497	0.784	0.229	0.356	0.410		0.763	0.898	0.250	0.883	0.559
Shrub cumulative cover	r	-0.452	-0.474	-0.082	0.870	0.687	0.692	-0.107	0.538	-0.614	-0.029	0.055	1.000	-0.030	0.000	-0.293	0.082
	p	0.008	0.005	0.650	0.000	0.000	0.000	0.553	0.001	0.000	0.873	0.763		0.869	0.010	0.098	0.650
Tree cumulative cover	r	0.178	0.168	-0.134	0.098	0.265	-0.028	0.067	0.448	-0.298	-0.081	-0.023	-0.030	1.000	0.152	-0.069	0.134
	p	0.323	0.351	0.459	0.589	0.137	0.879	0.712	0.009	0.092	0.655	0.898	0.869		0.399	0.703	0.459
Annual grass cumulative cover	r	-0.355	-0.258	0.322	0.008	0.364	0.036	-0.098	0.051	-0.480	0.076	-0.206	0.000	0.152	1.000	-0.307	-0.322
	p	0.042	0.148	0.068	0.967	0.037	0.843	0.586	0.778	0.005	0.673	0.250	0.010	0.399		0.082	0.068
Other annual species cumulative cover	r	0.559	0.458	0.459	-0.400	-0.401	-0.356	-0.017	-0.203	0.427	0.126	0.027	-0.293	-0.069	-0.307	1.000	-0.459
	p	0.001	0.007	0.007	0.021	0.021	0.042	0.927	0.257	0.013	0.486	0.883	0.098	0.703	0.082		0.007
Bare surface cumulative cover	r	-0.265	-0.114	-1.000	0.243	0.225	0.230	0.107	0.188	-0.309	-0.278	-0.106	0.082	0.134	-0.322	-0.459	1.000
	p	0.137	0.528	0.000	0.174	0.208	0.199	0.554	0.295	0.080	0.117	0.559	0.650	0.459	0.068	0.007	

4.3.3 Total cumulative vegetation cover and cumulative life / growth form cover

Cumulative vegetation cover in the dune crest habitat decreased significantly ($p=0.000$, Table 4.4) as range condition decreased (Figure 4.8). Cumulative vegetation cover on the dune slope was high in the farms that had the highest range condition scores (exception Eersterus) and low in the farms with the lowest range condition scores (Figure 4.9; $p=0.042$), whereas cumulative vegetation cover was variable in the farms with the moderate range condition scores. In the dune street habitat cumulative vegetation cover was variable across the range condition gradient and not significantly correlated with range condition (Figure 4.10; $p=0.932$). For the farms as a whole, across habitats, cumulative vegetation cover ($p=0.019$) was significantly positively correlated with range condition (Table 4.4).

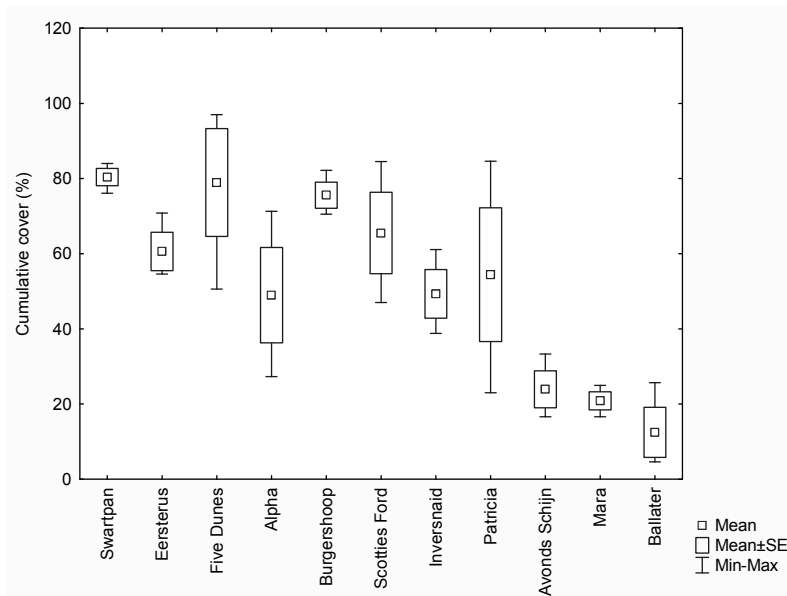


Figure 4.8 Cumulative vegetation cover for the dune crest habitat on 11 farms in the southwestern Kalahari arranged from good to poor along a range condition gradient.

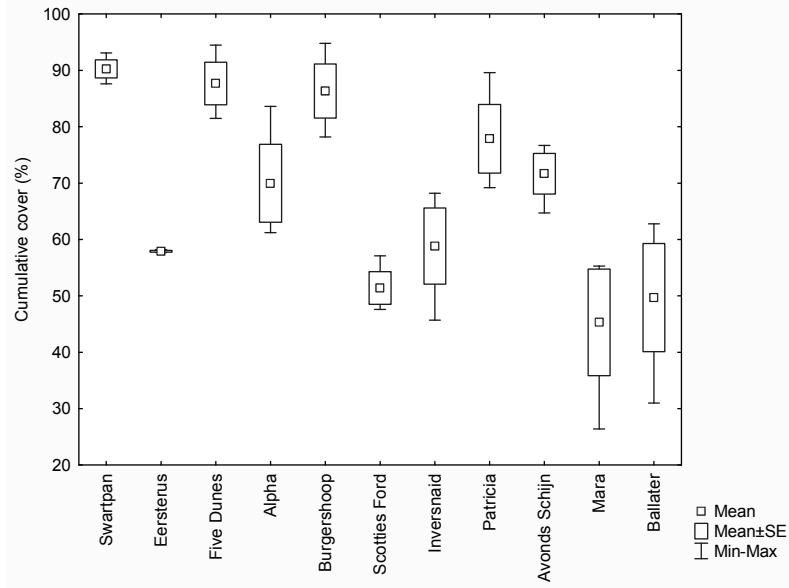


Figure 4.9 Cumulative vegetation cover for the dune slope habitat on 11 farms in the southwestern Kalahari arranged from good to poor along a range condition gradient.

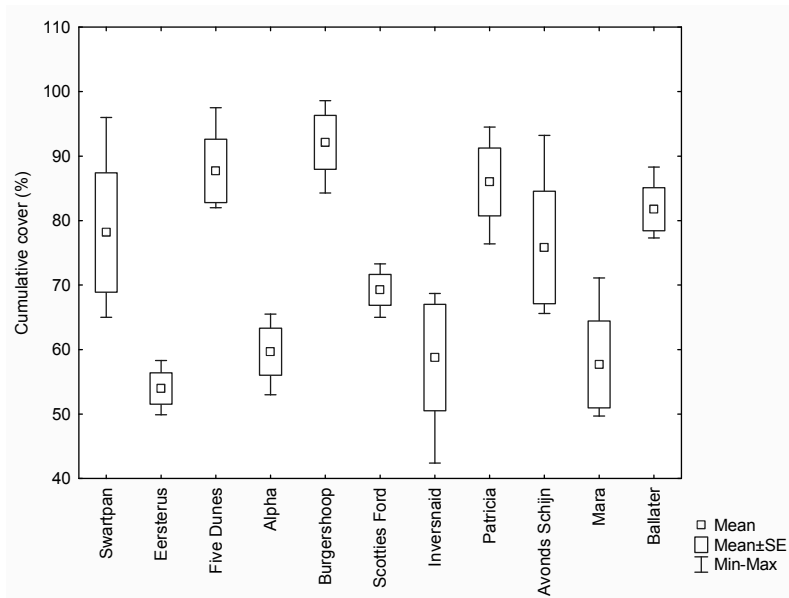


Figure 4.10 Cumulative vegetation cover for the dune street habitat on 11 farms in the southwestern Kalahari arranged from good to poor along a range condition gradient.

In the dune crest habitat perennial grass cover decreased significantly ($p=0.000$) and bare surface area increased significantly ($p=0.000$) with lower range condition scores (Figure 4.11a). None of the other life/growth form categories showed any significant relationships with range condition. Similarly, in the dune slope habitat perennial grass cover was significantly lower ($p=0.001$) and bare surface area significantly greater ($p=0.042$) on the farms with lower range condition scores than on the farms with higher range condition scores (Figure 4.11b). Farms with a low range condition score also showed higher cumulative vegetation cover for perennial herbs ($p=0.080$) and annual grasses ($p=0.162$), although not significantly so. In the dune street habitat there was a significant reduction in perennial grass cover ($p=0.000$) and an increase in shrub cover ($p=0.016$) and annual grass cover ($p=0.007$) as range condition decreased (Figure 4.11c). Perennial herb cover increased as range condition decreases but not significantly so ($p=0.100$).

For the farms as a whole, across habitats, perennial grass cover ($p=0.000$) and shrub cover ($p=0.026$) increased significantly with a decrease in veld condition.

4.3.4 Cover of selected species

Mean percentage cover of two of the three most prominent dune crest perennial grass species, *Stipagrostis amabilis* and *Eragrostis trichophora* decreased noticeably along the range condition gradient from good to poor (Figure 4.12a). *Eragrostis lehmanniana* is not a typical dune crest species and generally had low cover values, but nevertheless also decreased along the range condition gradient from good to poor. *Stipagrostis amabilis* and *E. lehmanniana* each have a Category 2 ecological status and *Eragrostis trichophora* a Category 3 status.

Three species typical of the dune slope habitat also decreased along the range condition gradient (Figure 4.12b). *Centropodia glauca* and *Eragrostis lehmanniana* each have a Category 2 ecological status, and *Aristida meridionalis* has a Category 3 ecological status.

Of the three most prominent dune street grass species *Stipagrostis ciliata* and *Stipagrostis obtusa* each have a Category 1 ecological status and *Stipagrostis uniplumis* has a Category 3 ecological status. *Stipagrostis ciliata* exhibited the greatest change in cover along the range condition gradient (Figure 4.12c), whereas *S. obtusa* only diminished markedly at the lowest (most degraded) end of the gradient and *S. uniplumis* showed no trend along the range condition gradient.

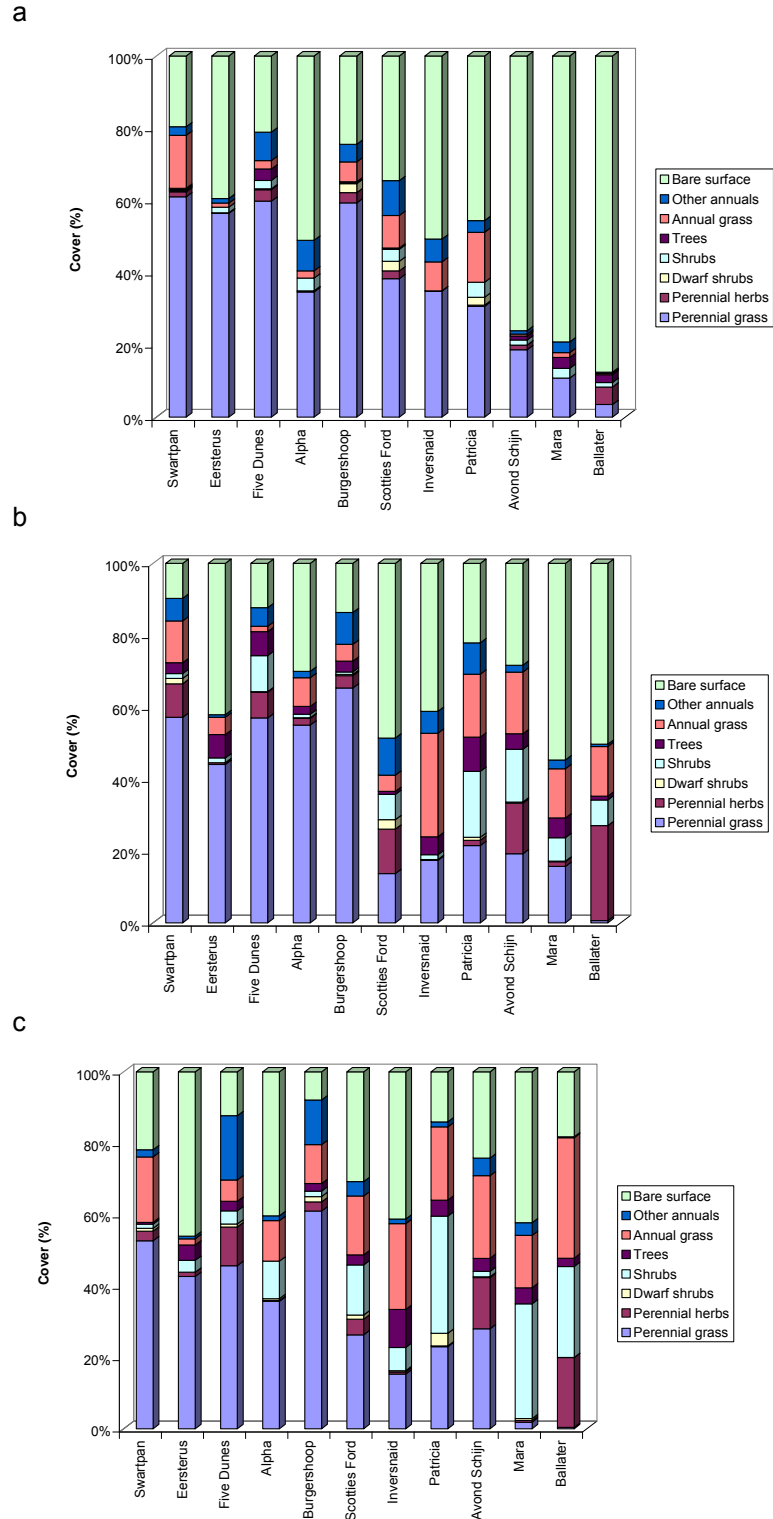


Figure 4.11 Contributions of different life/growth forms to vegetation cover (as percentage of total cumulative cover) across the range condition gradient from good (left) to poor (right) condition in the (a) dune crest (b) dune slope and (c) dune street habitats of the southwestern Kalahari.

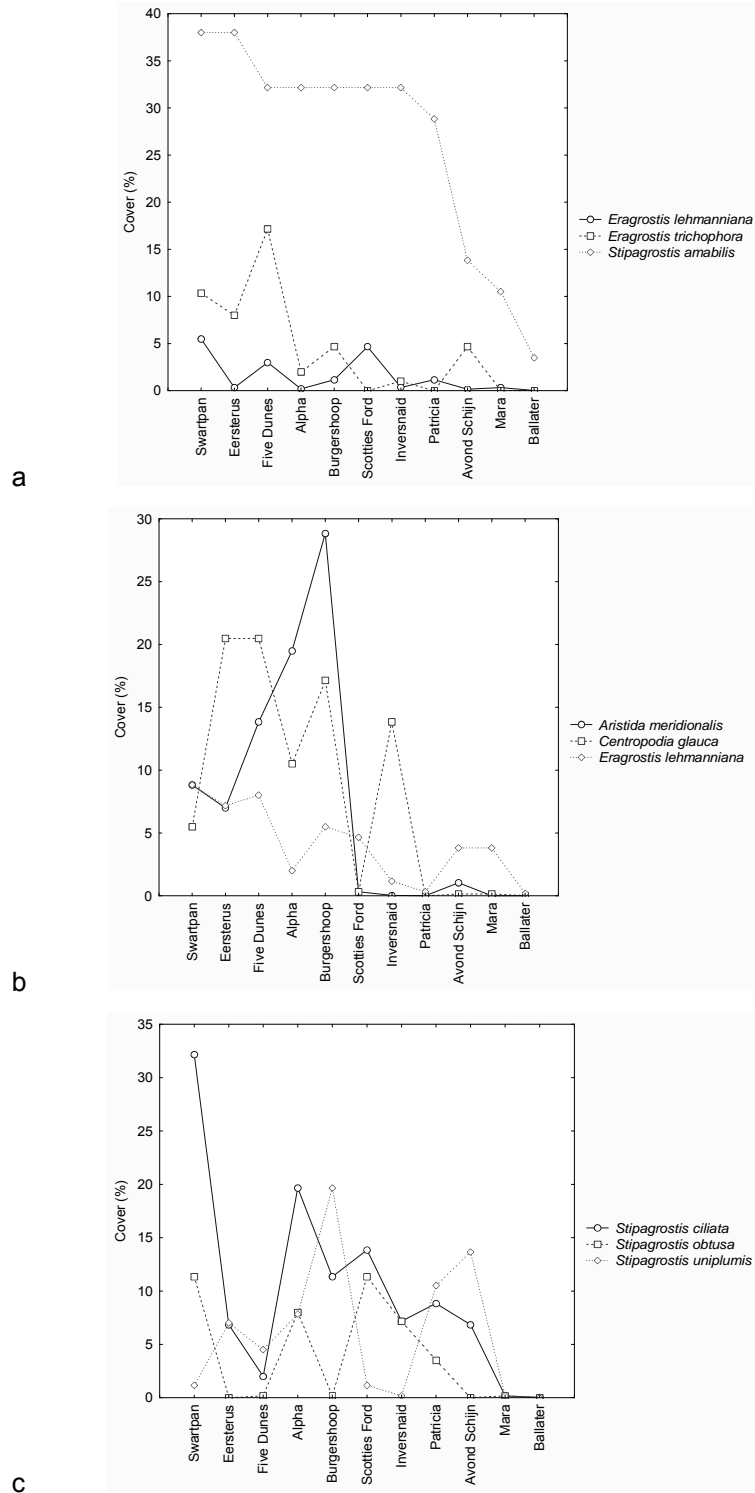


Figure 4.12 Mean percentage cover of prominent perennial grass species across the range condition gradient from good (left) to poor (right) condition in the (a) dune crest, (b) dune slope and (c) dune streets habitats of the southwestern Kalahari.

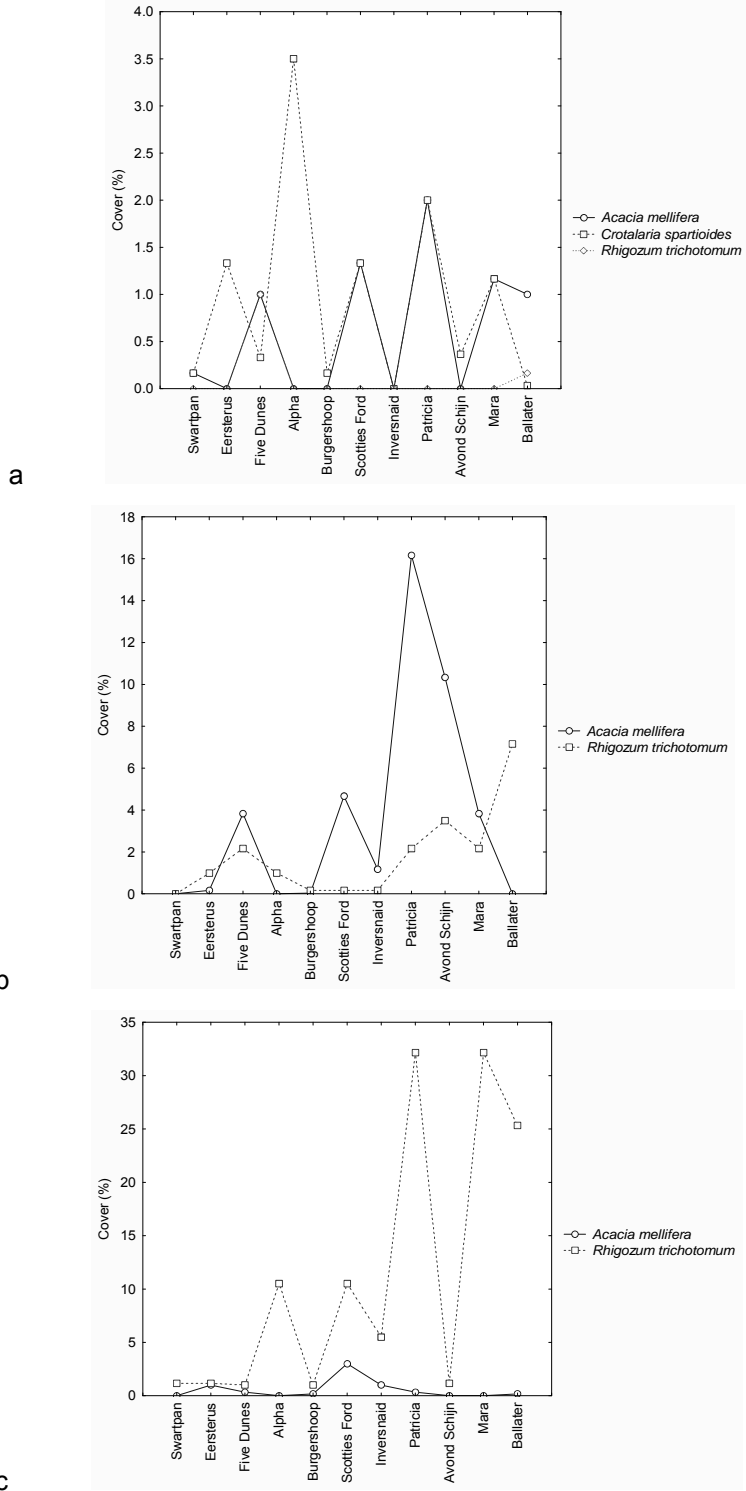


Figure 4.13 Percentage cover of the most prominent shrub species across the range condition gradient from good (left) to poor (right) condition in the (a) dune crest, (b) dune slope and (c) dune streets habitats of the southwestern Kalahari.

Overall shrub cover was low ($\leq 3.5\%$ cover) in the dune crest habitat for all common shrub species (Figure 4.13a). *Acacia mellifera* cover was variable across the range condition gradient but still low overall. *Crotalaria spartioides*, a typical dune crest species, did not show any relationship with the range condition gradient. *Acacia mellifera* and *Rhigozum trichotomum* were the most prominent shrub species in the dune slope and dune street habitats with cover of *A. mellifera* up to 16% in the dune slope habitat (Figure 4.13b) and *R. trichotomum* up to 32% in the dune street habitat (Figure 4.13c). *Rhigozum trichotomum* cover increased as the range condition decreased in the dune slope and dune street habitats. *Acacia mellifera* cover was fairly low ($\leq 3\%$ cover) throughout the gradient in the dune street and no discernible trend was visible, but increased on the dune slope with poor range condition. *Acacia mellifera* cover decreased again at the extreme end of the gradient.

4.3.5 Species richness and Shannon-Wiener index of diversity

Species richness (Figure 4.14a; $p=0.050$) was marginally significantly correlated with the range condition gradient in the dune crest habitat, but the Shannon-Wiener index of species diversity was not (Figure 4.14b; $p=0.486$). In the dune slope habitat the Shannon-Wiener index of diversity was significantly higher in the farms with high range condition scores (Figure 4.15b; $p=0.035$) but species richness was not significantly correlated (Figure 4.15a; $p=0.320$). In the dune street habitat species richness was marginally significantly correlated with the range condition gradient (Figure 4.16a; $p=0.042$), but the Shannon-Wiener index of diversity increased significantly with better range condition (Figure 4.16b; $p=0.16$). The overall mean Shannon-Wiener index of species diversity score decreased significantly across the range condition gradient ($p=0.043$) but total species richness did not ($p=0.300$) (Figure 4.17).

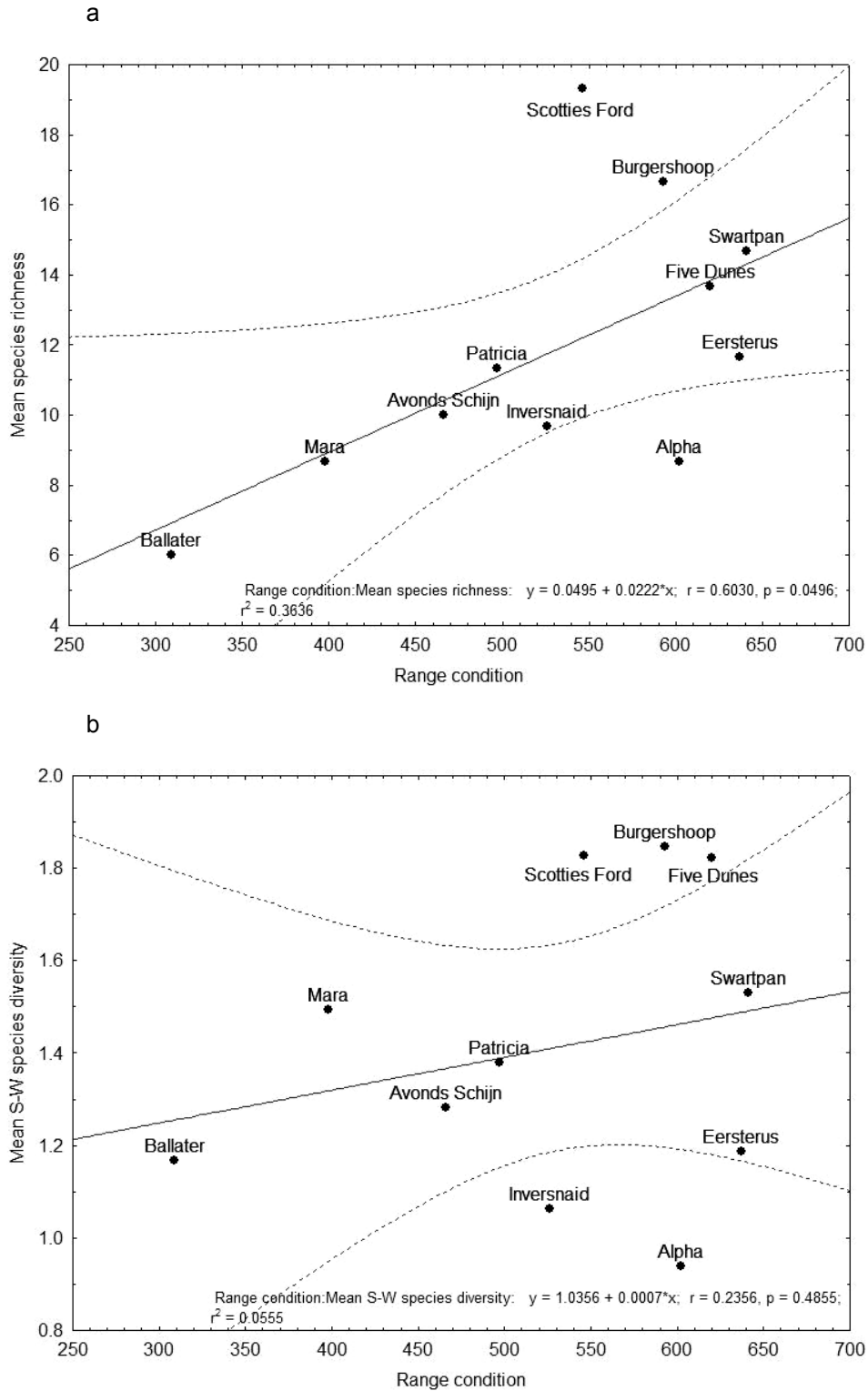


Figure 4.14 Changes in (a) species richness and (b) Shannon-Wiener index of diversity over the range condition gradient for the dune crest habitat. Dotted lines indicate 95% confidence levels.

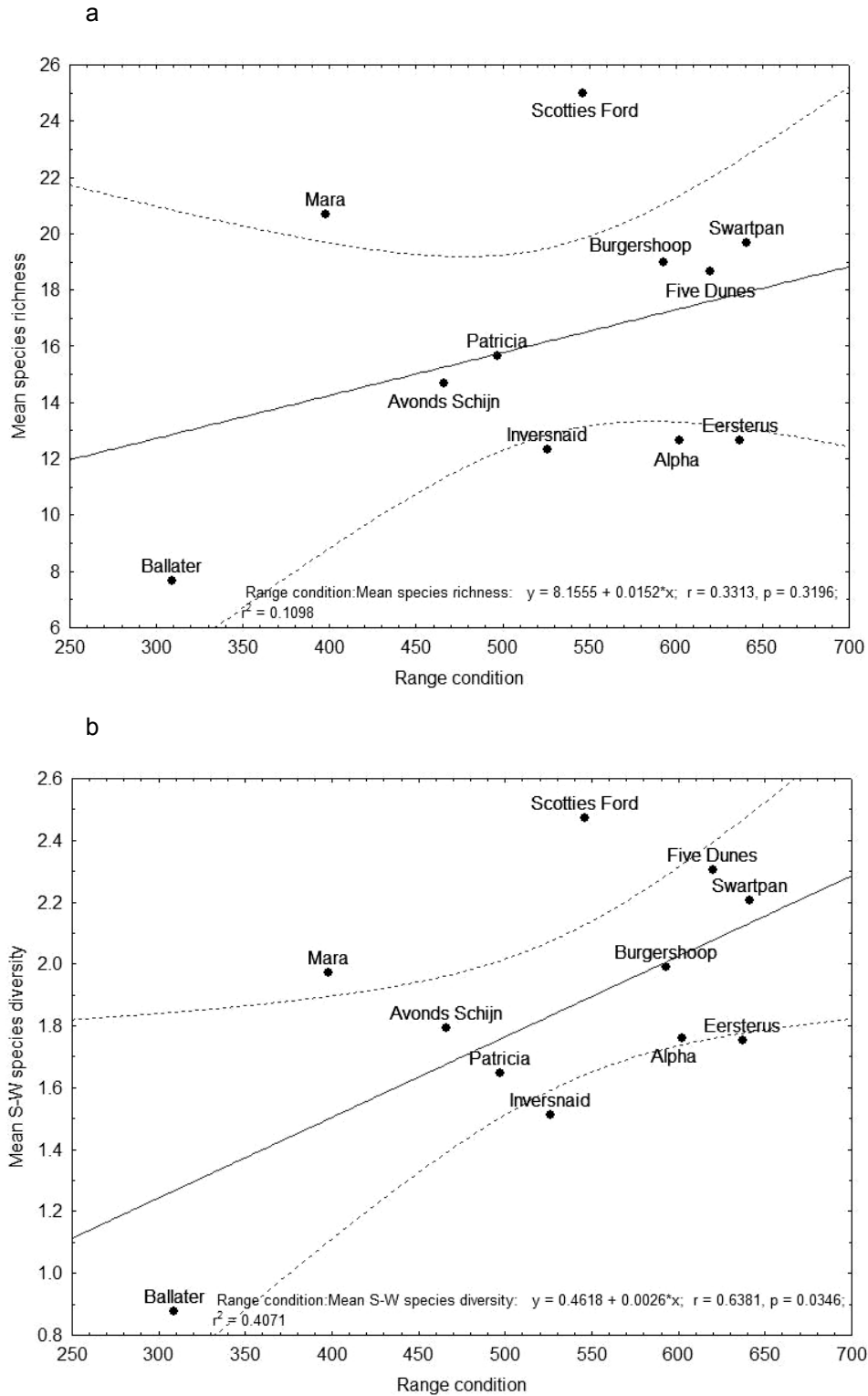


Figure 4.15 Changes in (a) species richness and (b) Shannon-Wiener index of diversity over the range condition gradient for the dune slope habitat. Dotted lines indicate 95% confidence levels.

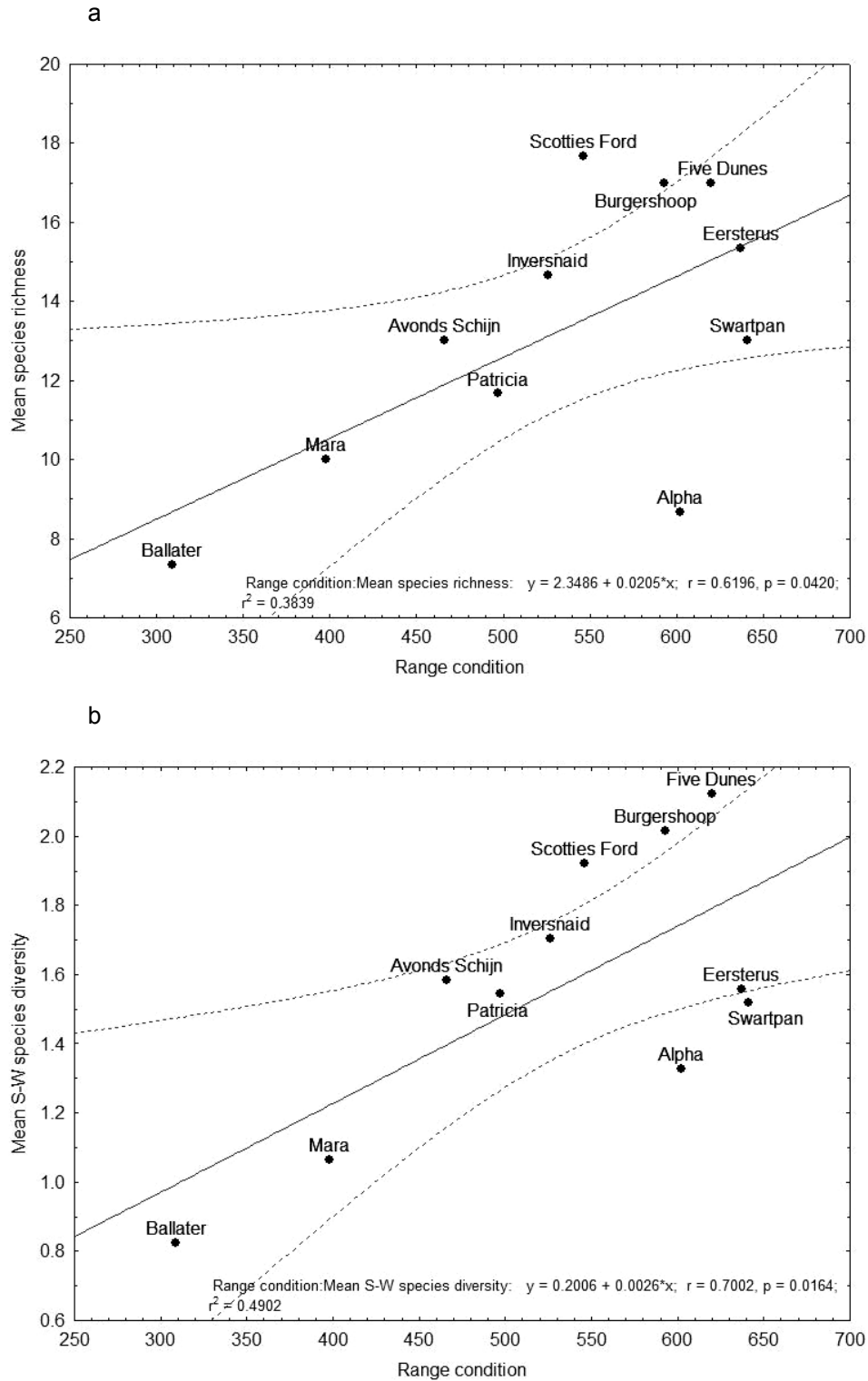


Figure 4.16 Change in (a) species richness and (b) Shannon-Wiener index of diversity over the range condition gradient for the dune street habitat. Dotted lines indicate 95% confidence levels.

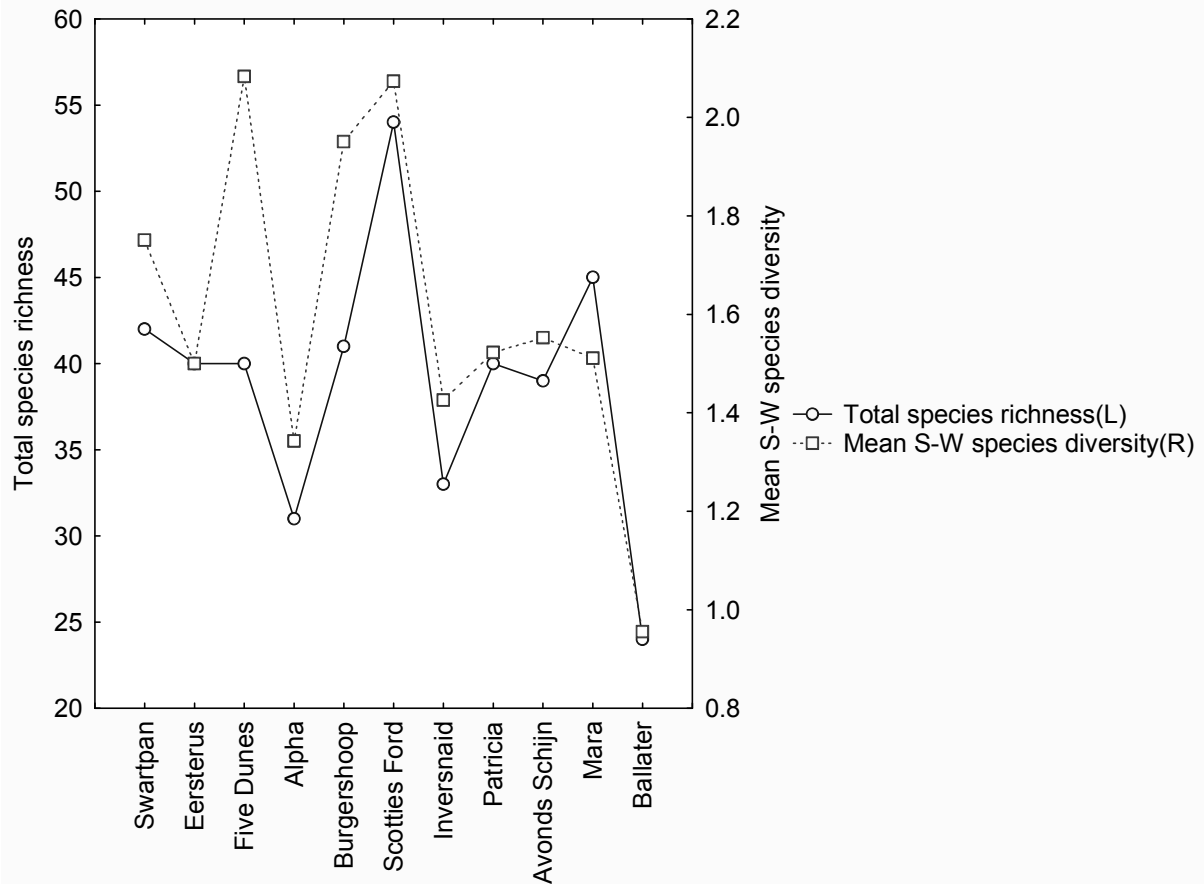


Figure 4.17 Total species richness and mean Shannon-Wiener index of species diversity for 11 farms along a degradation gradient in the southwestern Kalahari.

4.4 General discussion

4.4.1 Range condition

In order to establish an objective grazing gradient across all the farms included in the study the range condition was calculated (Figure 4.1). Based on the range condition gradient the farms could subjectively be separated into two groups: (1) five farms that were in good condition (scores from 593 to 641) and (2), six farms that were moderately to severely utilised and in an average to poor condition (scores from 309 to 546). The range condition gradient corresponded well with the initial broad classification of each of the farms in which farms were categorized as being in good to very good condition, average to below average condition or poor to very poor condition.

Bush encroachment has been associated with overgrazing (Skarpe, 1990b; Ringrose *et al.*, 1996; Palmer & Van Rooyen, 1998) and shrub cover (mostly *Rhigozum trichotomum* and *Acacia mellifera*) should therefore be a valuable parameter to identify a grazing gradient. Overgrazing also leads to an increase in annual plant cover (Van Rooyen *et al.*, 1991) and bare surface area of especially the dunes (Palmer & Van Rooyen, 1998) and a decrease in perennial grass cover (Van Rooyen *et al.*, 1991; Palmer & Van Rooyen, 1998). An increase in bare surface area would conversely imply a decrease in overall cumulative cover and basal cover. *Schmidtia kalahariensis* is the main contributor to annual grass cover. Although a characteristic, omnipresent species in the Kalahari, the grass is only palatable when dry (Du Toit, 2001) and should increase under intense grazing as annuals have been reported to do (Leistner, 1967; Van Rooyen *et al.* 1994). Total cumulative cover and perennial grass cover showed significant positive correlations with the range condition whereas evidence of bush encroachment, grazing and browsing as well as shrub cover and bare surface cover showed significant negative correlation with range condition (Table 4.4).

4.4.2 Correspondence analysis of floristic data

Dune veld vegetation is grouped into four classes by Leistner (1967) *viz.* dune valleys, foot slopes, slopes and crests according to sand compactness (sand grades 1–4), each with prominent plant species. The CA ordination of the relevé data produced a distribution of samples where the dune crest habitat was clearly distinguished from the dune slope and dune street habitats (Figure 4.2). Several species were characteristic of the dune crest habitat even in intensely utilized areas, although palatable species were reduced to some degree due to intense utilisation. *Stipagrostis amabilis*, *Crotalaria spartioides*, *Boscia albitrunca*, *Eragrostis trichophora* and *Limeum arenicum* were all examples of such dune crest specific species.

The distribution of dune slope and dune street relevés did not appear to be well separated. However, when farms with high range condition scores were separated from those with low range condition scores, dune slope relevés of the farms with high range condition scores aggregated at the top of the CA ordination plane (Figure 4.3), while dune street relevés stretched from the dune slope aggregation to the bottom-right. The dune slope and dune street relevés appeared to migrate to the bottom right of the ordination space if range condition decreased and veld was overutilized. Due to the loss of especially perennial grass species that were characteristic of the dune slope habitat (e.g. *Aristida meridionalis*, *Centropodia glauca* and *Eragrostis lehmanniana*) during intense utilization, dune slope relevés became more similar to dune street relevés. This shift was enhanced by the colonization of the dune slope habitat by annual grass species, notably *Schmidtia kalahariensis*, and shrubs such as *Rhigozum trichotomum* during overutilisation, which

caused homogenization of the dune slope and dune street habitats. The transition between the dune slope and dune street habitats can be very gradual with a broad ecotonal region.

Dune crest relevés 30, 33 and 36 of the farm Ballater stood out from the distribution pattern described previously. This farm was exceptional in that some areas on the farm had been severely degraded. Typical dune topography had been altered by the flattening and lowering of the denuded dune crests (Figure 2.19 in Chapter 2). Mean cover by *Stipagrostis amabilis* had been reduced to only 3.5%, whereas mean cover of the unpalatable shrub *Hermannia tomentosa* increased to 4.7%. The only other perennial grass species found in this habitat was *Eragrostis lehmanniana* (mean cover of 0.03%). Rutherford & Powrie (2009) conducted a comparative study of the adjacent farms Ballater and Avond Schijn (both also included in this study) and also observed lower total perennial cover and lower graminoid cover on Ballater, which experienced high utilisation pressure.

From the distribution of habitat relevés in the ordination plane (Figures 4.2 – 4.4) it was observed that the three different habitats were separated along the x-axis: dune crest on the left, dune slope in the center and dune street on the right. Furthermore, a degradation gradient existed along the x-axis within each habitat subgroup. Dune crest relevés span from lower degradation on the left to higher degradation on the right. Dune slope and dune street relevés also respectively span from low degradation on the left to higher degradation on the right. The dune crest appeared to be robust as a distinct habitat type, even under intensive utilisation. The farms with low range condition scores all exhibited a marginal shift. It was only when this habitat was severely overutilized that it changed its characteristics as illustrated by the farm Ballater. Under these utilisation pressures dunes become bare and mobile, as is also observed in the degraded Mier area of the Kalahari (Van Rooyen, 1998). The less pronounced shift of degraded dune crest relevés can be attributed to the unique habitat and species composition, limiting its affinities with degraded dune slope and dune street habitats. Furthermore, herbivores first utilise the dune street, followed by the dune slope and then the dune crest. The first signs of degradation would therefore become apparent in the dune streets, and the dune crests later. Dune crests are more demanding for large herbivores and have less palatable species (e.g. *Stipagrostis amabilis*, *Requienia sphaerosperma*) than the dune slope (e.g. *Centropodia glauca*) and dune street (*S. obtusa*, *S. ciliata*) habitats (Van Rooyen *et al.*, 1994). The dune streets also have a greater cover of annual grass and forb species during the rainy season (Thomas *et al.*, 2000), which would attract herbivores (*S. kalahariensis* is only palatable in its senescent form). This robustness as a habitat type could mask signs of overutilisation of the dune crest.

4.4.3 CCA-based dune crest grazing gradient

In the dune crest habitat there were two major groups of explanatory variables that stood out. The first group consisted of total cumulative cover, perennial grass cover and species richness, which were strongly correlated with each other ($p=0.000$ in all cases). Farms with high range condition scores were positively associated with each of these parameters. The arrows of these parameters in the ordination therefore point in the direction of lower utilisation and better veld condition. The second group of variables of note consisted of grazing evidence, browsing evidence, trampling evidence, bush encroachment evidence and bare surface cover, which all shared strong positive correlations ($p\leq 0.027$ in all cases, except bush encroachment evidence vs. bare surface cover where $p=0.053$). The direction of the arrows of these habitat parameters in the ordination pointed in a direction of greater utilisation and poorer veld condition. Importantly, the parameters of the first group mostly showed a significant negative correlation with the parameters of the second group (Table 4.5). The strong association within the two groups, the negative correlation between the two groups and the diverging directions of change of the two groups made it possible to identify a grazing or utilisation gradient in the ordination, which is indicated by the dashed arrow.

In the ordination the farms can subjectively be arranged from underutilized to overutilized in the following sequence:

Burgershoop → Eersterus → Swartpan → Five Dunes → Inversnaid → Alpha → Scotties Ford → Patricia → Avonds Schijn → Mara → Ballater

This sequence corresponded well with the range condition gradient with only minor changes in the order. Farms with high range condition scores were generally on the left in the ordination plane and farms with low range condition scores to the right. However, the distinction is not very pronounced, with only the severely degraded sites clearly shifting to the right.

4.4.4 CCA-based dune slope grazing gradient

In the case of the dune slope habitat, two groups of environmental variables were evident. The first group of parameters that showed significant positive correlations with each other were perennial grass cover and cumulative cover ($p\leq 0.000$; Figure 4.6). These two variables were also strongly positively correlated with range condition ($p=0.001$ and $p=0.042$ respectively; Table 4.4). This grouping was similar to that identified in the dune crest habitat except for the absence of species richness. A decrease in these variables should point to overgrazing. The second group of

environmental variables consisted of bare surface cover, annual grass cover, grazing evidence, browsing evidence, trampling evidence and bush encroachment evidence (Figure 4.6 and Table 4.6). This group was also similar to that of the dune crest habitat except for the addition of annual grass cover. Increases in these factors should point towards overgrazing. Due to the common occurrence of *Schmidtia kalahariensis*, its increased cover should not be seen as an indicator on its own, but in conjunction with changes in other parameters such as shrub cover, perennial grass cover and bare surface cover. Many significant negative correlations between the variables in the two groups were also found in the dune slope habitat.

A subjective grazing gradient from underutilized to overutilised range could be constructed arranging the farms in the following sequence:

Burgershoop → Eersterus → Alpha → Five Dunes → Swartpan → Inversnaid → Mara → Scotties Ford → Avonds Schijn → Patricia → Ballater

This sequence again corresponded well with the range condition gradient except for the farm Mara that was placed higher up the gradient, but still among the group of low range condition farms.

4.4.5 CCA-based dune street grazing gradient

Two main groups of environmental variables also emerged from the dune street CCA ordination (Figure 4.7). The first group that showed consistent significant positive correlation among its members ($p \leq 0.001$; Table 4.7) and negative correlation with the grazing gradient ($p \leq 0.028$; Table 4.4) consisted of shrub cover, browsing evidence, grazing evidence and bush encroachment evidence. This was similar to the groupings identified in the dune crest and dune slope habitats but shrub cover was a new addition. The dune street habitat carries a high animal load because much of the fodder is located in this habitat and it is also easier for animals to move around on the firmer substrate of the dune street (Van Rooyen *et al.*, 1994). High animal traffic around water holes located in dune streets is therefore consistent with overgrazing. Higher shrub cover also points to overgrazing. The second group consisted of perennial grass cover, Shannon-Wiener diversity, species richness and other annual cover (herbs). In the dune street habitat Shannon-Wiener diversity increased significantly with higher range condition scores (Figure 4.16b) and species richness increases weakly with higher range condition scores (Figure 4.16a). Cover by other annual species could potentially point to higher utilisation, but differences may be due to local soil moisture content.

Many significant negative correlations occurred between the two groups (Table 4.5). A subjective grazing gradient could be identified with the farms subjectively arranged from underutilized to overutilised in the following sequence:

Burgershoop → Five Dunes → Eersterus → Swartpan → Avonds Schijn → Alpha → Inversnaid
→ Scotties Ford → Ballater → Patricia → Mara

The arrangement found here is somewhat different from that produced by the range condition scores and the dune crest and dune slope ordinations. However, in general, the grazing gradients derived from the CCA ordinations of the three habitat types corresponded well with the range condition gradient. The gradient as produced in the range condition assessment was therefore accepted as a fair reflection of the grazing gradient.

4.4.6 Cumulative cover and life / growth form cover

In the dune crest habitat significant positive correlations existed between range condition and the mean total cumulative cover ($p=0.000$), perennial grass cover ($p=0.000$) and bare surface cover ($p=0.000$) (Table 4.4). Because *Stipagrostis amabilis* was such a dominant perennial grass species in the dune crest habitat (Figure 4.12a), changes in its presence had a big influence on perennial grass cover. *Stipagrostis amabilis* and *Eragrostis lehmanniana* are Category 2 grass species and declined as expected with increased grazing pressure, although overall cover of *E. lehmanniana* was low throughout. Cover of *Eragrostis trichophora*, classified as a Category 3 species, was generally higher in high range condition farms than in low range condition farms. *Stipagrostis amabilis* is a robust and woody grass species not preferred by herbivores and only utilised in the absence of other sources of fodder. Its young shoots are eaten by wildlife (Van Rooyen, 2001). Its decline can therefore be viewed as a good indicator of veld degradation.

All other life/growth form types occurred in low proportions irrespective of range condition and no significant correlations occurred with range condition. *Crotalaria spartioides* was the only shrub species specifically associated with the dune crest and although unpalatable and toxic (Van Rooyen, 2001), did not increase in overutilized veld (Figure 4.13a). The deep, unstable and infertile sands on dune crests prohibit shallow rooted shrubs such as *Rhigozum trichotomum* from flourishing on dune crests and therefore preclude shrub encroachment in this habitat.

Schmidtia kalahariensis, an annual grass species, reacts quickly to favourable local environmental conditions and can even tolerate the unstable and variable conditions on dune crests. Mace (1991) and Van Rooyen *et al.* (1994) state that annual grass species in the Kalahari

do not only act as the classical early succession/pioneer species, because annual grass and herb dominance also occurs after overutilisation as well as in seasons with a high rainfall. As long as plants receive some protection from sandblasting, by mostly *Stipagrostis amabilis* plants, and have sufficient moisture supply *S. kalahariensis* will persist on the dune crests. Denuding of dune crests also leads to the removal of seeds from the substrate which makes reclaiming of dune crests very difficult.

Mean cumulative cover showed a significant positive relationship ($p=0.042$) with the grazing gradient in the dune slope habitat (Table 4.4). In arid regions such as the Kalahari good rainfall years, as experienced during the survey period, can cause flushes of annual vegetation. The owner of the farm Swartpan reported 287 mm for the 2004/2005 season and the owner of the farm Alpha 365 mm for the same period. The high total vegetation canopy cover after high rainfall events can mask the real veld condition of habitats. The canopy cover of different life/growth forms in the dune slope indicated that farms at the lower end of the grazing gradient had high total cover, but that perennial grasses made a small contribution to total cover. Contributions by annual grass species and other annual species together with encroaching shrubs increased total cover markedly. *Aristida meridionalis* is a Category 3, *Centropodia glauca* a Category 1 and *Eragrostis lehmanniana* a Category 2 grass species. These grass species declined as veld was more intensely grazed. The relationship between bare surface cover and the range condition gradient is weaker than in the dune crest habitat, but still significant ($p=0.042$).

Total tree cover was higher in the dune slope habitat than in the dune crest habitat. This was because *Acacia haematoxylon*, *Acacia erioloba* and *Boscia albitrunca* were all prominent in this habitat. Tree cover was not correlated with range condition on the dune slopes. Large trees are able to persist during overutilization, provided their canopies are out of reach of herbivores (Skarpe, 1990a), because of their deep root systems that both anchor and supply sufficient resources to the plants. Skarpe (1990b) observed that *Boscia albitrunca* trees have higher cover in areas overgrazed for 12 years than in undisturbed veld, but that cover decreased again in areas overgrazed for more than 30 years. In the same study *Acacia mellifera* was observed to increase dramatically with overgrazing. Shrub cover was also not significantly correlated with range condition in the dune slope but cover of *Rhigozum trichotomum* and *Acacia mellifera* was distinctly higher in low range condition farms. *Hermannia tomentosa* was the dominant perennial herb although it occurred in veld that was in good condition it increased when veld was overgrazed (Figure 4.11b & c). On the farm Ballater some areas of extreme overutilisation had *H. tomentosa*, *B. albitrunca* and *R. trichotomum* as the only species present in all habitats (see photographs in Figure 2.19).

No significant correlation existed between mean total cumulative cover and range condition in the dune street habitat ($p=0.932$). Mean cumulative cover was however frequently higher in overgrazed farms than in underutilized farms (Figure 4.12). This was largely due to the increased presence of *Rhigozum trichotomum* and *Schmidtia kalahariensis*. A significant positive correlation existed between perennial grass cover and range condition ($p=0.000$) and a significant negative correlation between both shrub cover ($p=0.16$) and annual grass cover ($p=0.007$) and the range condition gradient. *Stipagrostis ciliata* decreased as grazing intensity increased and *S. obtusa* diminished under high grazing intensity. *Stipagrostis uniplumis* had a large canopy and in terms of plant numbers may not be as common as Figure 4.12c suggests. This grass species also had high cover percentages under strong grazing pressures. Although *Schmidtia kalahariensis* occurred throughout the region, its growth was favoured under conditions of overutilisation where competition from perennial grasses was diminished. Neither tree cover nor other annual cover showed any relationship with grazing intensity.

In all three habitat types dwarf shrub species occurred in such low numbers that it was impossible to deduce any relationship between species' cover and range condition.

Some authors have reported no relationship between range degradation and distance from artificial watering points. Van Rooyen *et al.* (1991, 1994) found no relationship between vegetation change and distance from watering points in the Kgalagadi Transfrontier Park, a large conservation area. Fourie *et al.* (1987) found no correlation between *R. trichotomum* dominance and livestock overgrazing over a 16 year period. A large number of savanna studies, especially in Botswana, have however reported distinct vegetation degradation and vegetation zoning ("piospheres") around watering points under livestock farming conditions which were observed both on the ground (Perkins and Thomas, 1993; Perkins, 1996; Brits *et al.*, 2000; Thomas *et al.*, 2000), by remote sensing (Ringrose *et al.*, 1996; Palmer & Van Rooyen, 1998) and by artificial modeling prediction (Jeltsch *et al.*, 1997; Weber *et al.*, 1998). Simultaneous soil chemistry gradients have also been recorded (Perkins & Thomas, 1993). Intensive livestock ranching within restricted boundaries (camps) and with few watering points limit the movements of herbivores, leading to concentrated and increased grazing pressure and grazing evidence on a farm as a whole when compared to the open systems of national parks. Livestock are also more water dependent than indigenous wildlife species such as springbok and gemsbok (Bergström & Skarpe, 1999), are less capable of moving to areas that can provide in their dietary requirements (Skarpe, 1991b) and may be less mobile on dune crests than dune streets than indigenous wildlife species, resulting in increased utilization of the dune street habitats. This also results in greater veld utilisation around watering holes which manifests as piospheres.

4.4.7 Species richness and Shannon-Wiener index of diversity

Species richness was marginally significantly correlated with the range condition gradient in the dune crest ($p=0.050$) and dune street ($p=0.042$) habitats but not in the dune slope habitat ($p=0.320$). On all except two farms the dune slopes produced the highest species richness scores, possibly because typical dune crest and dune street species may also be encountered on the dune slopes that inflated species counts. The total species richness recorded for each farm (all habitats combined) did not show significant correlation with the range condition gradient ($p=0.300$). Leistner and Werger (1973) reported a decrease in species richness from the dune crests to the dune valleys (streets), whereas in the present study, dune slopes had the highest species richness. Rutherford and Powrie (2009) observed significantly lower species richness (38 vs. 16) and species evenness (0.63 vs. 0.07) on Ballater than Avond Schijn, but this was an extreme contrast in range condition that did not reflect a moderated gradient of range condition as is presented in the present study. Of interest was the relative classification of Rutherford and Powrie (2009) of the two respective properties as high utilisation (HU) and low utilisation (LU), although with the gradient identified in this study, Avond Schijn was observed to be a farm of poor range condition.

The farm Scotties Ford stood out as the farm with the highest species richness in all habitats. This could be attributed to its recent management history. The farm became the property of the local Khomani San community in 1999. The farm had previously been a commercial farm as all other farms in this study. Since the transfer of ownership, management emphasis had changed from commercial to subsistence farming with different stocking densities and livestock species proportions. On commercial farms the emphasis is on sheep farming, whereas the San community favour farming with goats. Goats are both browsers and grazers, but sheep are only grazers. Differences in feeding behaviour may cause plant diversity to increase with goat farming. Goats for example utilize a greater number of species and may aid the dispersal of plant species not utilized by sheep.

The Shannon-Wiener index of diversity correlated significantly with range condition in the dune slope ($p=0.035$) and dune street ($p=0.016$) habitats. As a result of the dominance of *Stipagrostis amabilis* on the dune crests when range was in a good condition, the Shannon-Wiener index of diversity did not increase as range condition improved ($p=0.485$). Van Rooyen and Van Rooyen (1998) showed that the Shannon-Wiener index is higher in dune crests and dune slopes (2.59-3.04) than in dune valleys (streets) and low in pan margins and floors (0.36-1.48). Although pans were not included in this study, the mean Shannon-Wiener index was found to be highest in the dune slopes (1.8), followed by dune streets (1.6) and dune crests (1.4) (Figures 4.14, 4.15 and

4.16). Rutherford and Powrie (2009) also observed higher overall Shannon-Wiener index of diversity for Avond Schijn than Ballater.

4.5 Conclusion

Dune crests, dune slopes and dune streets are distinct habitat types with differences in substrate composition, abiotic influences (e.g. wind) and plant communities. Floristically, dune crests were clearly separated from the other habitats. However, the floristic composition of dune slopes and dune streets grade into each other with the level of similarity depending on the grazing pressure. Perennial grass cover was reduced by grazing intensity in all habitats and could be witnessed in local grazing and browsing evidence. A reduction in cumulative cover and an increase in bare surface cover were indicative of greater grazing intensity in the dune crest and dune slope habitats. In the dune streets shrub cover and annual grass cover increased when veld was overgrazed.

Species richness increased when veld condition improved in the dune crest and dune street habitats, although the significance of this relationship was marginal. When viewed across all habitats on farms however, species richness did not change significantly with range condition. The Shannon-Wiener index also increased when veld condition improved in the dune street and dune slope habitats as well as across all habitats. This relationship was not however found in the dune crest habitat.

Degradation of dune veld occurs in a specific sequence. The first habitat to be affected by overgrazing is the dune street habitat, because (a) it is an easy corridor for movement for especially livestock, (b) watering points are positioned in dune streets, (c) most of the palatable grass species are found in the dune streets and (d) most of the prominent perennial grass species are Category 1 grasses. Overgrazing leads to the loss of perennial grasses and an increase in shrub cover (bush encroachment) and annual grass cover in the dune street. If overgrazing persists these effects extend to the dune slopes, where bare surface patches also start to emerge. As dune streets and slopes become severely depleted grazing animals move to the dune crests and start to graze the tough *Stipagrostis amabilis* which is normally avoided when other fodder is available. This species is essential to stabilize and protect the dune crest. Overutilisation of this grass species leads to bare dune crests.

It is possible to use the range condition score to establish a gradient reflecting past utilisation pressure. This gradient agreed well with the gradient established by multivariate analysis. The direct gradient analysis (CCA) clearly demonstrated which environmental variables were

associated with this gradient. In future, additional variables e.g. current stocking densities, historic stocking densities, and distance from watering points, can be incorporated into analyses to investigate their relationships.

Moisture plays a critical role in arid systems such as the Kalahari and has a profound influence on vegetation dynamics. Vegetation cover increases rapidly after rainfall events largely as a result of annual species that grow vigorously under these favourable conditions. It is hoped that the relatively close proximity of the farms to each other in this study reduced the effects of localized rainfall events to some extent.

Chapter 5

A plant functional trait analysis of selected dominant Kalahari plant species

Abstract

Environmental factors act as filters that select for those plant trait categories that promote species establishment, persistence and reproduction. Edaphic conditions, moisture availability and utilisation pressure are among the key abiotic and biotic variables affecting vegetation composition and dynamics of arid and semi-arid ecosystems. The underlying homogeneous edaphic properties of the soil in the dunefields of the southern Kalahari allowed for trait attribute comparisons across a grazing gradient without the compounding effect of soil variability. A selection of 112 Kalahari plant species was investigated for a set of traits that were regarded as important in grazing response evaluation. Different functional groups were identified and compared when the trait pool was composed of either the entire trait data set, the vegetative traits data set only or the reproductive traits data set only. Vegetative traits exerted a strong influence over functional group composition when the entire trait data set was evaluated. The reproductive trait analysis differed from analyses of the entire trait data set and the vegetative traits data set. Prominent growth forms such as trees, shrubs, grasses and perennial or annual herbs were identifiable in all trait sets, but to a lesser degree in the reproductive trait set.

5.1 Introduction

The occurrence and proliferation of specific species in certain habitats can not be seen as an entirely random selection. There are criteria or assembly rules that should make it possible to predict the subset of the total species pool of a region that would occur in a specific habitat (Diaz *et al.*, 1999a). Environmental influences such as climate, disturbance and site productivity act as successive filters (assembly rules) that select for certain traits and functions out of the species pool (Woodward & Diament, 1991; Diaz *et al.*, 1999b).

If a habitat is characterized by a heterogeneous and diverse set of environmental filters that act on trait selection, for example diverse geology, climate, soil, grazing regimes and susceptibility to fire, it becomes difficult to attribute traits to a specific filter or filters. The southern Kalahari duneveld is a relatively homogeneous environment with presumably less diverse filters in operation at the landscape level and is therefore ideally suited for a study of grazing related traits. It must be stressed though that the southern Kalahari duneveld vegetation in its entirety is distinct from other regional vegetation types, mostly by virtue of its unique sandy soils with reduced water availability and nutrients (Van Rooyen & Van Rooyen, 1998).

Within the southern Kalahari duneveld mean annual rainfall for Twee Rivieren to the north of the study area is 220 mm per annum (Van Rooyen *et al.*, 1991) and 189 mm for Upington on the southern border (electronic data supplied by the South African Weather Service, 16 Feb 2006), but large variation in annual rainfall is common. For the small village of Askham just south of Twee Rivieren Leistner (1967) reported a mean annual rainfall from 1933 to 1950 of 176 mm, but with extremes of 72.9 mm per annum to 295.8 mm per annum. Great extremes in temperatures occur throughout the region, from -10°C in winter to highs of 45.4°C in summer (Van Rooyen *et al.*, 1990). Similar geological and edaphic conditions occur across vast expanses in the southern Kalahari (see Figure 2.3 in Chapter 2). Within this largely homogeneous environment it should be possible to separate grazing-dependent functional traits, thereby assembling functional types according to land use intensity. Although mean annual rainfall is approximately similar across the region, annual rainfall in different areas or even within the same area is an unpredictable variable. Skarpe (1996) foresaw that alterations in human land use would be the most important reason for large scale change in most savanna ecosystems in the near future and it could therefore be argued that human induced pressure would be a stronger driver of vegetation change than climatic factors or underlying edaphic conditions.

The plant functional type (PFT) concept was previously defined in Chapter 1 as “a set of trait states that represent a unified response to changes in the environment or have similar effects on the environment”. The species belonging to a PFT group therefore have similar

combinations of functional attributes (Navarro *et al.* 2006). Traits should not be considered in isolation but be compared with other traits, because some traits are often strongly related and represent a combined strategy distilled from a set of several traits (Westoby & Wright, 2006). Different combinations of PFTs may be employed within one locality for persistence within regional environmental parameters. Plant functional types assist in describing the changes that vegetation assemblages undergo over time by simplifying the component species set into sets of species with similar function/adaptation to disturbance (Grime *et al.* 1996; Gitay & Noble, 1997). Through modeling exercises predictions can also be made regarding possible changes to plant communities or landscapes in future (Körner & Jeltsch, 2008)

A universal plant functional group classification would be very difficult to achieve because plant functional types are specific to a region or a set of conditions (Skarpe 1996; Hadar *et al.*, 1999; Lavorel *et al.*, 1999). Therefore, the classification (trait set and trait categories) that is used in this study may not be directly applicable to other regions and should be employed with the necessary circumspection (McIntyre *et al.* 1999b), (for example, the canopy diameter categories used here may not be useful in tropical forests). As data sets for different regions of the world are accumulating however, our understanding of trait-environment linkages are improving, but more information is required on for example the cost-benefit relationships (Westoby & Wright, 2006) and the identification of traits that represent the real drivers of specific ecosystem functioning (Grime, 2006). Species diversity is still a prominent avenue to explore community theory, but emphasis on ecological-trait differences is increasing (Westoby & Wright, 2006). Development of trait databases is such that soon it may be possible to make use of this information for predictions on ecological change (Grime, 2006). It would be advantageous to have a wide range of trait information available on species from which to explore trait-environment linkages. A plant-based or “bottom-up” approach was used here, where plant traits thought to be important for growth, reproduction and survival were quantified (Scholes *et al.*, 1997; Weiher *et al.*, 1999). This is in contrast to the environmental “top-down” approach where main environmental parameters are segmented into ranges within which selected species may function (Scholes *et al.*, 1997).

The objectives of this part of the study were to investigate:

- Trait assemblages and the identification of Plant Functional Types among 112 common Kalahari plant species
- How PFT groups and assemblages are affected by reducing the trait sets to only vegetative traits or reproductive traits, or a more constrained set of both reproductive and vegetative traits
- Whether there are distinct associations and correlations between some specific pairs of traits

5.2 Materials and methods

One hundred and twelve common Kalahari plant species were investigated for 49 traits (Table 5.1). The trait selection was done according to the procedure described previously in section 3.3.1 of Chapter 3. Trait categories were defined by consulting the sources cited in Table 5.1. Trait evaluations that required field surveys were investigated according to the procedures described in section 3.3.2 of Chapter 3.

Multivariate analyses of species trait data were performed with Principal Co-ordinate Analysis (PCoA) in the software programme Syntax (Podani, 2000). Principal Co-ordinates (PCoA or Principal Co-ordinate Analysis) is a more general form of Principal Component Analysis (PCA) that allows the use of a wide array of distance measures and can give a marked improvement over PCA (McCune & Grace, 2002). The programme also allows for the simultaneous analysis of binary, ordinal and categorical data in a single data set. Trait categories are explained in Table 5.1.

A Principal Co-ordinates analysis (PCoA) was conducted on all species and all traits, except for specific leaf area (SLA) and leaf dry matter content (LDMC). This is because data on these two traits were not available for all species (56 of 112 species have data for these traits). The trait “plant and flower gender” was also removed because scores for these traits showed almost no variation among species. A total of 46 traits were therefore used in the complete trait analysis. Ordinations were investigated for groups which were interpreted as functional groups. The functional groups produced through the complete trait set PCoA were investigated in detail for trait attributes.

Trait data were subsequently split into vegetative (27) and reproductive (20) traits and analysed separately. The functional groupings based on vegetative and reproductive traits were also produced by PCoA analysis. Functional groups thus identified were explained in detail and the vegetative functional groups compared with reproductive functional groups. The variation in the composition of the groups was compared with the full trait data set analysis. A Product-Moment correlation analysis was conducted in STATISTICA (StatSoft, Inc., Tulsa, U.S.A.) to compare trait affinities for the complete 112 species data set and the 15 traits that had continuous variable scores. The 56 species for which SLA and LDMC data were available were subjected to a separate Product-Moment correlation analysis in conjunction with the same 15 continuous traits.

Table 5.1 Traits investigated in this study with a description of the trait categories, definitions of traits and sources for trait definitions. The trait sequence follows an intuitive approach for grouping traits for example plant physical dimensions and forms, leaf traits and stem traits.

Trait	Trait categories	Definition	Information source (Reference)
Plant height (cm)	≤3; >3–10; >10–50; >50–100; >100–150; >150–200; >200–300; >300	The vegetative vertical maximum height of a plant, discounting any abnormal protrusions. In grasses the inflorescences are included in height measurements, due to the photosynthetic capability of culms.	Ecological Flora of California ^a Author ^b
Canopy diameter (m)	≤0.2 m; >0,2–0.5; >0.5–1; >1.0–2.0; >2.0;	The vegetative horizontal maximum width of the canopy, discounting any abnormal protrusions. Should preferably be the mean of two perpendicular measurements.	Author ^b
Canopy density (%)	≤25; >25–50; >50–75; >75	The theoretical “footprint” of the canopy on the ground when viewed from above, expressed as a percentage of total possible cover (100%)	Author ^b
Raunkier life form	Phanerophyte – nano (≤2 m); Phanerophyte – micro (>2–5 m); Phanerophyte – Meso (>5–50 m); Chamaephyte – woody dwarf shrub (frutescent); Chamaephyte – semi-woody dwarf shrub; (suffrutescent); Chamaephyte – herbaceous; Hemicryptophyte – caespitose; Hemicryptophyte – reptant; Geophyte – bulbous (bulbs, tubers); Geophyte – rhizome; Therophyte – caespitose; Therophyte – reptant; Liana - phanerophytic/chamaephytic Liana – hemicryptophytic	See Appendix B	Mueller-Dombois & Ellenberg (1974)
Life span (years)	<1; 1–2; >2–5; >5–25; >25–50; >50		BIOTA AFRICA ^c
Organs shed	Plant; Shoot; Leaf; Evergreen	Organs shed during dry season or under unfavourable conditions.	Own interpretation
Shoot architecture	Appressed basal rosette; Raised basal rosette; Caespitose tuft; Sub-caespitose tuft; Hydra; Broom; Fountain; Caespitose shrub; Semi-circular shrub; Rhizomatous shrub; Procumbent; Scandent; Liana; Fan; Decumbent cup; Erect		BIOTA AFRICA ^c and own interpretation. Compare Appendix B
Stem density	Herbaceous; Hemixylous (suffrutescent); Ligneous	See definition list	BIOTA AFRICA ^c
Trophic type	Nitrogen fixing; No nitrogen fixing		BIOTA AFRICA ^c
Photosynthetic pathway	C ₄ ; C ₃		BIOTA AFRICA ^c
Clonality	None; Aboveground; Belowground; Lying branches sometimes rooting		BIOTA AFRICA ^c
Spinescence: Stem (Modified stems and stipules although a stipule is an outgrowth of the leaf base)	None; Slightly spiny; Intermediately spiny; Very spiny		BIOTA AFRICA ^c
Spinescence: Leaf (Modified leaves)	None; Slightly spiny; Intermediately spiny		BIOTA AFRICA ^c
Leaf area (mm ²)	Leptophyll (≤25); Nanophyll (>25–225); Microphyll (>225–2025); Mesophyll (>2025–18225); Macrophyll (>18225–164025)	The one-sided projected surface area of an average leaf or leaf lamina	Ecological Flora of California ^a Cornelissen <i>et al.</i>
Specific leaf area (mm ² .mg ⁻¹)	≤ 0.5; > 0.5–1.0; > 1.0–1.5; > 1.5–2.0; > 2.0	The one-sided area of a fresh leaf divided by its oven-dry mass	Author ^b Cornelissen <i>et al.</i>
Leaf dry matter content (mg.g ⁻¹)	≤ 200; > 200–300; > 300–400; > 400–500; > 500	The oven-dry mass (mg) of a leaf divided by its water-saturated fresh mass (g)	Author ^b Cornelissen <i>et al.</i> (2003)
Leaf colour	All green; All glaucous (blue-greyish green); Green plus glaucous or with white markings, all on one surface (including spines); Discolourous		Author ^b
Leaf angle (leaf blade angle with respect to substrate)	Vertical or oblique upwards; Horizontal to slightly oblique upwards or downwards; Vertical to horizontal Hanging; Spiral; No specific orientation		BIOTA AFRICA ^c
Leaf hairiness adaxial	Glabrous; Sparse; Intermediate; Dense		BIOTA AFRICA ^c
Leaf hairiness abaxial	Glabrous; Sparse; Intermediate; Dense		BIOTA AFRICA ^c
Leaf consistency	Semi-succulent; Malacophyllous (mesomorph); Semi-sclerophyllous; Sclerophyllous		BIOTA AFRICA ^c and author ^b
Leaf/stem exudates	Wax; Latex; Resinous (Gum); Aqueous; Sticky; None		Author ^b



Leaf longevity	≤3 months; >3–6 months; >6–12 months; >12 months	Author ^b
Leaf type	Simple; Pinnate; Bipinnate; Palmate or trifoliolate	Ecological Flora of California ^a and
Leaf shape	Linear; Strap-shaped; Oblong; Lance-shaped; Inverse Lance-shaped; Spoon-shaped; Oval; Elliptic; Ovate; Rounded; Heart-shaped; Kidney-shaped; Obovate; Diamond-shaped; Triangular	Brickell (2003)
Leaf margin	Entire; Dentate; Denticulate; Serrate; Crenate; Lobed; Pinnatifid; Palmatifid; Undulate; Revolute	Barnard <i>et al.</i> (2004)
Carbohydrate storage	Specialized organs; No storage organs	Kahmen & Poschlod (2004)
Response to fire	Killed; Resprouts from aboveground buds; Resprouts from belowground buds	Author ^b
Palatability to livestock	Toxic; Unknown; Unpalatable; Limited palatability; Palatable; Very palatable	BIOTA AFRICA ^c
Growth phenology	Warm and dry season (ca. April/May; September/October); Hot and humid season (ca. November–March); Cold and dry season (ca. June–August)	Author ^b
Flowering phenology	Warm and dry season (ca. April/May; September/October); Hot and humid season (ca. November–March); Cold and dry season (ca. June–August)	Author ^b
Fruiting phenology	Warm and dry season (ca. April/May; September/October); Hot and humid season (ca. November–March); Cold and dry season (ca. June–August)	Author ^b
Germination phenology	Warm and dry season (ca. April/May; September/October); Hot and humid season (ca. November–March); Cold and dry season (ca. June–August)	Author ^b
Sociability	Single; Loose groups; Dense clumps; Large herds	BIOTA AFRICA ^c and
Pollination mode	Wind; Specialized zoochorous; Unspecialized zoochorous; Self; Water	BIOTA AFRICA ^c and author ^b
Plant and flower gender	Monoecious; Dioecious	Author ^b
Inflorescence prominence	Exposed; Indeterminate	Faegri & van der Pijl (1979)
Inflorescence type	Solitary, Cluster; Cyathium; Capitulum; Umbel; Cyme; Spike; Raceme; Thyrses; Panicle	Brickell (2003)
Flower shape	Bell-funnel; Bowl-dish; Trumpet; Brush; Tube; Flag; Floret; Gullet	Brickell (2003); Faegri & van der Pijl
Flower colour	Brown; Green-grey; Pink-red; Purple; Purple-green; Purple-red; White; White-brown; White-green; White-pink; White-pink-purple-blue; White-purple-blue; White-yellow; White-yellow-green; White-yellow-pink-purple; Yellow; Yellow-brown; Yellow-green; Yellow-pink-purple	Author ^b
N seeds per fruit	≤ 2; >2–5; >5–10; >10;	Author ^b
Seed mass class (mg)	≤ 0.1; >0.1–1; >1–10; >10–100; >100–1000	Author ^b
Fruit type	Achene; Berry; Capsule; Caryopsis; Drupe; Nut; Pepo; Utricle	BIOTA AFRICA ^c , Ecological Flora of
Diaspore morphology	Bristled seed; Burred seed; Winged seed; Plumed seed; Glandular seed; Burred fruit; Winged fruit; Fleshy pulp fruit; Tumbleweed; No fruit or seed attachments	
Telechory	No obvious agent; Anemochory; Epizoochory; Endozoochory; Autochory (includes ballism)	BIOTA AFRICA ^c
Antitelechory	No antitelechory; Synaptospermy; Heterodiaspory; Trypanospermy; Hygrochasy; Myxospermy;	Author ^b
Fecundity (seeds per plant per reproductive event)	≤200; >200–500; >500–1000; >1000–5000; >5000	BIOTA AFRICA ^c and author ^b
Seed dormancy	None; Moderate; Strong	Ecological Flora of California ^a and own
Seed bank type	None; Transient; Permanent	BIOTA AFRICA ^c

^a Ecological Flora of California forms part of the Jepson Flora Project of the University of California, Berkeley

(<http://ucjeps.berkeley.edu/efc/categories-table.htm>, 21 November 2006).

^b Author refers to trait categories that were compiled by the author based on literature descriptions and the spread of trait scores for specific traits, personal field experience and interpretations of what appropriate categories would be.

^c BIOTA AFRICA Field Forms 2005, February 19 (unpubl.)



Table 5.2 The occurrence of nodulation in Leguminosae taxa investigated in this study (De Faria *et al.*, 1989)

Leguminosae species investigated in this study	Sufamily	Tribe	Genus	No. of spp. in genus	No. of spp with data	Nodulation present	Nodulation absent	Nodulation conclusion for species
<i>Acacia erioloba</i>	Acacieae	Mimosoideae	<i>Acacia</i>	~1200	216	204	12	Yes
<i>Acacia haematoxylon</i>								
<i>Acacia hebeclada</i>								
<i>Acacia mellifera</i> subsp. <i>detinens</i>								
<i>Acacia reficiens</i>								
<i>Crotalaria podocarpa</i>	Crotalarieae	Papilionoideae	<i>Crotalaria</i>	~600	136	136	0	Yes
<i>Crotalaria spartioides</i>								
<i>Crotalaria sphaerocarpa</i>								
<i>Cyamopsis serrata</i>	Indigofereae	Papilionoideae	<i>Cyamopsis</i>	3	3	3	0	Yes
<i>Indigofera alternans</i> var. <i>alternans</i>	Indigofereae	Papilionoideae	<i>Indigofera</i>	~700	187	184	3	Yes
<i>Lebeckia linearifolia</i>	Crotalarieae	Papilionoideae	<i>Lebeckia</i>	35	7	7	0	Yes
<i>Lessertia physodes</i>	Galegeae	Papilionoideae	<i>Lessertia</i>	50	17	17	0	Yes
<i>Lotononis densa</i> subsp. <i>gracillius</i>	Crotalarieae	Papilionoideae	<i>Lotononis</i>	~100	32	32	0	Yes
<i>Lotononis platycarpa</i>								
<i>Parkinsonia africana</i>	Caesalpinieae	Caesalpinioideae	<i>Parkinsonia</i>	~15	4	0	4	No
<i>Prosopis glandulosa</i> var. <i>glandulosa</i>	Mimoseae	Mimosoideae	<i>Prosopis</i>	44	10	7	3	Yes
<i>Ptychlobium biflorum</i>	Millettieae	Papilionoideae	<i>Ptychlobium</i>	3	3	3	0	Yes
<i>Requienia sphaerosperma</i>	Millettieae	Papilionoideae	<i>Requienia</i>	3	2	2	0	Yes
<i>Senna italica</i> subsp. <i>arachoides</i>	Caesalpinieae	Cassieae	<i>Senna</i>	~240	57*	3	46	No

* The total of 57 is more than the nodulation present/absent total of 49 because in eight species evaluated nodulation reports were both positive or negative (3+46+8=57).

The potential nitrogen fixing capability of legume species in this study was derived from an assessment of the frequency of occurrence in Leguminosae genera (De Faria *et al.*, 1989, Table 5.2).

5.3 Results

In the PCoA of 46 plant traits the species formed clusters that were strongly linked to major life forms (Figure 5.1). From right to left across the ordination plane the groups were identifiable as trees and large shrubs (Group I) leading into medium woody shrubs (Group II), small to medium woody shrubs (Group III), geophytes perennial creepers and lianas and semi-woody shrubs (Group IV), perennial grasses semi-woody shrubs (Groups VIII and IX), herbaceous perennials and annuals (Group V) erect or creeping annuals (Group VI) and annual grasses and non creeping annuals (Group VII).

In the restricted analysis, groups of major life forms were also identifiable (Figure 5.2). Trees and large shrubs were distinct (Group III). The medium woody shrubs of Figure 5.1 were divided in the restricted analysis into medium-large and small to large perennial shrubs (Groups I and II). Small to medium woody perennial shrubs and perennial geophytes of Figure 5.1 still grouped in similar fashion in the restricted analysis (Group IV), but with some degree of mixing with closely associated groups in Figure 5.1 (Groups IV and IX in Figure 5.1). In the restricted analysis perennial and annual grasses aggregated together (Group VI) rather than apart. The closely associated herbaceous perennials and annuals (Group V) and erect or creeping annuals (Group VI) in Figure 5.1 were still closely associated in the restricted analysis but with some degree of interchanging. Due to the similarity in the distribution of species between the complete and restricted analysis an in depth analysis of the functional groups of the complete analysis was made.

5.3.1 Complete trait data set PCoA

The trait attributes for each of the functional groups identified in Figure 5.1 through the complete trait analysis were investigated in detail (Table 5.3). This detail table is for a selection of 18 of the 46 traits used in the analysis. Some of the trait attributes were illustrated in the ordination (Figure 5.3 to Figure 5.5). Functional groups were labelled according to dominant growth forms because these traits are most prominent. Results were accordingly summarized by describing the main distinguishing characteristics of each of the groups.

- Group I – Trees and large shrubs

This group was distinguished as nitrogen fixing, C₃ phanerophytes with caespitose, semi-circle shrub or hydra shoot architectures (Figure 5.2). Height and canopy diameter were largest of all groups. Stems were ligneous and intermediately spiny with leaves mostly glabrous and sclerophyllous. Brush flower types and white and yellow flower colour combinations were common as well as unspecialized zoochorous pollination (Figure 5.3). Large seeds often without diaspore dispersal aids, except for fleshy pulp occasionally, were coupled with endozoochorous dispersal (Figure 5.4).

- Group II – Medium woody shrubs

C₃ nanophanerophytes or various chamaephytic Raunkier life forms were typical of the group in conjunction with caespitose shrub or semi-circle shrub shoot architectures. Plant height was taller than most groups except for Group I, but canopy diameter was variable. Similarly stems were more ligneous than other groups except Group I. Stem spinescence, leaf hairiness, and leaf consistency were variable, but leaves were mostly small. Flower type and pollination mode were variable, although fruit types were often fleshy diaspores or capsules. Dispersal mode and seed mass were variable.

- Group III – Small to medium woody shrubs and geophytes

C₃ suffruticose and fruticose chamaephytes and bulbous geophytes were representative of the group, but shoot architecture was very variable, although the caespitose shrub or semi-circle shrub forms were most common. Plants were of intermediate height and stems on the cusp of hemixylous to herbaceous, but without spines. Leaf hairiness, leaf consistency and leaf size were variable as was flower type and pollination mode. Diaspores of the capsules, achenes or nuts had no attachments, plumes or fleshy pulp. Dispersal mode and seed size were variable, but with anemochory common.

- Group IV – Geophytes, perennial creepers, lianas and perennial herbs

This group exhibited C₃ photosynthesis and no nitrogen fixing, but carbohydrate storage was common. A variety of hemicryptophyte life forms occurred as well as some bulbous or rhizomatous geophytes. Shoot architecture was scandent, procumbent or liana types. Plant height and canopy diameter were variable and stems were mostly herbaceous and without spines. Leaf hairiness, leaf consistency and leaf size were variable. Flowering occurred in the hot and humid season and flower shapes included bell-funnel, trumpet and gullets shapes of various colour combinations with specialized zoochorous pollination. Fruit type, diaspore morphology and dispersal mode were variable, but diaspores without attachments were common.

- Group V – Herbaceous perennials and annuals

Mostly C₃ plants without carbohydrate storage consisting of chamaephytes and therophytes in a variety of shoot architectures from erect to procumbent. Plant height and canopy diameter were low and stems were herbaceous. Leaf hairiness was common with intermediate, microphyllous leaf size across a wide range of leaf consistencies. Flower shape, flower colour and pollination mode were variable and fruit capsules or nuts had either no attachments or burrs or wings. Dispersal mode was variable, but often anemochorous with seed size of great variation.

- Group VI – Erect or creeping annuals

C_3 and sometimes C_4 plants were characteristic of the group and without carbohydrate storage organs. Procumbent or erect therophytes of low height and canopy diameter were coupled with herbaceous spineless stems. Leaves were small and ranged from glabrous to densely hairy and malacophyllous to semi-sclerophyllous. Flowering occurred in the hot and humid season with flowers of various shapes, flower colour combination and pollination modes. Fruit were mostly capsules and diaspores without any attachments. Anemochory was dominant as was small seeds.

- Group VII – Annuals grasses and non-creeping annuals

This group exhibited no nitrogen fixing or carbohydrate storage but C_4 photosynthesis was common. The therophytes with procumbent to decumbent cup or sub-caespitose tuft architectures had a range of plant heights but low canopy width. Stems were herbaceous and spineless and leaves often glabrous with a variety of consistencies and sizes. Flowering typically occurred in the hot and humid season with bowl-dish, brush or floret flower types exhibiting unspecialized zoochorous or wind pollination. The small seeds of the capsule or caryopsis fruits either had no attachments or a variety of burrs, bristles or wings with either anemochorous or epizoochorous dispersal.

- Group VIII – Perennial grasses and herbs

The group typically showed no nitrogen fixing or carbohydrate storage but either C_3 or C_4 photosynthesis. Medium-sized hemicryptophytes and therophytes with variable canopy sizes Caespitose, sub-caespitose tuft or semi-circle shrubs shoot architectures were typical and stems were herbaceous without spines. Leaves were glabrous and semi-sclerophyllous to sclerophyllous, but variable in size. Flowering occurred in the hot and humid season and floret or brush flower types often had drab colour combinations of white, green, blue and purple. Pollination was by unspecialized zoochory or wind. The small seeds and associated diaspores of the achene, caryopsis or capsule fruit types had either no attachments or often plumes or bristles. Anemochory was dominant.

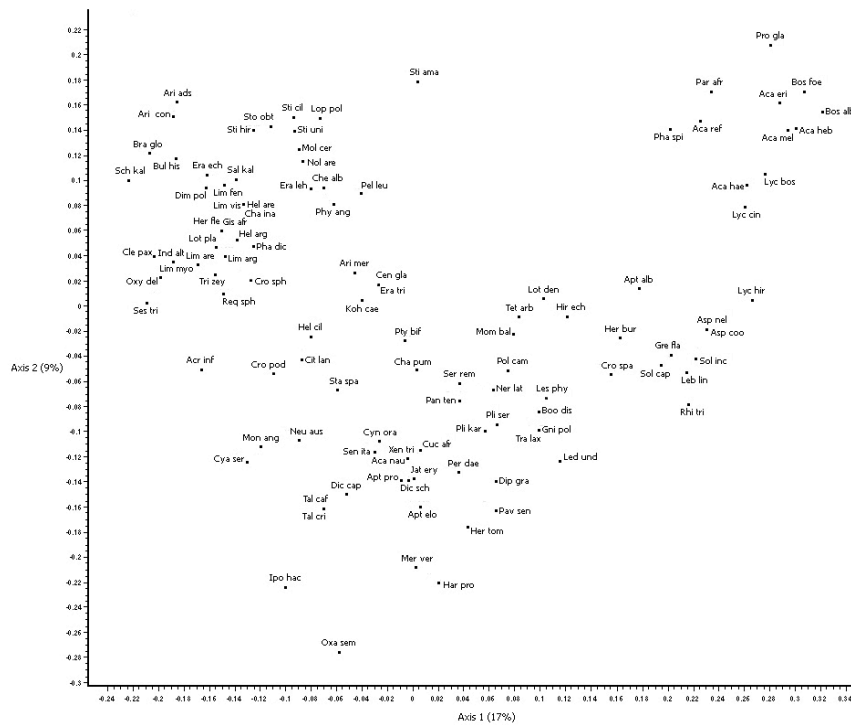
- Group IX – Perennial grasses and herbs

No nitrogen fixing occurred in the group but C_4 photosynthesis was common. Hemicryptophytes and less common chamaephytes of the group had caespitose, sub-caespitose tuft or semi-circle shrub shoot architectures as in Group VIII. The group exhibited medium plant height and canopy diameter with spineless, herbaceous stems. Leaves were semi-sclerophyllous and glabrous and of various sizes. Flowering occurred in the hot and humid season and the white, yellow, blue or purple floret or tube flower types had wind or unspecialized zoochorous pollination. The mostly caryopsis fruit had no attachments or less commonly burrs. Seeds were small and dispersal anemochorous, or sometimes epizoochorous.

Stem density, stem spinescence, plant height and life span increased along the x-axis from left to right (Figure 5.2). Leaf dry matter content, although not included in the ordination, was also inferred to increase along the x-axis from left to right by virtue of the significant positive association of the trait ($p \leq 0.05$) with stem density ($r=0.41$), stem spinescence ($r=0.41$), plant height ($r=0.57$) and life span ($r=0.61$). Similarly specific leaf area was not included in the analysis but had significant ($p \leq 0.05$) negative correlation with stem density ($r=-0.52$), stem spinescence ($r=-0.34$), plant height ($r=-0.42$) and life span ($r=-0.60$).



a



b

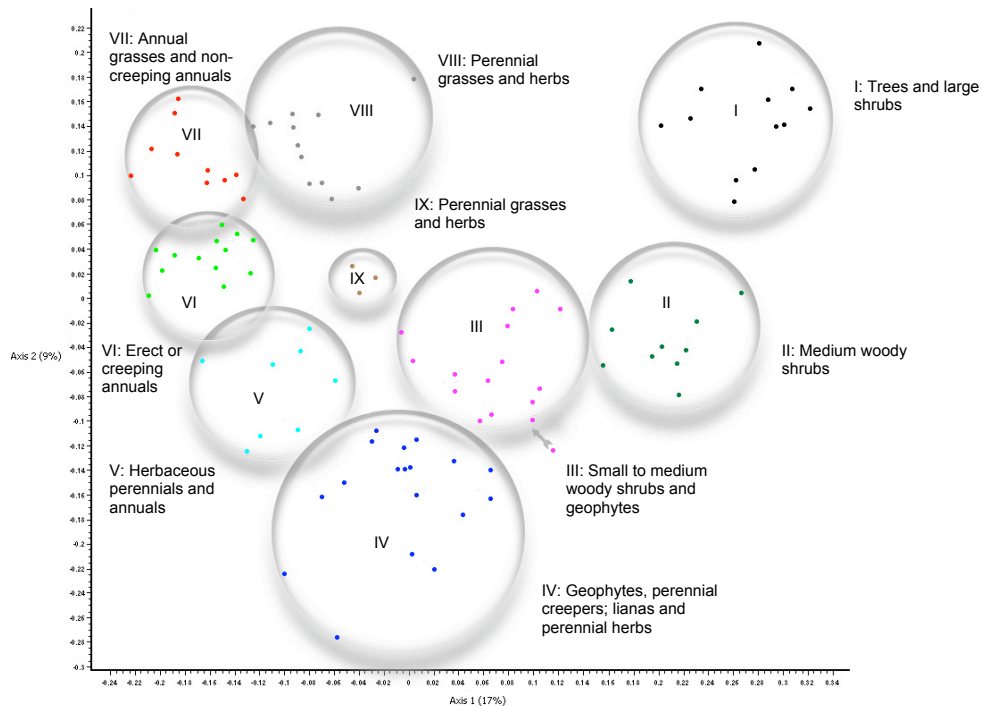


Figure 5.1 (a) Principal Coordinates Analysis (PCoA) scatter diagram of 112 Kalahari plant species for a set of 46 plant traits and (b) the subsequent groups identified. The percentage of the variance explained by each axis is indicated in brackets after each axis label.



Table 5.3 Detailed descriptions of functional groups identified by PCoA of 46 traits (Figures 5.1 & 5.3, 5.4, 5.5)

	Group I Trees and large shrubs	Group II Medium woody shrubs	Group III Small to medium woody shrubs and geophytes	Group IV Geophytes, perennial creepers, lianas and perennial herbs	Group V Herbaceous perennials and annuals	Group VI Erect or creeping annuals	Group VII Annuals grasses and non-creeping annuals	Group VIII Perennial grasses and shrubs	Group IX Perennial grasses and shrubs
Number of species	12	11	17	20	8	16	12	12	4
Trophic type	Nitrogen fixing common	Nitrogen fixing uncommon	Nitrogen fixing uncommon	No nitrogen fixing	Nitrogen fixing uncommon	Nitrogen fixing uncommon	No nitrogen fixing	No nitrogen fixing	No nitrogen fixing
Photosynthetic pathway	C ₃	C ₃	C ₃	C ₃	C ₃ , rarely C ₄	C ₃ , uncommonly C ₄	C ₄ , uncommonly C ₃	C ₃ or C ₄	C ₄ , uncommonly C ₃
Carbohydrate storage	No carbohydrate storage	Uncommon	Uncommon	Common	Rare	No carbohydrate storage	No carbohydrate storage	No carbohydrate storage	Uncommon
Raunkia life form	Nano- or micro-phanerophyte;	Nano-phanerophyte; fruticose or suffruticose or herbaceous chamaephyte	Suffruticose chamaephyte or bulbous geophyte, uncommonly fruticose chamaephyte	Replant hemicryptophyte; also commonly caespitose hemicryptophyte, bulbous or rhizomatous geophyte, or hemicryptophytic liana	Herbaceous chamaephyte, caespitose therophyte or reptant therophyte	Caespitose therophyte or reptant therophyte	Caespitose therophyte or uncommonly reptant therophyte	Caespitose hemicryptophyte or caespitose therophyte	Caespitose hemicryptophyte, uncommonly suffruticose chamaephyte
Shoot architecture	Caespitose or semi-circle shrub, uncommonly hydra, rarely rhizomatous shrub	Caespitose or semi-circle shrub, rarely broom	Caespitose or semi-circle shrub, uncommonly raised basal rosette, rarely broom, fountain, liana, fan or decumbent cup	Procumbent, scandent or liana	Semi-circle shrub or erect, also commonly broom, procumbent or scandent	Procumbent or erect	Sub-caespitose tuft, procumbent and decumbent cup	Caespitose tuft, sub-caespitose tuft, semi-circle shrub or erect	Caespitose tuft, sub-caespitose tuft or semi-circle shrub
Plant height (cm)	>100, often >300	>50–200	>10–50, uncommonly >50–100	>3–50, rarely ≤3 or >50	>10–50.	≤3–50	≤3–100	>10–100	>50–100, uncommonly >100–150
Canopy diameter (m)	>2	>0.5–2	>0.2–1	≤0.2 to >2	≤0.2–0.5, rarely >0.5	≤0.2–1	≤0.2–0.5, rarely >0.5	≤0.2–2	>0.5–2
Stem density	Ligneous	Ligneous or hemixylous	Hemixylous or herbaceous	Herbaceous, rarely hemixylous	Herbaceous, rarely hemixylous	Herbaceous	Herbaceous	Herbaceous, rarely hemixylous	Herbaceous, rarely hemixylous
Stem spinescence	Intermediately spiny	None to intermediately spiny	None	None	None	None	None	None	None
Leaf hairiness adaxial	Glabrous, uncommonly sparse to intermediate	Glabrous to dense	Glabrous, uncommonly sparse to dense	Glabrous to dense	Intermediate to dense	Glabrous to dense	Glabrous, uncommonly sparse to intermediate	Glabrous	Glabrous
Leaf hairiness abaxial	Glabrous, uncommonly sparse to intermediate	Glabrous to dense	Glabrous, uncommonly sparse to dense	Glabrous to dense	Intermediate to dense	Glabrous to dense	Glabrous, uncommonly sparse to intermediate	Glabrous to sparse	Glabrous to sparse
Leaf consistency	Semi-sclerophyllous to sclerophyllous	Malacophyllous to sclerophyllous	Malacophyllous to sclerophyllous	Malacophyllous to semi-sclerophyllous	Malacophyllous to semi-sclerophyllous	Malacophyllous to semi-sclerophyllous	Malacophyllous or semi-sclerophyllous	Semi-sclerophyllous to sclerophyllous	Semi-sclerophyllous
Leaf area (mm²)	Nanophyll to microphyll	Leptophyll to nanophyll, rarely mesophyll	Leptophyll to mesophyll, rarely larger	Nanophyll to microphyll, uncommonly mesophyll	Microphyll, rarely mesophyll	Nanophyll, uncommonly microphyll	Leptophyll to microphyll	Leptophyll to microphyll	Leptophyll to microphyll
Flowering phenology	Warm and dry or hot and humid season	Warm and dry or hot and humid season	Hot and humid season, uncommonly warm and dry season	Hot and humid season	Hot and humid season	Hot and humid season	Hot and humid season	Hot and humid season	Hot and humid season
Flower shape	Brush, rarely trumpet or tube	Bell-funnel, brush, flag or gullet	Bell-funnel, brush, tube, flag or gullet	Bell-funnel, bowl-dish, trumpet, brush or gullet	Bowl-dish, flag or gullet	Bell-funnel, bowl-dish or flag	Bowl-dish, brush or floret	Floret or brush	Floret or tube
Flower colour	See Figure 5.4								
Pollination mode	Unspecialized zoochorous, uncommonly specialized zoochorous	Unspecialized or specialized zoochorous	Unspecialized or specialized zoochorous	Specialized zoochorous, uncommonly unspecialized zoochorous or wind	Unspecialized or specialized zoochorous	Specialized or unspecialized zoochorous, rarely wind	Unspecialized zoochorous or wind	Unspecialized zoochorous or wind	Wind, uncommonly specialized zoochorous
Fruit type	Berry or capsule	Berry or capsule, rarely a drupe	Capsule, uncommonly an achene or nut	Capsule, uncommonly an achene or pepo	Capsule or nut, uncommonly a pepo	Capsule, rarely an achene or nut	Capsule or caryopsis, uncommonly an achene	An achene, capsule or caryopsis	Caryopsis, uncommonly a capsule
Diaspore morphology	No fruit or seed attachments, uncommonly winged fruit or fleshy pulp fruit	No fruit or seed attachments or fleshy pulp fruit, rarely winged seeds	No fruit or seed attachment, plumed seeds or fleshy pulp fruit, rarely winged or glandular seeds	No fruit or seed attachments, uncommonly plumed seeds or fleshy pulp fruit, rarely bristled or winged fruit	No fruit or seed attachments, uncommonly burred seeds, winged fruit or fleshy pulp fruit	No fruit or seed attachments, rarely bristled or winged seeds or burred fruit	No fruit or seed attachments or burred seeds, uncommonly bristled or winged seeds or winged fruit	No fruit or seed attachments or plumed seeds, rarely bristled seeds	No fruit or seed attachments, uncommonly burred seeds
Telechory	Endozoochory	Endozoochory or autochory, uncommonly anemochory	Anemochory, uncommonly endozoochory or autochory	Anemochory or autochory, uncommonly endozoochory, rarely epizoochory	Anemochory, uncommonly epizoochory, endozoochory or autochory	Anemochory, rarely epizoochory or autochory	Anemochory or epizoochory	Anemochory, rarely autochory	Anemochory, uncommonly epizoochory
Seed mass class (mg)	>1–1000	>1–10, uncommonly ≤0.1–1	>0.1–10, uncommonly >10–100	>0.1–100	>0.1–10, rarely >10–100	≤0.1–10	≤0.1–10	≤0.1–10	≤0.1–10

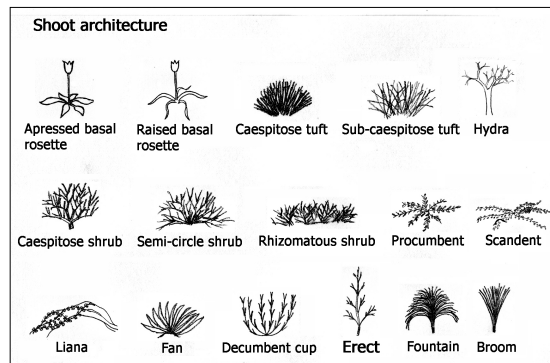
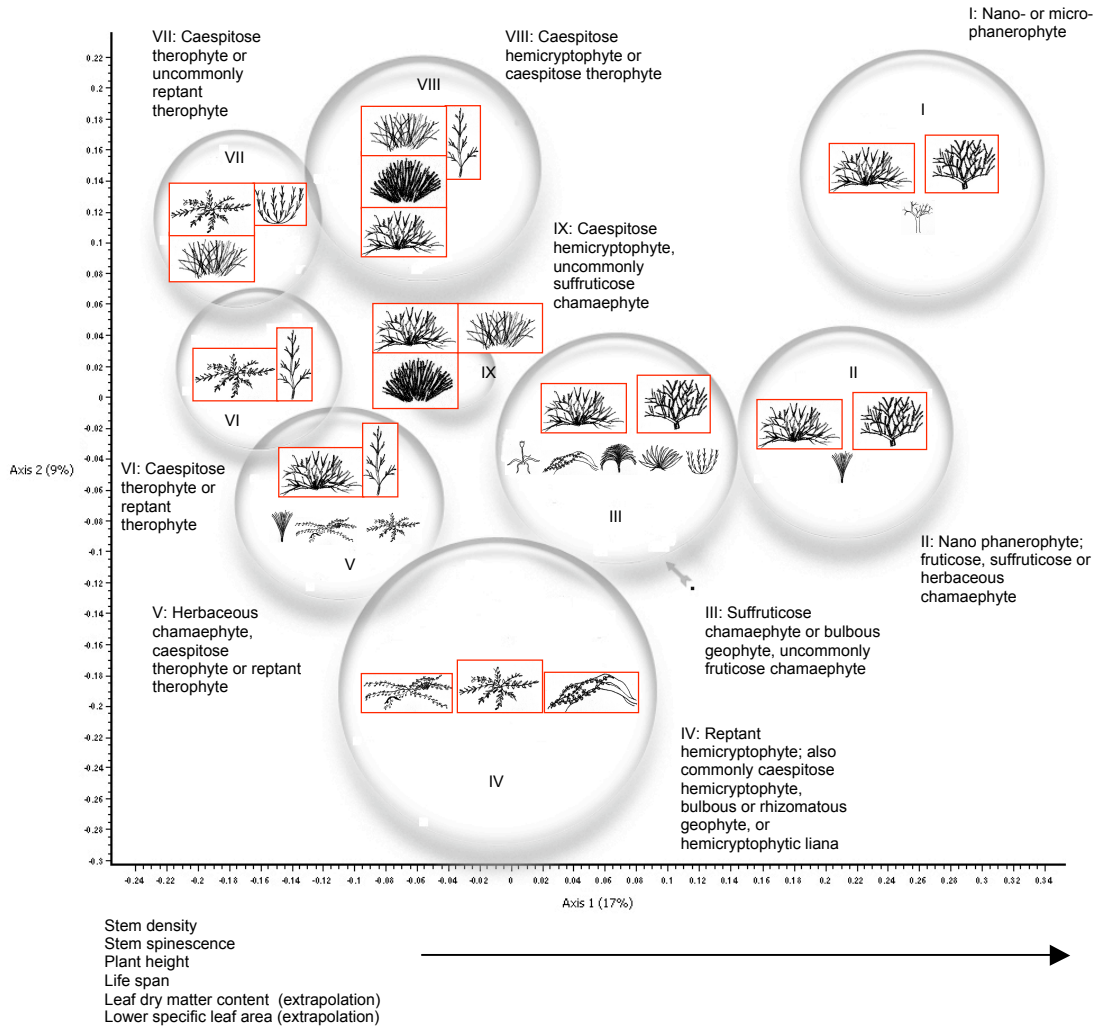


Figure 5.2 Principal Coordinates Analysis (PCoA) scatter diagram of 112 Kalahari plant species for a set of 46 plant traits and the subsequent groups identified. Raunkier life forms are noted and shoot architecture types per group are illustrated with boxed larger icons denoting dominant architecture types and smaller icons less dominant types. The percentage of the variance explained by each axis is indicated in brackets after each axis label

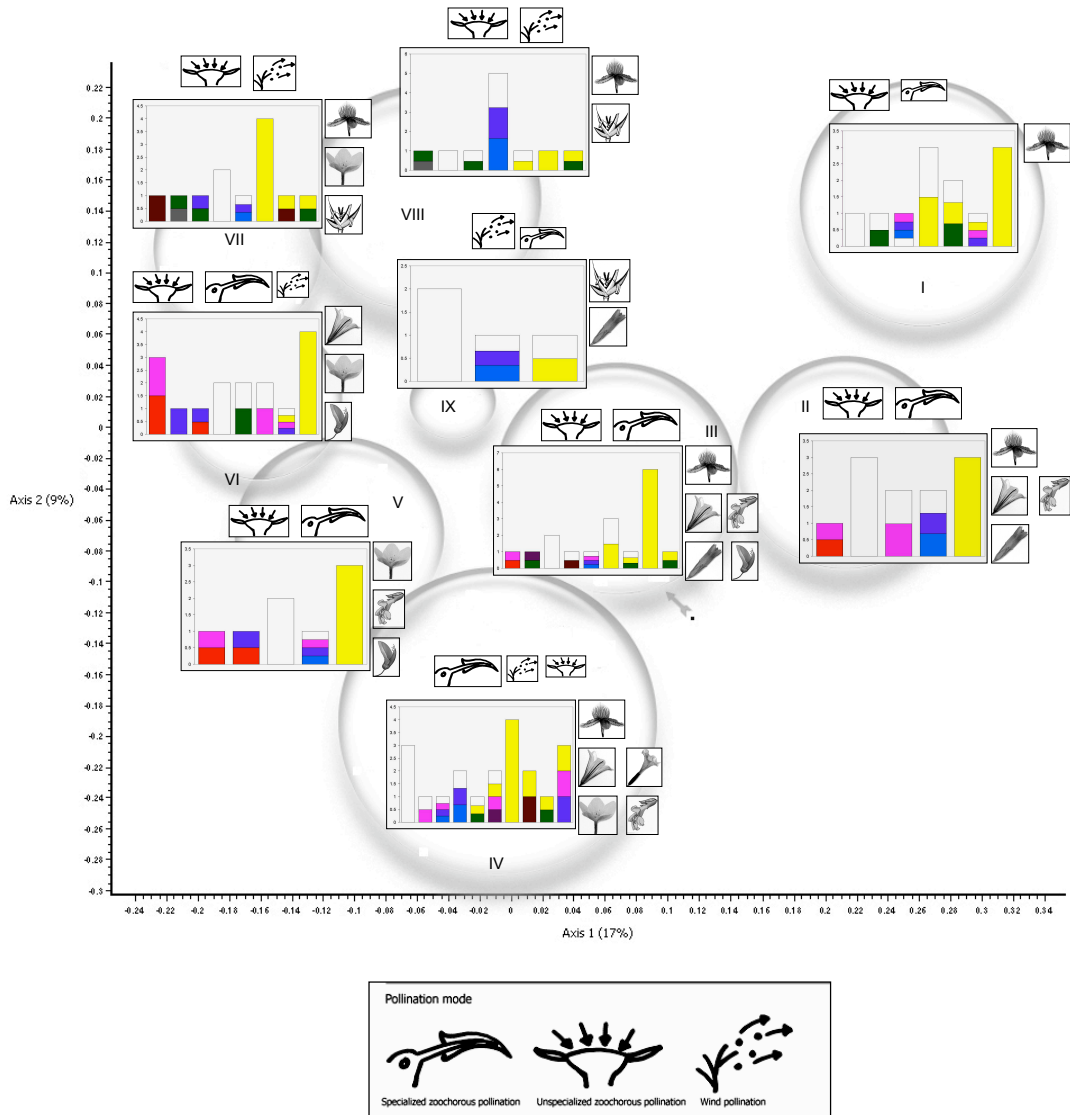


Figure 5.3 Principal Coordinates Analysis (PCoA) scatter diagram of 112 Kalahari plant species for a set of 46 plant traits and the subsequent groups identified. The traits Family, Status and Plant and flower gender have been removed from the analysis. Pollination mode, flower type (right side of each graph) and flower colour for the groups have been highlighted. Larger pollination mode icons denote more dominant states. Flower colour is indicated by the number of species that have specific flower colour combinations, for example in Group II three species have white flowers and two species have white and pink combination flowers. The percentage of the variance explained by each axis is indicated in brackets after each axis label

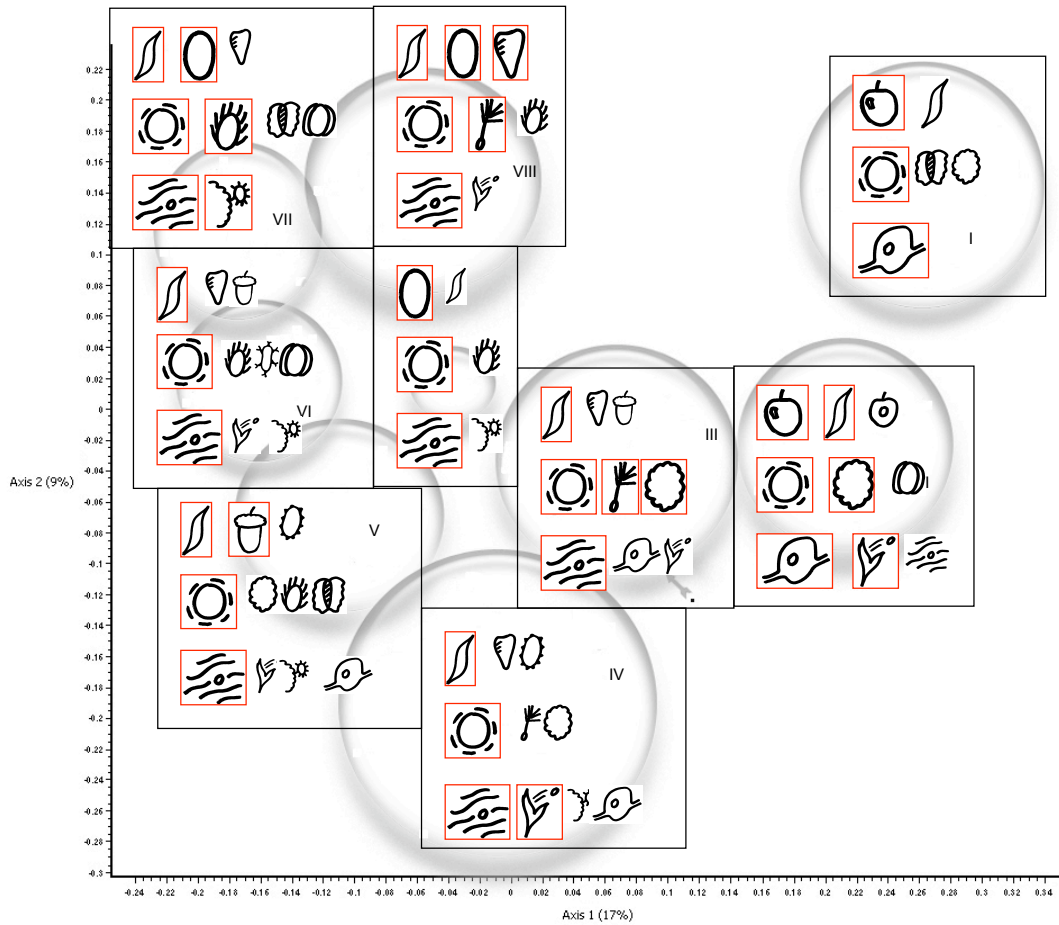


Figure 5.4 Principal Coordinates Analysis (PCoA) scatter diagram of 112 Kalahari plant species for a set of 46 plant traits and the subsequent groups identified. Fruit type, diaspore morphology and telechory have been highlighted consecutively from top to bottom per group. Larger boxed icons denote more dominant states.

5.3.2 Vegetative traits data set PCoA

The trait attributes for each of the functional groups identified in Figure 5.6 through the vegetative trait analysis were investigated in detail (Table 5.3) and compared with the groupings produced in the complete data set analysis. The functional groups according to vegetative traits were aligned according to prominent growth forms as with the complete data set analysis, although some interchanging of species within groups were observed (Figure 5.6). In the vegetative trait analysis trees and large shrubs were located on the right of the ordination, grading into medium and small perennial shrubs from right to left. Perennial herbs and grasses were located at the centre to left of the ordination and small or prostrate annuals at the far left. Parallel to this pattern were the increase in stem density, plant height, life span and leaf spinescence from left to right (Figure 5.7).

- Group I – Trees and large shrubs

The group consisted of C₃ nano- to mesophanerophytes with nitrogen fixing capability, but no carbohydrate storage. Plants were tall with wide canopies and caespitose or semi-circle shrub shoot architecture often with belowground clonality and leaf shedding only. Stems were ligneous and spiny and leaves spineless, green, glabrous and semi-sclerophyllous to sclerophyllous. Aqueous or resinous leaf or stem exudates occurred. Leaves were mostly bipinnate or pinnate and leaf margins always entire with leaf size ranging from nanophyll to microphyll. Growth occurred in the warm and dry season.

- Group II – Trees and large to small woody shrubs

C₃ nano- or microphanerophytes, or fruticose chamaephytes mostly exhibiting leaves shedding were typical. Predominantly caespitose shrub or semi-circle shrub shoot architecture coupled with medium to tall plant height and ligneous stems. Leaf and stem spinescence were variable and leaves were mostly glabrous and sclerophyllous. Leaf type was simple, leaf margins entire and leaf size small ranging only from leptophyll to nanophyll. Growth was restricted to the warm and dry season.

- Group III – Large to small woody shrubs

The group was typified by C₃ photosynthesis, no carbohydrate storage and mostly nanophanerophytes, fruticose chamaephytes or suffruticose chamaephytes. As with Groups I and II caespitose shrub or semi-circle shrub shoot architecture together with leaf shedding were predominant. The group had medium plant height, ligneous or hemixylous stems without spines as well as spineless or slightly spinescent leaves. The small to medium-sized, simple leaves were mostly glabrous (less consistently than Groups I and II), had very variable leaf consistency and entire margins. Growth season was variable.

- Group IV – Woody and semi-woody perennial shrubs

No nitrogen fixing occurred in this group and C_3 photosynthesis was a feature. A range of life forms were observed, but suffrutescent hemicryptophytes were most common displaying either leaf or shoot shedding. Caespitose shrub or semi-circle shrub shoot architecture was dominant and coupled with hemixylous to herbaceous stem density and no clonality, but plant height and canopy diameter were variable. Leaf and stem spinescence were low or absent and leaves were often intermediate to densely hairy. Leaves were simple, often malacophyllous, of wide ranging size, and the leaf margins often entire, but sometimes lobed to serrated.

- Group V – Semi-woody perennial shrubs, perennial grasses and geophytes

This group had no nitrogen fixing and a variety of life forms, notably caespitose chamaephyte or therophyte or less commonly non-frutescent chamaephytes or geophytes. Whole plants or shoots were shed on a variety of shoot architectures, although sub-caespitose tufts and semi-circle shrubs were most prominent. Plant height and canopy diameter were variable. Stems were herbaceous and spineless, and no clonality was observed. Leaves were spineless, all green, mostly glabrous and mostly semi-sclerophyllous. Leaves were also simple with entire margins and were of small to medium size.

- Group VI – Perennial creepers, lianas and herbaceous perennials

In this group no nitrogen fixing was observed, C_3 photosynthesis was typical and carbohydrate storage common. Life form was wide ranging from reptant or caespitose hemicryptophyte to bulbous geophyte to liana to herbaceous chamaephyte. Shoot shedding was common from procumbent or liana shoot architectures, although other forms were also evident. Plants height was low to medium, stems herbaceous and no clonality the norm, as spineless stems and leaves. Leaves were all green, mostly glabrous and malacophyllous, although leaf hairiness and semi-sclerophyllous leaves were observed. Leaves were simple and leaf margins often entire or lobed, or sometimes of various margins types. Leaf size was most variable of all groups ranging from small (nanophyll) to large (macrophyll).

- Group VII – Perennial and annual creepers

Features of this group were no nitrogen fixing, C_3 photosynthesis, no carbohydrate storage and reptant hemicryptophyte or hemicryptophytic liana life forms. Shoot architecture was the procumbent or fan forms and shoot or entire plants shedding was typical. Plant height and canopy diameter ranged from small to medium without clonality, stems were herbaceous and leaves and stems spineless. Leaf colour was glaucous or discolourous, never all green, leaves intermediate to densely hairy and malacophyllous or semi-sclerophyllous. The small to medium sized, simple leaves had entire, dentate or undulate margins and growth was confined to the hot and humid season.

- Group VIII – Perennial and annual creepers

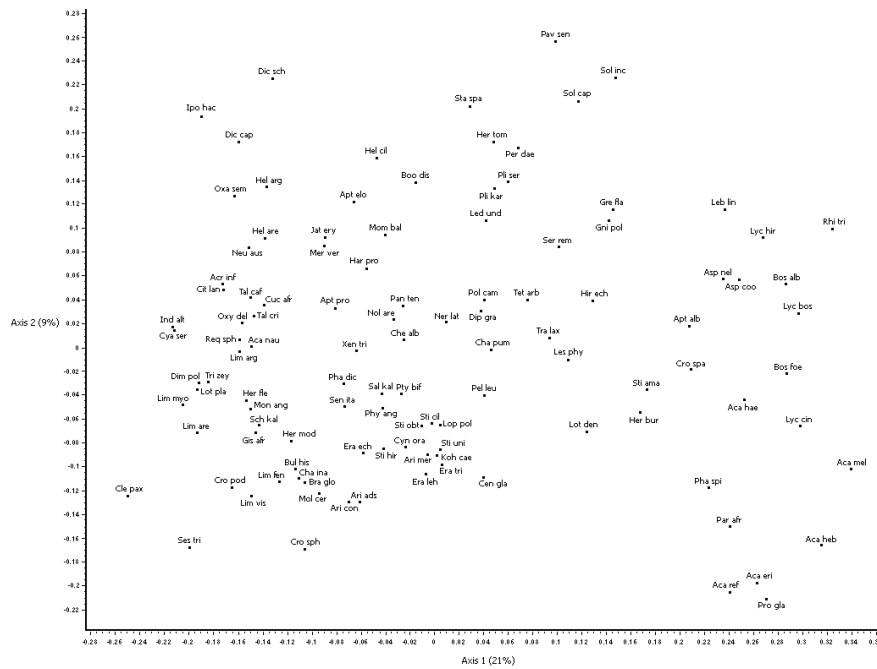
C₃ photosynthesis and also commonly carbohydrate storage were coupled to reptant or caespitose therophytes, reptant hemicryptophytes or rhizomatous geophytes. Shoot architecture was mostly procumbent, sometimes scandent or erect, plants of low height but varying canopy sizes and whole plants or shoots commonly shed. Leaves and stems were spineless, stems herbaceous and the variously coloured leaves intermediate to densely hairy. Leaf consistency ranged from malacophyllous to semi-sclerophyllous, with extremes of semi-succulent leaves occasionally observed. Leaf shape was simple and margins entire or lobed, but occasionally of various margin types. Leaves were small to medium sized and growth occurred in the hot and humid season.

- Group IX – Erect or creeping annuals and annual grasses

This group occasionally displayed nitrogen fixing ability and either C₃ or C₄ photosynthesis, but no carbohydrate storage. Life forms were caespitose or reptant therophytes where whole plants are shed from varying shoot architectures, but predominantly procumbent or erect forms. Plant height and canopy diameter ranged from low to medium. The absence of clonality is typical and stems were herbaceous. Stems were spineless, as were the all green leaves. Leaf hairiness was observed ranging from glabrous to intermediately dense and coupled with mostly semi-sclerophyllous leaves, although malacophyllous leaves were also observed. The highest incidence of aqueous, sticky or latex leaf/stem surface exudates were observed in this group, although it was still not a common feature. Leaves were mostly simple, but palmate or trifoliolate types were also observed. Leaf margins were mostly entire and leaf size ranged from very small to medium. Growth was restricted to the hot and humid season.



a



b

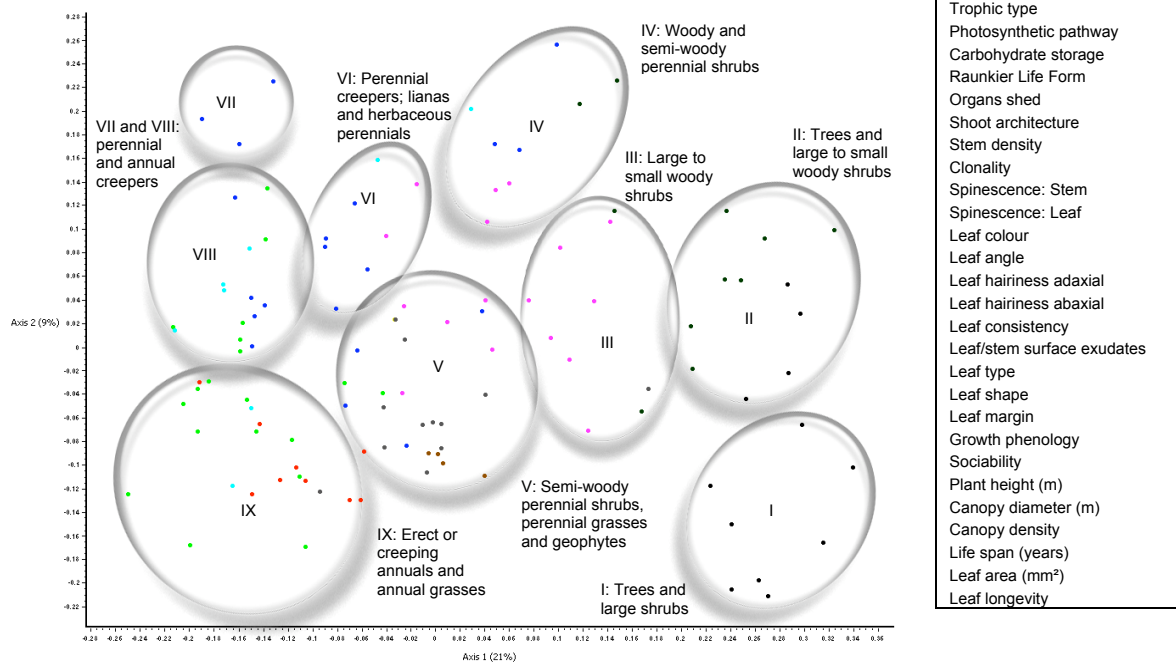


Figure 5.5 (a) Principal Coordinates Analysis (PCoA) scatter diagram of 112 Kalahari plant species for a reduced set of 27 vegetative plant traits and (b) the subsequent groups identified. The traits included in the analysis are indicated. Colour coding is according to the groups identified in Figure 5.1 for comparison. The percentage of the variance explained by each axis is indicated in brackets after each axis label.



Table 5.4 Detailed descriptions of vegetative trait categories for functional groups identified by PCoA of 27 vegetative plant traits (Figures 5.6 & 5.7)

	Group I Trees and large shrubs	Group II Trees and large to small woody shrubs	Group III Large to small woody shrubs	Group IV Woody and semi-woody perennial shrubs	Group V Semi-woody perennial shrubs, perennial grasses and geophytes	Group VI Perennial creepers, lianas and herbaceous annuals	Group VII Perennial and annual creepers	Group VIII Perennial and annual creepers	Group IX Erect or creeping annuals and annual grasses
Number of species	8	11	10	9	26	8	3	15	22
Trophic type	Nitrogen fixing common	Nitrogen fixing uncommon	Nitrogen fixing uncommon	No nitrogen fixing	No nitrogen fixing	No nitrogen fixing	No nitrogen fixing	Uncommon nitrogen fixing	Uncommon nitrogen fixing
Photosynthetic pathway	C ₃	C ₃	C ₃ , rarely C ₄	C ₃	C ₃ or C ₄	C ₃ , rarely C ₄	C ₃	C ₃	C ₃ or C ₄
Carbohydrate storage	No carbohydrate storage	Uncommon	Rarely	Uncommon	Uncommon	Common	No carbohydrate storage	Common	No carbohydrate storage
Raunkier life form	Nano- or micro- phanerophyte; uncommonly meso- phanerophyte	Nano- or micro- phanerophyte or fruticose chamaephyte	Nano- phanerophyte; fruticose or suffruticose chamaephyte; rarely caespitose hemicyptophyte or rhizomatous geophyte	Suffruticose hemicyptophyte; uncommonly herbaceous chamaephyte, bulbous geophyte, caespitose therophyte or phanerophytic/ chamaephytic liana	Caespitose hemicyptophyte or caespitose therophyte; uncommonly suffruticose or herbaceous chamaephyte or bulbous geophyte	Reptant hemicyptophyte or bulbous geophyte; uncommonly herbaceous chamaephyte, caespitose hemicyptophyte or any liana.	Reptant hemicyptophyte or hemicyptophytic liana	Reptant therophyte or uncommonly replant hemicyptophyte, rhizomatous geophyte or caespitose therophyte	Caespitose or replant therophyte
Organs shed	Leaves, rarely evergreen	Leaves, rarely shoots	Leaves, rarely shoots	Leaves or shoots	Whole plant or shoots, rarely leaves	Shoots, rarely leaves	Plant or shoots	Whole plant or uncommonly shoots	Whole plant
Shoot architecture	Caespitose or semi-circle shrub, rarely rhizomatous shrub or hydra	Caespitose or semi-circle shrub, rarely hydra or broom	Caespitose or semi-circle shrub, rarely caespitose tuft, broom or fountain	Caespitose or semi-circle shrub, rarely raised basal rosette, broom or liana	Sub-caespitose tuft or semi-circle shrub, uncommonly appressed basal rosette, caespitose tuft or erect	Procumbent or liana, uncommonly broom, semi- circle shrub, scandent or fan	Procumbent or fan	Procumbent, uncommonly scandent or erect	Procumbent or erect, uncommonly sub-caespitose tuft, caespitose shrub or decumbent cup
Plant height (cm)	>100, commonly >300	Mostly >50–200, uncommonly <50 or >200	>50– 150, uncommonly >150	<10–100, uncommonly >100	<10–100, uncommonly <10 or >100	>3–50, uncommonly ≤3	>3–50	<50, often ≤3	>10–50, also commonly <10 or <100
Canopy diameter (m)	>2	>0.5, often >2	>0.2– 2, rarely >2	>0.2, often >2, rarely ≤0.2	≤0.2–2	>0.2–2, rarely ≤0.2	>0.2–1	≤0.2 to >2	≤0.2–1, rarely >1
Stem density	Ligneous	Ligneous, uncommonly hemixylous	Ligneous or hemixylous	Hemixylous, uncommonly herbaceous	Herbaceous, rarely hemixylous	Herbaceous	Herbaceous	Herbaceous	Herbaceous
Clonality	None or belowground clonality	None, uncommonly belowground clonality	None, uncommonly belowground clonality	None, rarely belowground clonality	None, rarely aboveground or belowground clonality	None, rarely belowground clonality	None	None, rarely belowground clonality	None, rarely belowground clonality
Stem spinescence	Intermediately spiny	None to intermediately spiny	None or rarely slightly spiny	None or uncommonly intermediately spiny	None	None	None	None	None
Leaf spinescence	None	None or uncommonly slightly or intermediately spiny	None or uncommonly slightly or intermediately spiny one	None or rarely slightly spiny	None	None or rarely slightly spiny	None	None	None
Leaf colour	All green	All green or all glaucous, rarely green plus glaucous or discolourous	All green, uncommonly discolourous, rarely all glaucous or green plus glaucous	All green, all glaucous or discolourous, rarely green plus glaucous	All green, rarely green plus glaucous or discolourous	All green, rarely all glaucous or discolourous	All glaucous or discolourous	All green, rarely all glaucous or discolourous	All green
Leaf angle	No specific orientation	Vertical or oblique upwards or no specific orientation	Vertical or oblique upwards, vertical to horizontal or no specific orientation	Vertical or oblique upwards, horizontal to slightly oblique, hanging or no specific orientation	No specific orientation, uncommonly horizontal to slightly oblique or vertical to horizontal	Horizontal to slightly oblique or vertical to horizontal, uncommonly no specific orientation	Horizontal to slightly oblique or vertical to horizontal	Horizontal to slightly oblique, vertical to horizontal or no specific orientation	Horizontal to slightly oblique, vertical to horizontal or no specific orientation
Leaf hairiness adaxial	Glabrous, uncommonly sparse	Glabrous, rarely sparse to dense	Glabrous, uncommonly sparse	Intermediate to dense, uncommonly glabrous or sparse	Glabrous, rarely sparse	Glabrous, uncommonly intermediate to dense	Intermediate to dense	Intermediate to dense, uncommonly glabrous or sparse	Glabrous to intermediate
Leaf hairiness abaxial	Glabrous, uncommonly sparse	Glabrous, rarely sparse to dense	Glabrous, uncommonly sparse to intermediate	Intermediate to dense, uncommonly glabrous or sparse	Glabrous, uncommonly sparse	Glabrous, uncommonly intermediate to dense	Intermediate to dense	Intermediate to dense, uncommonly glabrous or sparse	Glabrous to intermediate, uncommonly dense
Leaf consistency	Semi- sclerophyllous to sclerophyllous	Sclerophyllous, rarely semi- sclerophyllous or malacophyllous	Malacophyllous to sclerophyllous	Malacophyllous, uncommonly sclerophyllous	Semi- sclerophyllous, uncommonly sclerophyllous or malacophyllous	Malacophyllous, uncommonly semi- sclerophyllous	Malacophyllous or semi- sclerophyllous	Malacophyllous, or semi- sclerophyllous, rarely semi- succulent	Semi- sclerophyllous, uncommonly malacophyllous
Leaf/stem surface exudates	Aqueous or none, rarely resinous	None, rarely resinous	None	None, rarely latex	None, rarely latex, wax or aqueous	None, rarely latex or aqueous	None	None, rarely aqueous	None, uncommonly aqueous, rarely sticky or latex
Leaf type	Bipinnate, uncommonly simple or pinnate	Simple, rarely bipinnate	Simple, rarely pinnate or palmate/ trifoliolate	Simple	Simple	Simple, rarely palmate/ trifoliolate	Simple	Simple, rarely pinnate or palmate/ trifoliolate	Simple, uncommonly palmate/ trifoliolate
Leaf shape	Mostly oblong or oval, uncommonly obovate, or linear	Linear, inverse lance-shaped, oval or obovate	Linear, oblong, oval or uncommonly lance-shaped, inverse lance- shape or elliptic	Oval, ovate, heart-shaped or uncommonly strap-shaped, oblong or inverse lance-shaped	Linear, rarely strap-shaped or oval	Elliptic or obovate, uncommonly strap-shaped, oval, elliptic or kidney shaped	Inverse lance- shaped, elliptic or triangular	Oblong, lance- shaped, obovate or triangular, rarely inverse- lance shaped, spoon-shaped, rounded or diamond-shaped	Linear, oblong or oval, uncommonly strap-shaped
Leaf margin	Entire	Entire, rarely revolute	Entire, rarely serrated, crenate or lobed	Entire, uncommonly lobed, rarely dentate or serrated	Entire, rarely serrated or lobed	Entire or lobed uncommonly denticulate, pinnatifid, palmatifid or undulate	Entire, dentate or undulate	Entire or uncommonly lobed or palmatifid, rarely dentate, serrated, pinnatifid or revolute	Entire, rarely dentate, serrated or pinnatifid
Leaf area (mm²)	Nanophyll to microphyll	Leptophyll to nanophyll	Leptophyll to microphyll	Leptophyll to mesophyll	Leptophyll to microphyll	Nanophyll to macrophyll	Nanophyll to microphyll	Nanophyll to microphyll	Leptophyll to microphyll



Growth phenology	Warm and dry season	Warm and dry season	Warm and dry season, uncommonly hot and humid season	Warm and dry season, also commonly hot and dry season	Warm and dry season or hot and humid season	Warm and dry season or hot and humid season	Hot and humid season	Hot and humid season, rarely cold and dry season	Hot and humid season
Sociability	Loose groups, also commonly dense clumps or large herds	Single, also commonly loose groups, uncommonly dense clumps or large herds	Loose groups, also commonly single, uncommonly dense clumps	Single or loose groups, uncommonly large herds	Loose groups, also commonly single, uncommonly large herds	Single or loose groups	Single	Loose groups or large herds, rarely single	Loose groups, uncommonly large herds
Canopy density (%)	25 to >75	25 to 75, rarely >75	<25 to >75	25 to >75, rarely <25	<25 to >75	<25 to 75	<25 to 50	<25 to 50, uncommonly >50	<25 to 75
Life span (years)	>5 (often >50)	>2-50,	>2-25	>5-25	<1 to 25	>2-25	<1 to 5	<1, uncommonly up to 5	<1, rarely up to 5
Leaf longevity (months)	>6 (often >12)	>6-12, uncommonly >12	>6-12	>6-12	>6-12, uncommonly >3-6	>6-12, rarely >3-6	>3-12	>3-12	>3-12, uncommonly <3

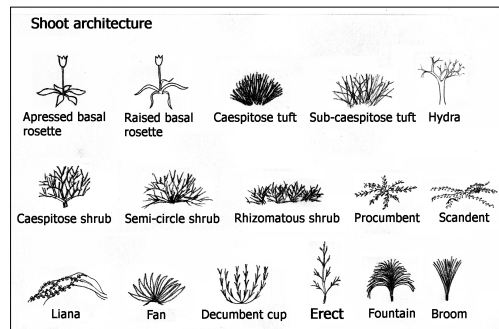
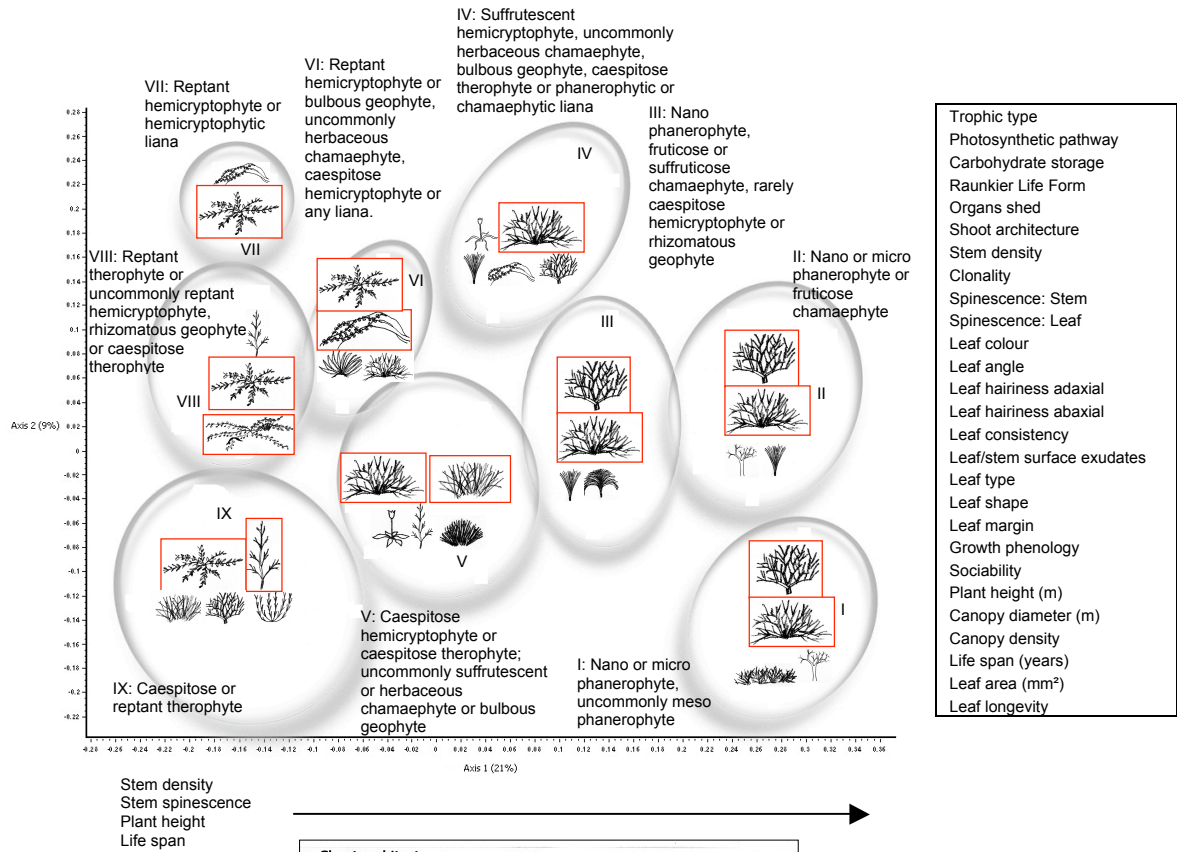


Figure 5.6 Principal Coordinates Analysis (PCoA) scatter diagram of 112 Kalahari plant species for a reduced set of 27 vegetative plant traits and the subsequent groups identified. Shoot architecture types per group are indicated with boxed larger icons denoting dominant architecture types and smaller icons less dominant types. The traits included in the analysis are indicated. The percentage of the variance explained by each axis is indicated in brackets after each axis label.

5.3.3 Reproductive traits data set PCoA

The trait attributes for each of the functional groups identified in Figure 5.7 through the reproductive trait analysis were investigated in detail (Table 5.5) and compared with the complete trait data set and vegetative trait data set groupings.

Although the reproductive traits data set did not include vegetative traits, the groupings that were produced to some degree still followed main life forms as was seen in the complete data set and vegetative trait data set analyses (Figure 5.7). Groups I and II were dominated by trees and small to large, semi-woody to woody shrubs, but with perennial creepers and bulbous geophytes intruding into Group II (compare Groups I to IV in Figure 5.1). Perennial and annual grasses mostly grouped together in the reproductive trait analysis instead of separately (Groups VI and VII). Prostrate and erect annuals were grouped separately in Groups IV and V with some transition into group VI. Group III consisted of an assemblage of herbaceous to semi-woody, small to large shrubs and perennial creepers, geophytes and lianas (compare Groups III, IV and V in Figure 5.1).

Inflorescence prominence, germination phenology and plant/flower gender trait categories were similar between groups and did not contribute to separation of groups.

- Group I – Trees and woody to semi-woody, medium to large shrubs
Occasional belowground clonality occurred in the group, mostly warm and dry season flowering, and hot and humid season fruiting. Unspecialized zoochorous pollination was typical on brush flower shapes which were carried in spike, raceme, capitulum or cluster inflorescences or as single flowers (Figure 5.8). Yellow and white flower colour combinations were dominant (Figure 5.8). Berries or capsules producing diaspores without any attachments or sometimes fleshy pulp fruit were dispersed through endozoochory (Figure 5.9). Antitelechory was either absent or anti-telechory was present in the form of synaptospermy. Several large seeds were produced per fruit (>5) delivering medium to high fecundity, but transient seed banks. Plant life span was generally long.
- Group II – Woody to semi-woody small to large shrubs, perennial creepers and bulbous geophytes
Clonality was absent, flowering associated with the warm and dry season and fruiting with the hot and humid season. Specialized or unspecialized zoochorous pollination was associated with brush, bell-funnel, flag or gullet flower shapes carried solitary, in clusters, or sometimes in capitulums. Yellow and white flower combinations were common with limited other colour combinations. Capsule fruit were most common with occasional achene, nut or drupe types. Diaspores of the medium sized seeds sometimes had fleshy pulp or plumes, but were otherwise without attachments and had anemochorous or autochorous dispersal. Several

seeds (>5) were produced per fruit generating transient seed banks and variable, although generally high fecundity. Life expectancy was of medium duration.

- Group III – Herbaceous to woody and small to large shrubs, perennial creepers, geophytes and lianas

Occasional underground clonality was observed in the group and typically flowering occurred in the hot and humid season and fruiting in the warm and dry season. Specialized or unspecialized zoochorous pollination was associated with the predominantly solitary inflorescences, although several other types were also observed. Predominantly bowl-dish and bell-funnel to tubular flowers has yellow as dominant colour. Diaspores without any attachment or with fleshy pulp were mostly carried in capsules, but sometimes berries or pepos were observed. Anemochory, endozoochory and autochory were dispersal mechanisms and antitelechory was either absent or took the form of synaptospermy. Medium seeds had transient to no seed banks, with the variable numbers of seeds per fruit producing low to medium fecundity. Plants had a medium expected life span.

- Group IV – Prostrate and erect annuals, few weak herbaceous perennials

The group exhibited no clonality and flowering was confined to the hot and humid season and fruiting mostly to the warm and dry season. Pollination was specialized or unspecialized zoochory. Flowers were mostly carried solitary, but at times in clusters, capitulum or spikes. Bowl-dish, flag or gullet flowers were most common and flowers colour yellow, but with shades of white, blue and purple also occurring. Capsules produced diaspores without seed attachments, or uncommonly burred fruit or plumed seeds. Dispersal by anemochory was most dominant, but epizoochory and autochory were also observed. Antitelechory was absent or by synaptospermy. Medium sized seeds were produced in variable quantities per fruit, culminating in low to medium plant fecundity and often permanent seed banks. Life expectancy was short to medium.

- Group V – Prostrate and erect annuals

Absence of clonality typified this group as well as flowering and fruiting associated with the hot and dry season. Unspecialized zoochorous pollination through capitulum, cymes or spikes was dominant. The bowl-dish or brush flowers were mostly of singular yellow, white or green colours, or combinations thereof. Capsules or achenes produced diaspores without attachments, but sometimes had winged or bristled seeds. Antitelechory was absent or took the form of trypanospermy. The small to medium sized seeds were produced in variable numbers per fruit, produced medium to high fecundity, and were delivered into permanent seed banks. Plant life span was short.

- Group VI – Perennial grasses and herbaceous annuals

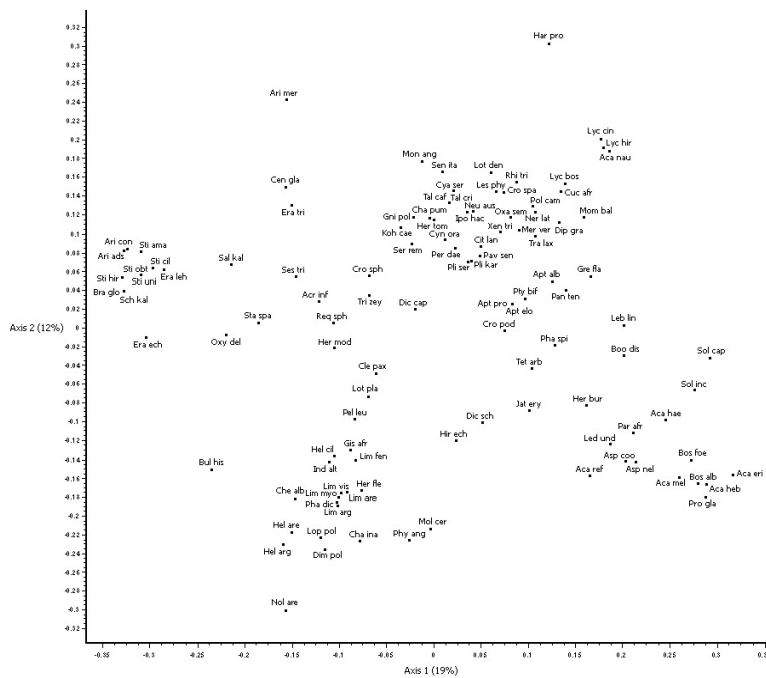
Aboveground or belowground were observed in the group, although not a common feature. Flowering occurred in the hot and humid season and fruiting in the warm and dry season. Wind was the common mode of pollination with bowl-dish, floret or gullet flower shapes often carried solitary or in panicles. Yellow flowers was almost absent, with white, orange to purple and brown colours dominating. Caryopsis or nut fruit types was most common as was diaspores without seed or fruit attachments, or winged or burred seeds, or winged fruit. Anemochorous dispersal was most common, with epizoochory only uncommonly found. Antitelechory was mostly absent. Small to medium size seeds were produced in medium numbers per fruit (2-5), delivering low to medium fecundity and either permanent or transient seed banks. Life expectancy was short.

- Group VII – Annual and perennial grasses

Clonality was mostly absent, flowering occurred in the hot and humid season and fruiting in the warm and dry season. Wind pollination facilitated through floret flower shapes and panicle inflorescences were typical. White, yellow and green flower colours were most common. The caryopsis most commonly had burred or plumed seed diaspores, but also at times had no attachments. Anemochory or epizoochory occurred and antitelechory was either absent or facilitated through trypanospermy. The small seeds were produced in low numbers per fruit (≤ 2), but produced variable fecundity. Permanent weed banks were typical. Life span was expected to be short to medium.



a



b

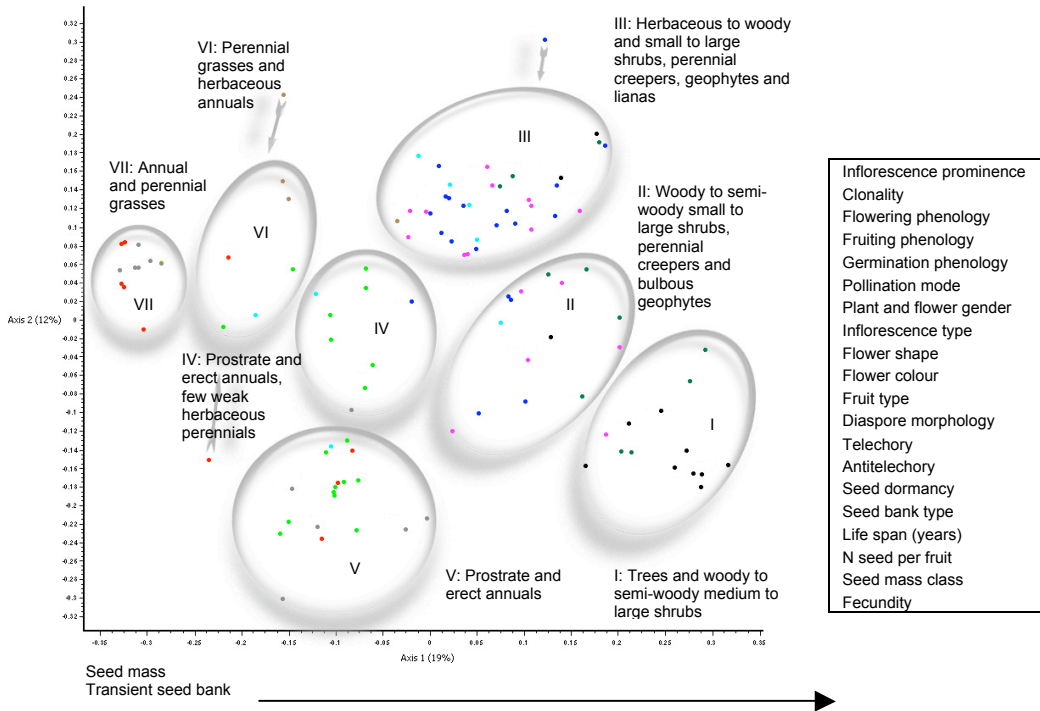


Figure 5.7 (a) Principal Coordinates Analysis (PCoA) scatter diagram of 112 Kalahari plant species for a reduced set of 20 reproductive plant traits and (b) the subsequent groups identified. The traits included in the analysis are indicated. Colour coding is according to the groups identified in Figure 5.1 for comparison. The percentage of the variance explained by each axis is indicated in brackets after each axis label.



Table 5.5 Detailed descriptions of reproductive trait categories for functional groups identified by PCoA of 20 reproductive plant traits (Figures 5.8, 5.9 & 5.10)

	Group I	Group II	Group III	Group IV	Group V	Group VI	Group VII
	Trees and woody to semi-woody, medium to large shrubs	Woody to semi-woody small to large shrubs, perennial creepers and bulbous geophytes	Herbaceous to woody and small to large shrubs, perennial creepers, geophytes and lianas	Prostrate and erect annuals, few weak herbaceous perennials	Prostrate and erect annuals	Perennial grasses and herbaceous annuals	Annual and perennial grasses
Number of species	14	15	36	9	19	8	11
Inflorescence prominence	Exposed	Exposed	Exposed, rarely indeterminate	Exposed, rarely indeterminate	Exposed, rarely indeterminate	Exposed	Exposed
Clonality	No clonality or uncommonly belowground	No clonality,	No clonality or uncommonly belowground	No clonality	No clonality,	No clonality, or uncommonly aboveground or belowground	No clonality, rarely aboveground or belowground
Flowering phenology	Warm and dry season, also commonly hot and humid season	Warm and dry season, or hot and humid season	Hot and humid season	Hot and humid season	Hot and humid season, rarely warm and dry season	Hot and humid season	Hot and humid season
Fruiting phenology	Hot and humid season	Hot and humid season, rarely warm and dry season or cold and dry season	Warm and dry season	Warm and dry season, uncommonly hot and humid season	Hot and humid season, rarely warm and dry season	Warm and dry season	Warm and dry season
Germination phenology	Warm and dry season	Warm and dry season	Warm and dry season, rarely cold and dry season	Warm and dry season	Warm and dry season, rarely hot and humid season or cold and dry season	Warm and dry season	Warm and dry season
Pollination mode	Unspecialized zoochorous	Unspecialized zoochorous or specialized zoochorous	Unspecialized zoochorous or specialized zoochorous, uncommonly wind	Unspecialized zoochorous or specialized zoochorous	Unspecialized zoochorous, rarely specialized zoochorous or wind	Wind, or uncommonly specialized zoochorous	Wind
Plant/flower gender	Monoecious	Monoecious	Monoecious	Monoecious	Monoecious	Monoecious	Monoecious
Inflorescence type	Solitary, cluster, capitulum, spike or raceme	Solitary or cluster, uncommonly a capitulum, rarely an umbel, cyme or spike	Solitary, uncommonly a cluster, umbel, spike or raceme	Solitary, uncommonly a cluster, capitulum or spike	Capitulum, cyme or spike, uncommonly a cluster or umbel	Solitary or a panicle, uncommonly a cluster, spike or thyse	A panicle
Flower shape	Brush	Bell-funnel, brush, flag or gullet	Bell-funnel or bowl-dish, uncommonly a trumpet, tube or flag	Bowl-dish, flag or gullet, uncommonly a bell-funnel	Bowl-dish or brush, rarely a bell-funnel, tube or flag	Bowl-dish, floret or gullet	A floret
Flower colour	See Figure 5.9						
Fruit type	Berry or capsule	Capsule, uncommonly an achene, drupe or nut	Capsule, uncommonly a berry or pepo	Capsule, rarely an achene or nut	An achene or capsule, rarely a nut	Caryopsis or nut, uncommonly a capsule or utricle	Caryopsis
Diaspore morphology	No fruit or seed attachments, uncommonly fleshy pulp fruit	No fruit or seed attachments, uncommonly fleshy pulp fruit or plumed seeds, rarely winged seeds or winged fruit	No fruit or seed attachments, or fleshy pulp fruit, rarely winged seeds, plumed seeds or winged fruit	No fruit or seed attachments, uncommonly plumed seeds or burred fruit	No fruit or seed attachments, uncommonly bristled seeds or winged seeds	No fruit or seed attachments, uncommonly burred seeds, winged seeds or winged fruit	Burred seeds or plumed seeds, uncommonly no fruit or seed attachments
Telechory	Endozoochory	Anemochory or autochory,	Anemochory, also commonly endozoochory, autochory	Anemochory, uncommonly epizoochory or autochory	Anemochory, rarely synaptospermy or heterodiaspory	Anemochory, uncommonly epizoochory	Anemochory or epizoochory
Antitelechory	None or synaptospermy	None or synaptospermy	None or synaptospermy, rarely autochory	None or synaptospermy	None or trypanospermy	None, rarely synaptospermy or trypanospermy	None or trypanospermy
Seed mass class (mg)	>100-1000, also commonly ≤0.1-100	>0.1-10, rarely >10-100	>0.1-10, rarely >10-100	>0.1-10, rarely >10-100	≤0.1-10	>1-10, uncommonly >0.1-1	>0.1-1, uncommonly >1-10 or ≤0.1
Seed dormancy	None or moderate	Moderate, uncommonly none	Moderate, uncommonly none	Moderate or strong, rarely none	Strong, rarely none or moderate	Moderate or strong	Strong, rarely moderate
Seed bank type	Transient, uncommonly none	Transient, uncommonly none	Transient, uncommonly none, rarely permanent	Permanent, uncommonly transient	Permanent	Permanent or transient	Permanent
Life span (years)	>2 to >50	>2 to 25	>2 to 25, uncommonly ≤1	≤1, uncommonly >2 to 25	≤1, rarely >1-5	≤1 or >2-5	≤1, >1-2 or >5-25
N seeds per fruit	>5-10, or >10, uncommonly ≤2 or >2-5	>5-10, or >10, also commonly ≤2	>2-5, or >10, uncommonly ≤2 or >5-10	≤2 to >10	≤2 to 5, or >10	≤2, uncommonly >2-5, or >10	≤2
Fecundity	>1000-5000 or >5000, uncommonly >200-1000	>1000-5000, also commonly ≤200-1000 or >5000	>200-1000, uncommonly ≤200 or >5000	>200-1000	>500 to >5000, rarely ≤200 or >200-500	>200-1000, uncommonly >1000	>500-5000

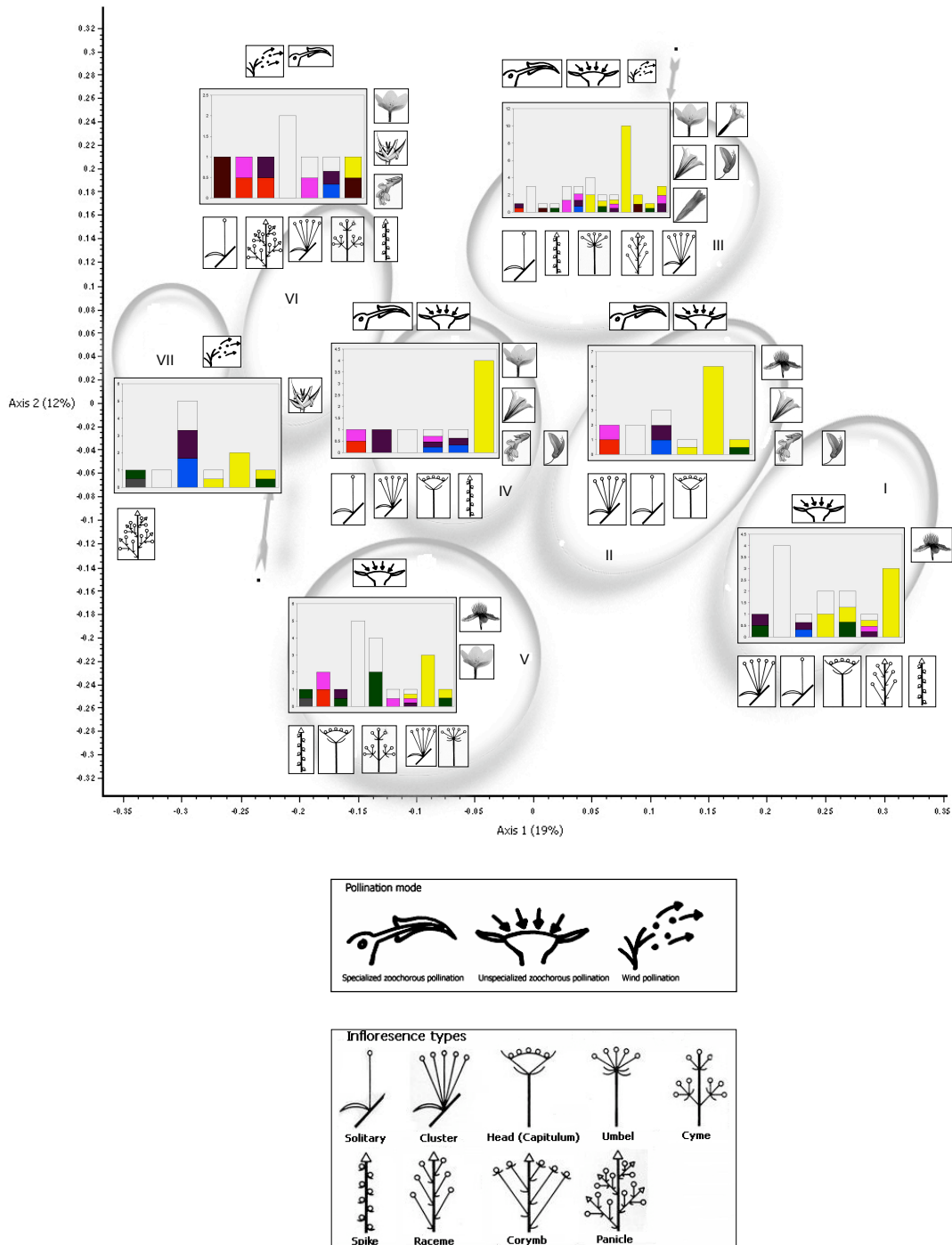


Figure 5.8 Principal Coordinates Analysis (PCoA) scatter diagram of 112 Kalahari plant species for a reduced set of 20 reproductive plant traits and the subsequent groups identified. Inflorescence type (below each graph), flower type (right side of each graph) and flower colour for the groups have been highlighted. Larger inflorescence icons denote more dominant states. Flower colour is indicated by the number of species that have specific flower colour combinations, for example in group V, five species have white flowers and four species have green and white combination flowers. The percentage of the variance explained by each axis is indicated in brackets after each axis label.

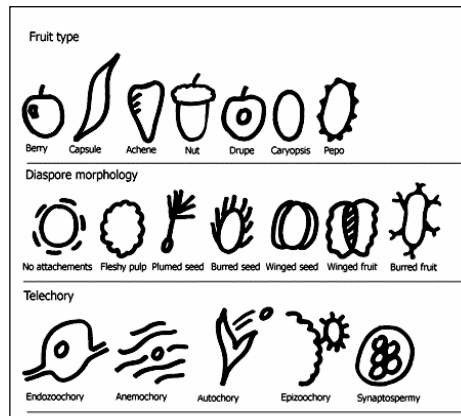
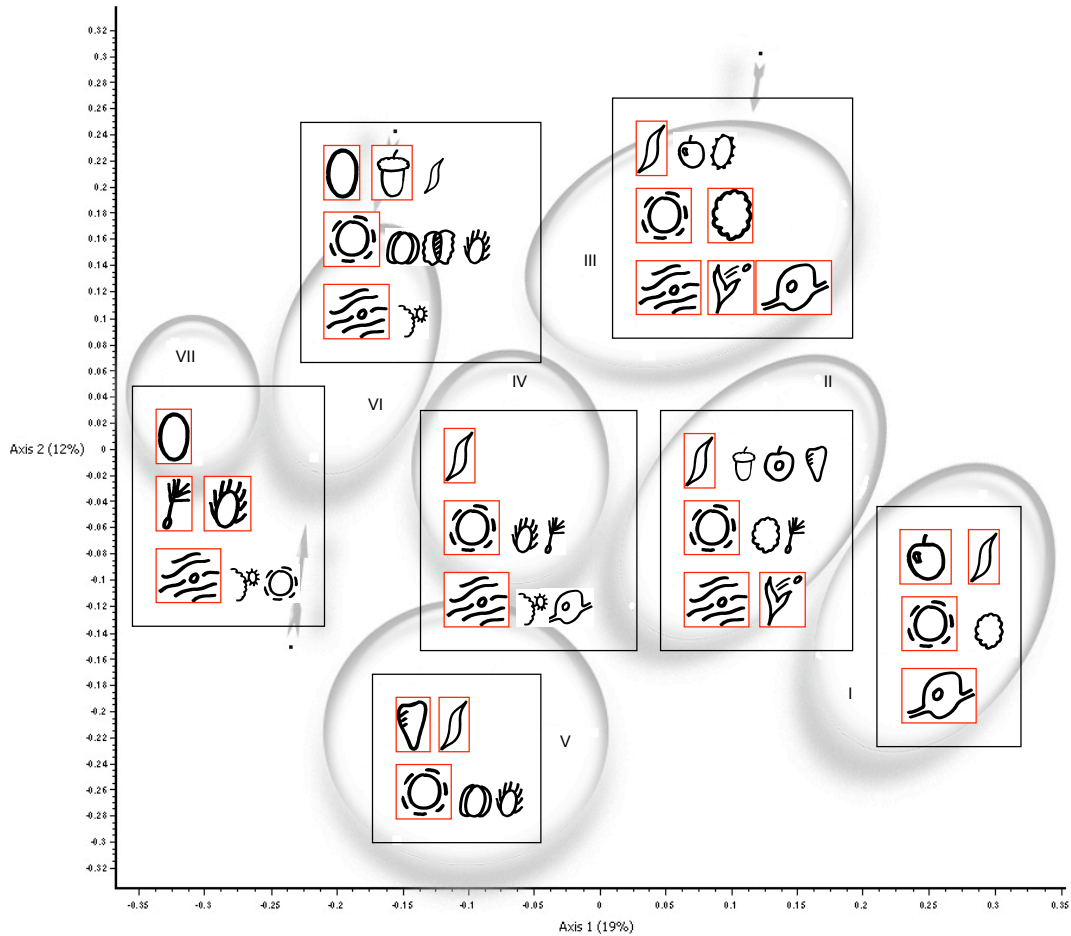


Figure 5.9 Principal Coordinates Analysis (PCoA) scatter diagram of 112 Kalahari plant species for a reduced set of 20 reproductive plant traits and the subsequent groups identified. Fruit type, diaspore morphology and telechory have been highlighted consecutively from top to bottom per group. Larger boxed icons denote more dominant states. The percentage of the variance explained by each axis is indicated in brackets after each axis label.

The product-moment correlation analysis of the group of 51 species that had data available for the traits specific leaf area and leaf dry matter content showed that these two traits had significant negative correlation with each other. Where correlations between both these two traits and other traits were significant, SLA and LDMC were always converse to each other. SLA showed significant negative correlation with the following continuous traits: stem density ($r=-0.52$), stem spinescence ($r=-0.34$), leaf consistency ($r=-0.40$), plant height ($r=-0.42$), canopy diameter ($r=-0.46$), canopy density ($r=-0.28$), life span ($r=-0.62$), and leaf longevity ($r=-0.49$). LDMC on the other hand exhibited significant positive correlation: stem density ($r=0.41$), stem spinescence ($r=0.41$), leaf consistency ($r=0.32$), plant height ($r=0.57$), canopy diameter ($r=0.38$), canopy density ($r=0.57$), life span ($r=0.61$), and leaf longevity ($r=0.53$). Scatterplot matrices between selected variables are shown in Figure 5.11. The complete analysis of the relationship between SLA, LDMC and other continuous traits is shown in Appendix A.1. Appendix A.2 also shows correlations between the continuous traits for the complete data set, not only the 51 species with SLA and LDMC data.

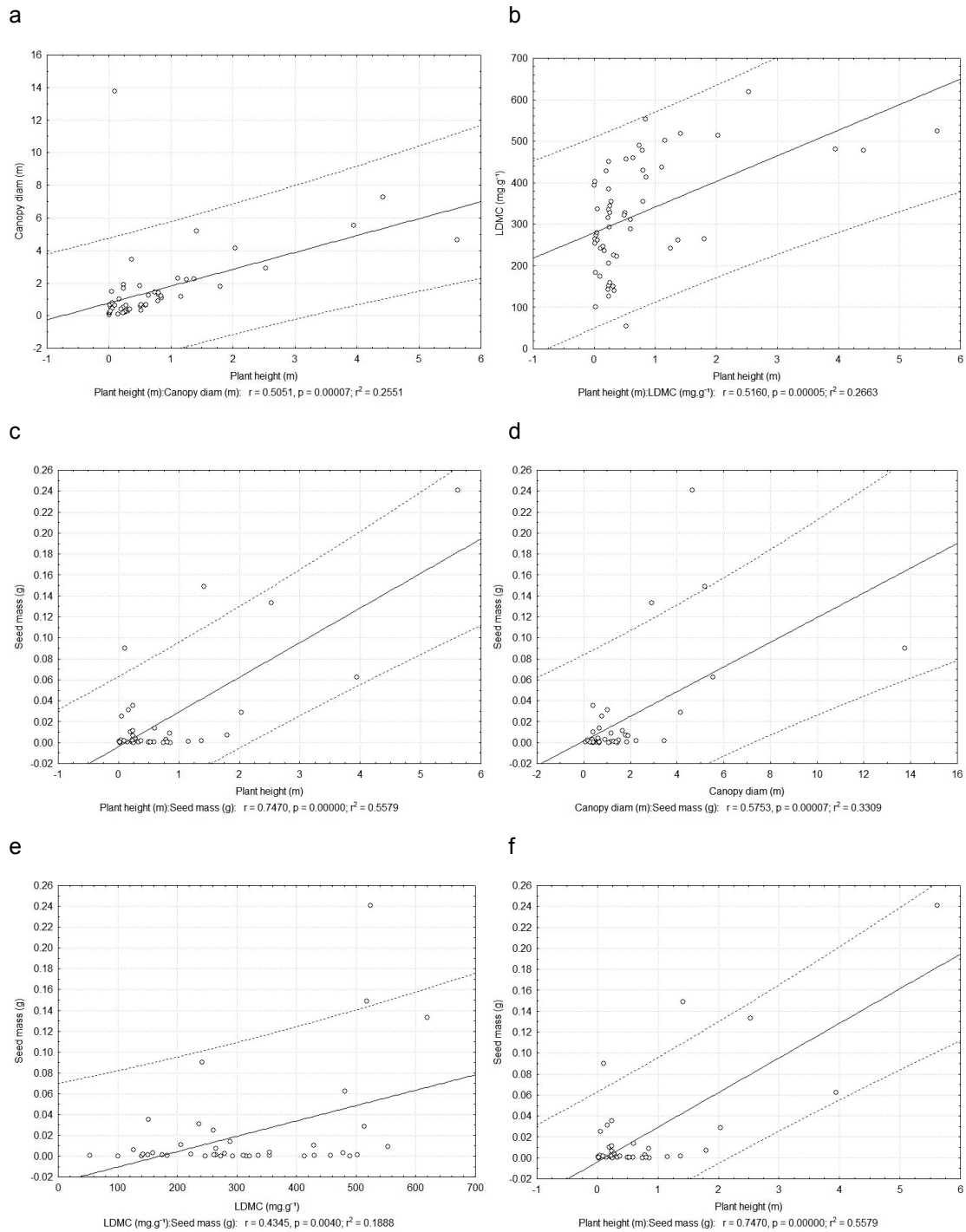


Figure 5.10 Product-Moment scatterplot matrices of species data sets for which specific leaf area (SLA), leaf dry matter content (LDMC) and seed mass data were available. SLA and LDMC analyses were conducted for 56 plant species and seed mass data is available for 42 plant species. The scatterplot matrices are (a) plant height vs. canopy diameter (N=56), (b) plant height vs. LDMC (N=56), (c) plant height vs. seed mass (N=42), (d) canopy diameter vs. seed mass (N=42), (e) LDMC vs. seed mass (N=42) and (f) plant height vs. seed mass (N=42). Double dotted lines denote predictions at the 95% level.

5.4 General discussion

The Kalahari is a semidesert and the primary driver of forage production is rainfall (Van Rooyen & Van Rooyen, 1998). Drought and water availability therefore act as strong filters of functional traits that will allow for the persistence and reproduction of species in such a region (Woodward & Diament, 1991). The species groups identified in the complete analysis represent different strategies of coping with the demands of the arid environment. Within these groups different adaptations with respect to vegetative persistence and reproduction were exhibited.

Although the aim of the current analyses was to classify functional groups, it should be noted that the distribution of species in the ordination plane occurred along a continuum for the respective traits and that the boundaries between functional groups were often not clear. The delineation of groups was therefore largely subjective. Two groups that were in close proximity in one analysis could be grouped together in the analysis of another set of traits, even though the absolute differences between the two analyses are small. Prominent life forms such as annual and perennial grasses, herbaceous annuals and woody or semi-woody shrubs were however evident. Upon closer investigation smaller subgroups of species also occurred within the major groups.

Vegetative traits and more specifically Raunkier life form, shoot architecture, plant height, stem density and life span were important traits that divided groups representing major life forms. In the complete (Figure 5.2) and vegetative (Figure 5.6) analyses the larger more frutescent trees and shrubs were always grouped distinctively on the right of the ordination plane with the herbaceous, small annuals grouped oppositely on the left of the ordination plane. Between these extremes were groups representing transitions from suffrutescent shrubs to perennial grasses and herbaceous perennials. The importance of the vegetative traits were evident from the observation that although major life forms were still evident in most of the groups in the reproductive analysis, plant sizes and stem densities for example (vegetative traits) were no longer strongly correlated with the first axis. Significant positive correlations were found between plant height, stem spinescence, leaf consistency, canopy density, canopy diameter and life span, whereas significant negative correlations were found between plant height and leaf hairiness (Appendix A).

Plant height is associated with competitive vigour, high fecundity and an increase in the interval between disturbances (Cornelissen *et al.*, 2003). A reduction in plant height has been associated with increased grazing pressure, in order to avoid predation (Landsberg *et al.*, 1999; Diaz *et al.*, 2001), but was not found by Vesk *et al.* (2004). Species with sprawling habits produced large canopy diameters in the current study. Lavorel *et al.* (1999) showed that grazing leads to smaller canopy diameters in grasses and forbs. A large canopy diameter

may be related to competitive vigour and more efficient use of sunlight (surface area), or more specifically large canopy at low height when growth occurs under the protection of other shrubs. Few of the prostrate or creeping species in the Kalahari have such protection, with most of these species growing in the open. Those that are associated with other plants often grow on top of other shrubs (e.g. *Momordica balsamina*) or are so vigorous that they outgrow the canopies of other plants (e.g. *Cucumis africanus* and *Acanthosicyos naudinianus*). Tall woody species are also more visible to grazers. In Mediterranean communities Hadar *et al.* (1999) reported that geophytes increased under extended heavy grazing because of their small size (height), but also due to their early flowering phenology (seed formation opportunities) and less dependence on seed in comparison with annual and perennial grass species.

Shoot architecture became less procumbent, decumbent or erect and more caespitose shrub, semi-circular shrub or tree-like from left to right across the complete (Figure 5.2) and vegetative ordinations (Figure 5.6). Shoot architecture may be closely related with plant height and grazing avoidance (Landsberg *et al.*, 1999; Diaz *et al.*, 2001; Cornelissen *et al.*, 2003). Trees may also outgrow the predation zone of large herbivores once a critical height is reached.

Stem density increased along the first axis. Higher stem density is related to plant longevity (resource investment), carbon storage, plant height (supporting structure) and stem palatability (Weiher *et al.*, 1999). Stem density was closely and positively correlated to leaf consistency ($p < 0.05$; $r = 0.29$), with leaves becoming more sclerophyllous in the suffrutescent shrubs, frutescent shrubs and trees. Sclerophyllous leaves have a higher construction “cost” per unit leaf area than malacophyllous leaves, which can only be recovered through reduced water loss in the short term as well as cumulative energy capture over the long term due to lower productivity (Skarpe, 1996). Leaf consistency (sclerophylly) is closely coupled with specific leaf area and leaf dry matter content (Skarpe, 1996; Diaz *et al.* 2001) and was also observed in this study ($p < 0.05$; $r = -0.40$ and $p < 0.05$; $r = 0.32$). The correlation analysis of 56 species with SLA and LDMC data showed that as SLA increases, LDMC decreases ($p < 0.05$; $r = -0.60$), with sclerophylly being positively aligned with LDMC. This result is supported by Wilson *et al.* (1999) and McIntyre (2008). SLA is associated with the relative potential growth rate of a species where large SLAs are associated with resource rich environments and low SLAs with resource-poor environments (Cornelissen *et al.*, 2003; McIntyre, 2008).

Leaf area however, was not significantly correlated with specific leaf area. Some of the large-leaved species in the study, such as *Acanthosicyos naudinianus*, and most of the grass species had large leaves in comparison with other species but the leaves had low SLA values (e.g. *A. naudinianus* $\leq 0.5 \text{mm}^2 \cdot \text{mg}^{-1}$) and were still semi-sclerophyllous to sclerophyllous. Diaz *et al.* (2001) observed that in a study of two grassland vegetation types, one site in Argentina

showed no link between SLA and leaf area whereas another site in Israel showed a significant negative relationship between the two traits. Small leaf area can be linked with environmental stresses such as high radiation and increased transpiration (water loss), low resource availability (cost of manufacture) and low temperatures (risk of freeze damage) (Skarpe, 1996; Cornelissen *et al.*, 2003). Leaf size decreases in phanerophytes and grasses when water availability decreases (Skarpe, 1996). Most perennial shrubby species are without leaves in the hot and dry periods (Van Rooyen, 2001). The leaves of most species were therefore not carried for more than one growing season. The leaves of ephemeral species were however, even more short lived.

Leaves were predominantly simple in all groups in the vegetative trait analysis except for Group I where bipinnate and pinnate leaves were common. Compound leaves, in conjunction with small leaflet size or sclerophylly, instead of single, large laminae provide the benefits of increased light infiltration through the canopy as well as reduced moisture loss through transpiration (Orians & Solbrig, 1977) and possibly the capability of partial leaf loss during herbivory instead of whole leaf (and resource investment) loss. Canopy cover in the Kalahari is generally low without closed canopy formation by phanerophytes that would limit light infiltration. Compound leaves as observed in Group I is therefore probably related to moisture loss reduction and herbivory loss limitation.

Stem spinescence increased along Axis 1 (Figure 5.6). Spines act as a deterrent against herbivore attack and may also have an additional role of reducing heat and drought stress (Cornelissen *et al.*, 2003; Hanley *et al.*, 2007). The long-lived species of Groups I and II had a higher degree of stem spinescence because of their need to conserve resources and the higher initial investment in leaf and stem production (higher LDMC). The present study showed a significant negative relationship between SLA and stem spinescence ($p < 0.05$; $r = -0.34$) whereby spinescence increased when SLA decreases, which supports the theory that spines have a primary defence function. The dense caespitose and semi-circle shrub shoot architecture types that were so common in several groups may also to some degree have a defence function. Even though spines may be absent, a dense woody structure would protect leaves towards the center of the plant, both from predation as well as abrasion and desiccation.

Life span increased with an increase in plant height, and stem density. In life history strategies species are either good competitors (K-selected) or ruderals (*r*-selected), where K-selected species are longer lived than *r*-selected species (Begon *et al.*, 1996). The *r*-selected species also have greater biotic potential to expand their populations during periods of abundant resource supply. Although K and *r*-selection does not refer to perennial versus annual life histories *per se*, K-selected species are associated with a long life span, whereas *r*-selected species are associated with a short lifespan.

Nitrogen fixing capability was common in Group I, but only uncommonly found in a few shrubs in Groups II and III as well as a few creeping annuals in Groups VIII and IX. Kalahari soil fertility is generally low (Buckley *et al.*, 1987b; Van Rooyen & Van Rooyen, 1998) and investment of resources into nitrogen fixing structures would be advantageous, especially for the long-lived Group I species. Milberg *et al.* (1998) reports a positive relationship between the three factors (a) seed size, (b) seed N, P and K content and (c) soil nutrient levels. The dual facility of large seeds and nodulation would therefore promote plant persistence in nutrient poor Kalahari soils, whereby large seeds would provide seedlings with a resource supply after germination and nodulation would increase N supply at a more mature life stage. *Parkinsonia africana* has very small leaves compared with other woody plant species of which a contributing factor may be the lack of nitrogen fixing capability.

C₄ photosynthesis was restricted to Groups VI to IX in the complete analysis, groups in which grasses were common. Several herbaceous annuals or weak herbaceous perennials also exhibited C₄ photosynthesis in these groups such as *Chamaesyce inaequilatera*, *Bulbostylis hispidula*, *Gisekia africana* and *Tribulus zeyheri*. This pathway is most efficient in hot and sunny habitats (Sage, 2004) and grass activity is therefore restricted to spring, summer and autumn. The hot and humid (and sunny) season is the optimal season for growth in the Kalahari for annuals, with C₄ photosynthesis being beneficial during this period. It has been shown that dominant C₄ species of the Kalahari have higher carbon assimilation rates than C₃ species, but interestingly that the rate in *Stipagrostis obtusa* and *S. uniplumis* was much lower than that of *S. ciliata*, *Eragrostis lehmanniana* and *Centropodia glauca* (Yu *et al.*, 2009). Rapid carbohydrate assimilation in the wet season would be a beneficial strategy for Kalahari species and may explain in part the dominance of grass in many areas.

Underground storage organs were common in Group IV and uncommon in Groups II, III and IX of the complete analysis which were the groups in which geophytes and perennial creepers such as *Cucumis africanus* and *Acanthosicyos naudinianus* were present. Species with underground storage organs are to some extent functionally comparable to ephemerals by avoiding environmental stress periods, although more reserve resources are immediately available upon regrowth in species with carbohydrate storage organs than annuals that rely on the restricted resource pool contained within the seed. The large available resource reserve with geophytes and perennial creepers could explain why these species often have some of the largest leaves which are metabolically expensive to produce. Replenishment of the underground storage organs would ironically also require a large amount of energy capture through a network of large leaves.

Clonality only occurred uncommonly in the groups dominated by trees, large shrubs or perennial grasses and rarely in other groups. Clonality is associated with competitive vigour, the ability to exploit resource-rich patches, or short-distance migration under poor seed

dispersal circumstances or poor seedling recruitment (Cornelissen *et al.*, 2003). The Kalahari has a low plant cover (Van Rooyen & Van Rooyen, 1998), relatively uniform resource distribution (few resource islands) and many species with telechoric mechanisms of seed dispersal, all of which confer little advantage to clonality. Because of the prominence of wind pollination and anemochory in the Kalahari, clonality probably has a more competitive or vegetative function than a reproductive one and is not common among Kalahari species.

Although no relationship was observed between leaf hairiness (leaf trichomes) and any of the axes, the significant negative relationship observed between leaf hairiness and plant height ($p < 0.05$; $r = -0.22$) indicates that taller, longer lived plants are investing more in these morphological structures. This may serve to offset the high water loss associated with elevated transpiration levels (Skarpe, 1996). Leaf hairs have the function of preserving moisture by reducing transpiration loss and excessive heat gain (Hanley *et al.*, 2007), but often causes a concomitant loss in photosynthetic rate (Skarpe, 1996). This action may be furthered by the grey-green colour of such hairy leaves which have higher light reflectance. Leaf hairs may also negatively affect palatability by providing structural defence against herbivory (Hanley *et al.*, 2007). Leaf hairiness has been shown to increase in some plant species following defoliation as possible deterrent against herbivory (Hanley *et al.*, 2007). In Tunisian steppes chamaephytes were more hairy in areas of low perennial plant cover (higher degradation) than areas of medium perennial plant cover (lower degradation) (Jauffret & Lavorel, 2003). Leaf hairiness was less common in hemicryptophyte (grass) dominated groups (Groups, VIII and IX of the complete analysis) where seasonal leaf shedding may make the investment in additional leaf structures uneconomical. Groups II to V in the complete analysis were noted for the occasional occurrence of large leaved (mesophyllous) species and these groups often had hairy leaves. No statistically significant relationship was however recorded.

Palatability is a difficult trait to quantify and attribute to a species, since palatability for the same species can change depending on numerous factors such as the herbivore species, seasonality, plant organs utilised, climate, soil and associated vegetation type (Du Toit, 2001). Toxicity, often associated with the bulbous species, was observed in several groups and perceived or subjectively estimated palatability was very variable within most groups. The Group VI herbaceous annuals, Group VIII perennial grasses (main fodder of large herbivores) and the *Acacia* dominated Group I had the highest palatability scores. Leaf or stem exudates may serve to deter herbivores (Landsberg *et al.*, 1999), but also reduce water loss (Orians & Solbrig, 1977). Such exudates were, however, only sporadically recorded in the analyses, but were most common in Groups I (trees and large shrubs) and IX (erect or creeping annuals and annuals grasses) of the vegetative analysis. In some annuals such as *Limeum arenicolum* and *Cleome paxii*, which exhibit this characteristic, the exudates may serve an

additional role of protection against wind and sand abrasion through adherence of sand particle to the plant parts (psammophory).

Most species grew actively in the periods from spring to autumn. The Kalahari is a summer rainfall region with cold winters during which frost occurs. This limits growth to the warm summers, but growth is nevertheless very dependent on rainfall. Leistner (1967) indicated that the growth period starts in early spring (August-September) even before the onset of rain for shrubs and trees and perennials with underground storage organs, and ends around May when frosts begin and summer annuals die off, grass leaves and culms dry up and perennials start to lose their leaves.

Single plants or plants in loose groups were the most common social structure in all groups. The sociability structure can be dependent on rainfall and isolated rainfall events may see annual species exhibiting different sociability structures within small distances. Competition for limited resources makes very close, dense growth undesirable. In the nutrient-poor soils of the Kalahari shrubs such as *Acacia mellifera* and *Lycium* sp. with extensive shallow root systems would only be able to increase in density up to a point where sufficient resources are available for each plant (Skarpe, 1990a and b). In such close proximity competitive effects will increase as observed in *Acacia mellifera* (Meyer *et al.*, 2008) and *Acacia erioloba* (Moustakas *et al.*, 2008). Underneath the canopy of encroaching species, e.g. *R. trichotomum*, there is usually little or no vegetation present due to the shallow root systems of these shrubs that monopolize resources. The grass and shrub layer dynamics and the dominance of either life form are dependent on rainfall, herbivory and fire (Jeltsch *et al.*, 1996; Jeltsch *et al.*, 1997; Weber *et al.*, 2000).

Very few species in the present study were considered to have had indeterminate inflorescences, where inflorescences were recessed or hidden within leaf or stem structure. Although several species had small flowers, these were not necessarily recessed (e.g. small seeded grass species). Most species had inflorescences that were clearly visible and exposed and those species, such as the grasses that had small flowers, carried them exposed. Although indeterminate may also purely refer to flower or inflorescence positions in the axils of leaves, in this study it refers to whether flowers are conspicuous or not.

Flowering in the hot and humid season (November to March) was common in all functional groups in both the complete trait and reproductive trait analyses. The Kalahari is a summer rainfall region and flowering is usually in response to rainfall events. Changes in flowering and fruiting phenology can be employed to avoid disturbances or competition (Weiher *et al.*, 1999), but because water is such a limiting factor growth, flowering and fruiting periods are limited to the rainy season from spring to autumn (Scanlon *et al.*, 2005). The availability of animal pollinators will also largely be limited to favourable environmental periods. In the tree

and shrub dominated groups, Groups I to III of the complete analysis, flowering before the onset of the first summer rains (September/October) were also common. Fruiting phenology followed the flowering phenology pattern, ranging from the hot and humid season to the warm and dry season (April/May).

Plant and flower gender were not included in the analyses because only one species were found to be dioecious and all others monoecious. According to Faegri & Van der Pijl (1979) dioecy has the advantage that autogamy is prevented, but has the disadvantage that only part of the population can produce seed. Mechanisms such as protandry or protogyny may however negate autogamy risk and gender ratios are also not necessarily equal in plant populations. Self incompatibility in Kalahari species was not investigated.

In this study the bell-funnel, bowl-dish and brush flower (or inflorescence) types were regarded as unspecialized zoochorous adaptations with the visual attraction being non-specific, mostly no nectar guides for pollinators and landing surface being available on any part of the flower for many types of pollinators (Faegri & Van der Pijl, 1979; Dafni, 1992). The trumpet, tube, flag and gullet were regarded as specialized zoochorous adaptations with more specific visual attractions (e.g. standard of the flag type or lips of the gullet type), the presence of nectar guides and more specific landing localities (Faegri & Van der Pijl, 1979; Dafni, 1992). The spikelet was regarded as an anemophilous adaptation with little to no visual pollinator attraction and small (but not necessarily hidden) flowers.

Yellow was the dominant flower colour in all groups in both the complete (Figure 5.3) and reproductive (Figure 5.8) trait analyses except for the groups that were dominated by grasses. In these groups (VIII and IX on Figure 5.3; VII in Figure 5.8) combinations of bluish-purple, green, grey, white and yellow were present. Grasses are known anemophilic species and the dull flower colours of these groups support this. The general relationship between flower type, flower colour and pollinator group is illustrated in Figure 5.11 (from Faegri & van der Pijl, 1979). According to the scheme, "open" flower (or inflorescence) types serve a great variety of animal pollinator groups, whereas "constricted" flower types such as gullets, flags and tubes serve a more limited pollinator assemblage of birds, butterflies, bees and moths. Group I in the complete analysis is therefore expected to have a broad range of pollinators whereas Groups II to VII could either have specialized or unspecialized pollination mechanisms. Group VII is a transitional Group between anemophilous and zoochorous pollination. Solitary or clustered inflorescence types were most common, except for panicles in the grass-dominated group VII (Figure VII), spikes, clusters and cymes in Group V and a combination of these types in Group I. It has been observed that (a) some species flower over an extended period with gradual maturation of flowers in an inflorescence over an extended period, (b) seed set decreases in an inflorescences' flowers the later pollination takes place in the season due to ovule competition and (c) larger floral displays place greater demands on plant resources and

puts pressure on seed production (Wyatt, 1982). Capitulum may be equivalent of single flowers in terms of pollinator attraction, but are superior in terms of outcrossing because several different “fathers” may be represented in the seed product of one inflorescence (Burt, 1961). In an arid system with limited resources, such as the Kalahari the investment of resources in smaller flowers or compact inflorescences (such as capitulum) and not large floral displays (except for large perennials such as *Acacias*) may therefore be beneficial. The semi-open Kalahari savanna also does not have the densely vegetated habitat of a forest that would require large floral displays to visually attract pollinators. Wind pollination is a common strategy, especially among the grasses, and therefore an investment is made in more, but smaller flowers (spikelets), which are carried in large inflorescences on long stalks to facilitate a higher dispersal point above ground level.

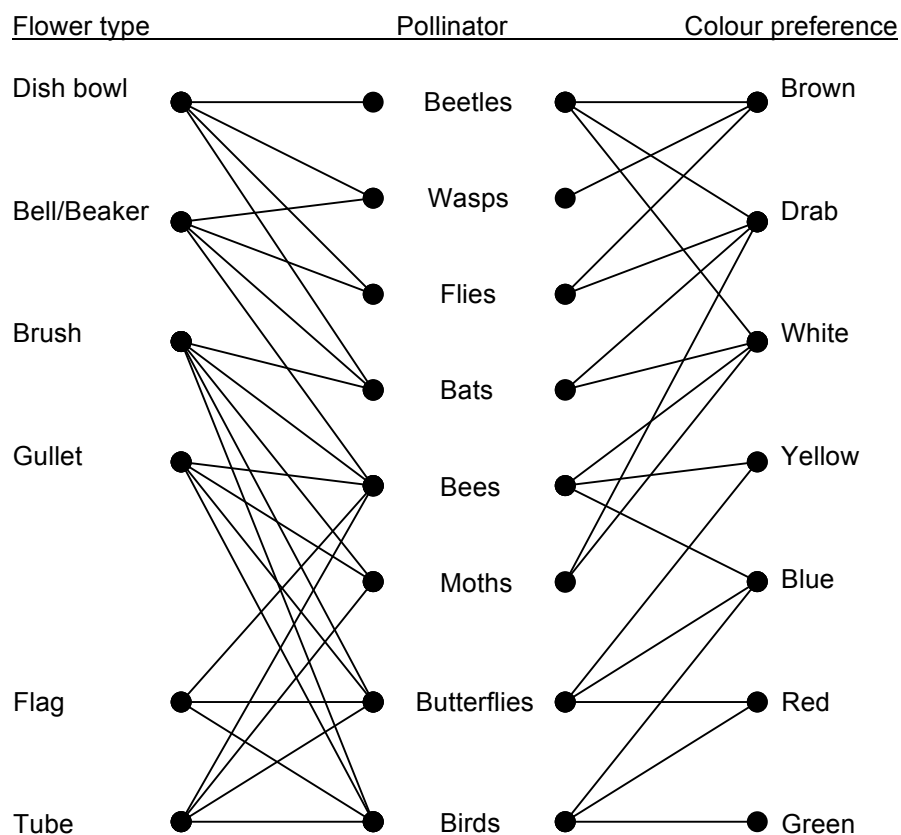


Figure 5.11 Relationship between flower type, flower colour and pollinator type (Faegri & Van der Pijl, 1979).

Endozoochorous dispersal was a common mechanism in Groups I and II in the complete analysis (Figure 5.4). In these groups berries and to a lesser extent drupes were present that are utilized by wildlife and livestock, as well as pods that are also eaten and that can be valuable sources of nutrition (e.g. *Acacia erioloba*, *Acacia haematoxylon* and the crosses of the two species and *Acacia mellifera* subsp. *detinens*; Van Rooyen, 2001, Skarpe *et al.*,

2007). The common occurrence of small seeded species where the diaspores either do not possess appendages or do possess wings (Groups V, VI, VII) or plumes (Groups III, IV, VIII) illustrate the importance of wind anemochory in the Kalahari. Diaspores sometimes appeared to have a duplicate strategy of both anemochorous and epizoochorous dispersal with the presence of bristles or burrs on small diaspores that could serve either function, as is found in *Schmidtia kalahariensis*, *Stipagrostis* species and *Brachiaria glomerata*. Although birds, small mammals, and insects such as ants may also play a role in diaspore dispersal among grass species, the primary dispersal agent, i.e. phase 1 dispersal *sensu* Chambers & McMahan, (1994) was considered, not secondary dispersal. Landsberg *et al.*, (1999) found that grasses in lightly grazed sites were wind dispersed and in heavily grazed sites diaspores were without dispersal aids. Also, forbs in lightly grazed sites had diaspores without dispersal aids and those in heavily grazed sites had animal dispersed seed.

Seed mass was greater in the functional groups consisting of perennials (Groups I to IV) than in the groups consisting of herbaceous annuals (Groups V to VII) and perennial grasses (Groups VIII and IX), (Table 5.3). Generally, species from open habitats have smaller seed mass than species from closed habitats, due to risks associated with shaded environments (Thompson & Hodkinson, 1998; Wright *et al.*, 2000). Annuals require sufficient open space for light and resource availability to develop quickly. Small seeded species are also more abundantly present and are present in more years than large seeded species in desert habitats (Guo *et al.*, 2000), which implies that small seeded species produce more seeds and have longer persisting seed banks (Guo *et al.*, 2000; Cornelissen *et al.*, 2003). In forbs it has been found that more fecund species are associated with heavily grazed areas (Landsberg *et al.*, 1999). Seed mass, rather than seed shape is more important in determining seed longevity, but a combination of the two attributes gives a good indication of seed infiltration depth into the soil (Bekker *et al.*, 1998), although this combined trait was not evaluated in this study. Smaller seeds are furthermore expected to have faster seedling growth rates (Swanborough & Westoby, 1996) but may produce smaller seedlings when nutrient availability is low (Milberg *et al.*, 1998). The organ growth priority may however be different between species of different seed mass, whereby shoot growth is more critical in small seeded species versus root growth in large seeded species to reach reliable water sources (Swanborough & Westoby, 1996; Schütz *et al.*, 2002). Large seeds do however put stress on resource allocation in the mother plant during the fruit formation stages and may limit vegetative growth (Castro-Diez *et al.*, 2003). This study found a significant positive relationship between seed mass and life span ($p > 0.05$; $r = 0.45$; Appendix A.2), indicating that annual species have lower seed mass than perennials. Seed mass was also higher in zoochorous dispersed species (Groups I and II in the complete analysis) than anemochorous species.

Synaptospermy, as a form of antitelechory was present in groups containing berries, pepos and indehiscent capsules. These groups were mostly zoochorously dispersed, indicating that it was preferable for seeds to stay together within a common “dispersal vehicle”. Trypanospermy was present in grass-dominated groups, where seed burial was improved through twisting of the awns when moistened. This promotes seed germination during favourable environmental conditions.

5.5 Conclusion

The Kalahari plant species discussed in this dissertation could be grouped into unique functional groups based either on vegetative or reproductive traits or all traits combined. The functional groups’ characteristics were quite similar between the total and vegetative trait analysis but the reproductive trait analysis revealed many differences due to the strong influence of vegetative traits on the ordinations. Many of the groups, especially with regards to vegetative traits were easily recognizable groups with distinct macrocharacteristics represented by the Raunkier life form type, shoot architecture or size for example.

Species differed in the effect that reproductive or vegetative traits had on their functional group affiliation. However, some correspondence could be found between the groups identified by both vegetative and reproductive traits. For example, phanerophyte species dominated Group I in the vegetative analysis as well as Group I of the reproductive analysis. However, some species of vastly different vegetative functional groups in the vegetative analysis, e.g. *Cucumis africanus*, *Momordica balsamina* and *Acanthosicyos naudinianus* were, closely associated with the phanerophytes of Group I in the reproductive analysis. This could be attributed to reproductive characteristics such as large seed size, internal zoochorous dispersal and synaptospermy.

The functional groups that consisted mostly of grasses in the vegetative analysis similarly formed unique reproductive functional groups, although the distinction was now on the basis of life history traits such as seed and diaspore morphology, seed dormancy and clonality. These traits grouped grasses, both annual and perennial, very closely in the reproductive trait analysis. In the vegetative trait analysis the perennial and annual grasses were relatively closely grouped in the ordination but were subjectively split into two groups where the annual grasses grouped with herbaceous annuals and the perennial grasses grouped with perennial shrubs.

The ecological significance of the traits evaluated was discussed. The combined reproductive and vegetative trait categories provided an overall strategy for survival and proliferation that may be more relevant to specific land use intensities. The relationship between the functional

groups identified in this chapter and the grazing gradient will be investigated in the next chapter.

5.6 Acknowledgements

- Prof. Anne Rasa of the farm Alpha, where most plant material for the functional analysis was obtained.
- Dr Anne Kraemer (Horn) for seed mass data on *Dicoma capensis*, *Eragrostis trichophora*, *Plinthus sericeus* and *Sericorema remotiflora*.
- Dr Martijn Kos for seed mass data on *Boscia albitrunca*.

Appendix A.1

Product-moment correlation matrix for 112 Kalahari plant species of 15 functional traits with continuous values. The r-values are quoted and red scores denote significance at the 95% level

	Stem density	Spinescence: Stem	Spinescence: Leaf	Leaf hairiness adaxial	Leaf hairiness abaxial	Leaf consistency	Plant height (m)	Canopy diameter (m)	Canopy density	Life span (years)	Leaf area (mm ²)	Leaf longevity	No. seed per fruit	Seed mass class	Fecundity
Stem density		0.65	0.18	-0.08	-0.09	0.29	0.70	0.62	0.38	0.66	-0.17	0.43	0.15	0.34	0.31
Spinescence: Stem	0.65		0.18	-0.11	-0.11	0.16	0.59	0.57	0.28	0.47	-0.03	0.29	0.19	0.29	0.26
Spinescence: Leaf	0.18	0.18		-0.18	-0.20	0.29	0.03	0.01	0.23	0.07	-0.26	0.09	-0.02	-0.10	0.06
Leaf hairiness adaxial	-0.08	-0.11	-0.18		0.93	-0.18	-0.22	-0.06	0.05	-0.15	0.06	-0.08	0.06	-0.05	0.00
Leaf hairiness abaxial	-0.09	-0.11	-0.20	0.93		-0.16	-0.20	-0.05	0.10	-0.12	0.09	-0.06	-0.01	-0.04	0.03
Leaf consistency	0.29	0.16	0.29	-0.18	-0.16		0.27	0.22	0.18	0.12	-0.43	0.16	-0.25	0.03	0.14
Plant height (m)	0.70	0.59	0.03	-0.22	-0.20	0.27		0.63	0.37	0.57	0.11	0.39	0.01	0.42	0.28
Canopy diameter (m)	0.62	0.57	0.01	-0.06	-0.05	0.22	0.63		0.28	0.55	0.15	0.43	0.06	0.43	0.41
Canopy density	0.38	0.28	0.23	0.05	0.10	0.18	0.37	0.28		0.33	0.10	0.40	-0.22	-0.01	0.33
Life span (years)	0.66	0.47	0.07	-0.15	-0.12	0.12	0.57	0.55	0.33		0.15	0.53	0.19	0.45	0.15
Leaf area (mm ²)	-0.17	-0.03	-0.26	0.06	0.09	-0.43	0.11	0.15	0.10	0.15		0.04	0.04	0.13	0.36
Leaf longevity	0.43	0.29	0.09	-0.08	-0.06	0.16	0.39	0.43	0.40	0.53	0.04		-0.09	0.23	0.10
No. seed per fruit	0.15	0.19	-0.02	0.06	-0.01	-0.25	0.01	0.06	-0.22	0.19	0.13	-0.09		0.07	0.00
Seed mass class	0.34	0.29	-0.10	-0.05	-0.04	0.03	0.42	0.43	-0.01	0.45	0.36	0.23	0.07		-0.11
Fecundity	0.31	0.26	0.06	0.00	0.03	0.14	0.28	0.41	0.33	0.15	-0.12	0.10	0.00	-0.11	

Appendix A.2

Product-moment correlation matrix for 51 Kalahari plant species of 15 continuous functional traits as well as the traits specific leaf area and leaf dry matter content. The r-values are quoted and red scores denote significance at the 95% level

	Stem density	Spine-science: Stem	Spine-science: Leaf	Leaf hairiness adaxial	Leaf hairiness abaxial	Leaf consistency	Plant height (m)	Canopy diameter (m)	Canopy density	Life span (years)	Leaf area (mm ²)	SLA (mm ² .mg ⁻¹)	LDMC (mg.g ⁻¹)	Leaf longevity	No. seed per fruit	Seed mass class	Fecundity
Stem density		0.71	0.27	-0.04	-0.11	0.44	0.71	0.62	0.39	0.77	-0.11	-0.52	0.41	0.57	0.30	0.49	0.18
Spinescence: Stem	0.71		0.19	-0.09	-0.11	0.28	0.62	0.62	0.35	0.56	0.04	-0.34	0.41	0.40	0.31	0.34	0.11
Spinescence: Leaf	0.27	0.19		-0.25	-0.30	0.35	0.05	0.00	0.21	0.09	-0.34	-0.02	-0.10	0.17	0.08	-0.16	0.06
Leaf hairiness adaxial	-0.04	-0.09	-0.25		0.92	-0.32	-0.29	-0.06	-0.17	-0.09	-0.06	0.11	-0.08	-0.22	0.10	-0.01	0.09
Leaf hairiness abaxial	-0.11	-0.11	-0.30	0.92		-0.31	-0.30	-0.08	-0.12	-0.09	-0.03	0.05	-0.01	-0.19	-0.02	-0.01	0.05
Leaf consistency	0.44	0.28	0.35	-0.32	-0.31		0.36	0.26	0.18	0.46	-0.28	-0.40	0.32	0.45	0.01	0.16	-0.18
Plant height (m)	0.71	0.62	0.05	-0.29	-0.30	0.36		0.66	0.50	0.73	0.32	-0.42	0.57	0.60	-0.02	0.57	0.16
Canopy diameter (m)	0.62	0.62	0.00	-0.06	-0.08	0.26	0.66		0.35	0.66	0.34	-0.46	0.38	0.56	0.13	0.48	0.33
Canopy density	0.39	0.35	0.21	-0.17	-0.12	0.18	0.50	0.35		0.51	0.16	-0.28	0.57	0.50	-0.25	0.02	0.44
Life span (years)	0.77	0.56	0.09	-0.09	-0.09	0.46	0.73	0.66	0.51		0.08	-0.62	0.61	0.66	0.20	0.52	0.22
Leaf area (mm ²)	-0.11	0.04	-0.34	-0.06	-0.03	-0.28	0.32	0.34	0.16	0.08		0.05	0.05	-0.03	-0.11	0.40	0.19
Specific leaf area (mm ² .mg ⁻¹)	-0.52	-0.34	-0.02	0.11	0.05	-0.40	-0.42	-0.46	-0.28	-0.62	0.05		-0.60	-0.49	-0.18	-0.33	-0.07
Leaf dry matter content (mg.g ⁻¹)	0.41	0.41	-0.10	-0.08	-0.01	0.32	0.57	0.38	0.57	0.61	0.05	-0.60		0.53	-0.15	0.21	0.18
Leaf longevity	0.57	0.40	0.17	-0.22	-0.19	0.45	0.60	0.56	0.50	0.66	-0.03	-0.49	0.53		-0.18	0.29	0.10
No. seed per fruit	0.30	0.31	0.08	0.10	-0.02	0.01	-0.02	0.13	-0.25	0.20	-0.11	-0.18	-0.15	-0.18		0.04	0.08
Seed mass class	0.49	0.34	-0.16	-0.01	-0.01	0.16	0.57	0.48	0.02	0.52	0.40	-0.33	0.21	0.29	0.04		-0.14
Fecundity	0.18	0.11	0.06	0.09	0.05	-0.18	0.16	0.33	0.44	0.22	0.19	-0.07	0.18	0.10	0.08	-0.14	

Chapter 6

The identification of grazing response functional types in dominant Kalahari plant species across a grazing gradient

Abstract

Common southern Kalahari plant species were investigated for a selection of traits and the changes in trait categories over a range condition gradient observed. The range condition gradient was established through a floristic analysis of a series of commercial farms that have been subjected to differing grazing intensities. A selection of 112 Kalahari species was investigated for a set of 17 traits thought to have relevance in grazing response and the trait data set analyzed by Principal Coordinates Analysis (PCoA). The distribution of the species according to trait categories in the ordination plane was used to identify functional groups. The functional groups represented species with similar trait attributes. The functional groups identified by PCoA were compared with the distribution of species over a range condition gradient that was identified through a Correspondence Analyses (CA) ordination. Prominent life and growth forms were identifiable in most instances in the functional groups and different associations with the range conditions were observed. Phanerophyte and chamaephyte dominated functional groups were mostly associated with low range condition scores and hemicytophyte dominated groups with high range condition scores, whereas herbaceous therophyte dominated groups did not show any specific association.

6.1 Introduction

The southern Kalahari savanna is susceptible to degradation due to overgrazing, which is related to the low rainfall, sparse grass cover and loose soil substrate (Leistner, 1967; Van Rooyen, 1998). Advancement in water extraction techniques has furthermore lead to an increase in stocking densities and utilisation of the veld because surface water could thus be made available artificially (Van Rooyen, 1998). It has also been suggested that degradation of veld condition in the Kalahari could be attributed to the crude and inaccurate assumptions of the fodder value of plant species such as the common grass species *Stipagrostis obtusa* (Du Toit, 2001). Overestimates of the fodder value of such grass species resulted in higher grazing capacity recommendations than would have been prudent (Du Toit, 2001).

Range overutilization is reported to (a) increase the cover of shrubs leading to bush encroachment, (b) increase bare soil cover, (c) reduce basal plant cover and (d) reduce cover of perennial (indicator) plant species (Kalikawe, 1990; Skarpe, 1996; Du Toit 2001). Moisture availability is, however, the overarching driver of vegetation dynamics in the Kalahari (Fourie *et al.*, 1987; Van Rooyen *et al.*, 1991; Van Rooyen & Van Rooyen, 1998). Large fluctuations in vegetation cover and species composition have been reported in response to drought and high rainfall cycles in the Kalahari (Van Rooyen *et al.*, 1994; Du Toit, 2001). After good rainfall events grass species, such as *Stipagrostis obtusa*, *S. ciliata* and *Eragrostis lehmanniana*, which are components of range in a good condition will re-establish quickly after drought. The shallow root systems of shrubs such as *Rhigozum trichotomum* and *Acacia mellifera* outcompete the grass component and other herbs for shallow soil layer moisture if the grass-shrub dynamic is disturbed (Skarpe, 1990a; Skarpe, 1990b; Hipondonka *et al.*, 2003). Reduction in the grass layer density further leads to reduced flammable biomass that would otherwise impact woody layer growth vigour (Skarpe, 1991a).

A plant functional group approach to studying the effects of overgrazing in this arid savanna region has not received significant attention in the past except for the work of Skarpe (1996) and Scholes *et al.* (1997). In these two studies a selection of plant traits (also labeled Plant Functional Attributes) were identified that the authors recommended for inclusion in plant functional classifications of African savannas. Most investigations into the Kalahari savanna vegetation dynamics and physiognomy focus mainly on life form and structural components of vegetation.

The components of species diversity that determines the expression of traits include species richness, diversity, evenness and their interactions (Chapin *et al.*, 2000). Species diversity has functional consequences whereby the number and kinds of species present influence ecosystem

processes as well as abiotic conditions (Chapin *et al.*, 2000). However, it is doubtful if the pure description of species diversity in isolation rather than in combination with physical traits provides enough information on ecological processes operating in the environment (Westoby & Wright, 2006). In the modern context of a changing global environment where the removal of species (sometimes referred to as keystone species) is investigated, it would be beneficial to understand how the functionality of the ecosystem is changed by such impacts (Grime, 2006). The plant species of any environment have a limited number of feasible adaptation options (survival strategies) available which are less than the number of species present (Scholes *et al.*, 1997). This implies that the study of functional groups represents a simplified and structured, but also more informative, interpretation with regard to describing the ecological components of a habitat.

Evidence is mounting that plant responses to disturbance vary according to resource availability, whereby plants in resource poor environments attempt to retain or protect acquired resources, but aim to counter resource loss through increased acquisition rates (tolerance) in resource rich environments (Grime *et al.*, 1997; Grime, 2006, Rusch *et al.*, 2009). In the resource poor Kalahari environment it is therefore expected that resource retention strategies would dominate and not tolerance strategies (increased acquisition rates), with identifiable functional adaptations to counter resource loss. In arid zones, determining the effects of overgrazing and agriculture on ecosystem functioning and changes in *inter alia* floristic composition and/or perennial plant cover can be achieved by the plant functional type approach (Gondard *et al.*, 2003). Various other physical plant parameters such as growth form, life form, leaf toughness and plant height serve as indicators of vegetation degradation (McIntyre *et al.*, 1999b; Adler, *et al.*, 2004; Navarro *et al.*, 2006) and some of these trait attributes may have particular relevance at different landscape levels (Diaz *et al.*, 2002).

Structurally the southern Kalahari dunefield is typified as a sparse, open savanna with low tree canopy cover (meso- and nanophanerophytes), the dominance of hemicryptophytes (perennial grasses) and the significant contribution of therophytes to the vegetation component during seasons with high rainfall (Van Rooyen & Van Rooyen, 1998; Lubbinge 1999). The dominance of hemicryptophytes may be related to the superior ability of these species to extract periodic moisture availability through their root systems in comparison with chamaephytes (Van Rooyen & Van Rooyen, 1998). According to Van Rooyen & Van Rooyen (1998) in the southern Kalahari the percentage contribution of different life form spectra are:

- i. Meso- and microphanerophytes 1%
- ii. Nanophanerophytes 8%
- iii. Chamaephytes 15%
- iv. Hemicryptophytes 31%

- v. Geophytes 13%
- vi. Therophytes 31%
- vii. Other 1%

This study follows the “bottom-up” approach of Scholes *et al.*, (1997), by investigating various plant trait attributes thought to be important in grazing responses (the Scholes *et al.*, 1997 study was not specifically grazing related). Grazing-related functional groups that can be identified in this manner (this chapter) are linked to veld condition assessments (Chapter 4) to form a holistic picture of the plant groups and trait attributes that prevail along a grazing gradient.

The sequence of research questions leading to the plant functional type and grazing response interaction are:

- Can a grazing gradient be identified on a number of commercial farms in the southern Kalahari and what are the floristic characteristics of farms along the gradient (Chapter 4)?
- Can functional groups be identified among the common plant species that have similar trait attributes? (Chapter 5).
- How do the functional groups identified among the common plant species set relate to the grazing gradient? What trait attributes and which species groups benefit at the opposite ends of the grazing gradient? These questions will be investigated in this chapter by limiting the trait set to those traits expected to have grazing response relevance.

6.2 Materials and methods

A correspondence analysis (CA) with CANOCO 4.5 (Microcomputer Power, Ithaca, New York) of the floristic data for 11 Kalahari farms was performed to investigate the relationships between relevés of different farms and of different habitats. The identification of a degradation gradient across all farms as a whole and the respective habitats individually was presented in Chapter 4.

One hundred and twelve common Kalahari plant species were investigated for a selection of traits. Multivariate analyses of species trait data were performed with Principal Co-ordinate Analysis (PCoA) in the software programme Syntax (Podani, 2000). The plant trait analyses were described in Chapter 5. Ordinations investigated for aggregate (functional) plant species groups with a set of 17 grazing related traits are discussed in this chapter.

The 17 traits included in the grazing related plant functional analysis were:

- Carbohydrate storage
- Raunkier Life Form
- Shoot architecture
- Plant height (m)
- Stem density
- Clonality
- Spinescence: Stem
- Spinescence: Leaf
- Leaf area (mm²)
- Leaf hairiness adaxial
- Leaf hairiness abaxial
- Leaf consistency
- Leaf/stem surface exudates
- Sociability
- Diaspore morphology
- Telechory
- Seed mass class (mg)

In this chapter the link between species distributions across the degradation gradients (CA analyses in CANOCO) and the functional groups identified (PCoA in Syntax) were made. Plant functional groups identified through PCoA analysis were assigned symbols and the corresponding species in the CA analysis were assigned the appropriate symbols. This enabled an investigation of functional group distributions across the degradation gradients for all farms and habitats as a whole and for each of the dune crest, dune slope and dune street habitats.

Some species occurred in the multivariate floristic analysis for the 11 farms, but were not evaluated for their trait attributes. Those species were:

- *Brachystelma* sp. (Brachyst)
- *Calobota linearifolia* E.Mey. = *Lebeckia linearifolia* E.Mey. (Leb lin)
- *Lotononis divaricata* (Eckl. & Zeyh.) Benth. (Lot div)
- *Nolletia rarifolia* (Turcz.) Steetz (Nol rar)

Some species evaluated for their trait attributes did not occur in the floristic habitat analysis. These species nonetheless contributed to the identification of functional groups. Those species were:

- *Acacia luederitzii* Engl. var. *luederitzii* (Aca ref)
- *Acrotome inflata* Benth. (Acr inf)
- *Aristida congesta* Roem. & Schult. subsp. *congesta* (Ari con)
- *Crotalaria podocarpa* DC. (Cro pod)
- *Cyamopsis serrata* Schinz (Cya ser)
- *Hermannia modesta* (Ehrenb.) Mast. (Her mod)
- *Ipomoea hackeliana* (Schinz) Hallier f. (Ipo hac)
- *Limeum myosotis* H.Walter var. *myosotis* (Lim myo)
- *Merremia verecunda* Rendle (Mer ver)
- *Neuradopsis austro-africana* (Schinz) Bremek. & Oberm. (Neu aus)
- *Plinthus karoocicus* I. Verd. (Pli kar)
- *Ptycholobium biflorum* (E.Mey.) Brummitt subsp. *biflorum* (Pty bif)
- *Salsola kali* L. (Sal kal)
- *Sesamum triphyllum* Welw. ex Asch. var. *triphyllum* (Ses tri)
- *Talinum cafferum* (Thunb.) Eckl. & Zeyh. (Tal caf)

6.3 Results

6.3.1 *Grazing related plant traits PCoA*

Nine functional groups were subjectively identified in a Principal Coordinates Analysis of Kalahari plant species based on the set of 17 traits that are assumed to have grazing relevance (Figure 6.1 and Table 6.1). Separation between the top and bottom functional groups was attributed to leaf hairiness. Stem density, stem spinescence, leaf consistency and plant height increased across the ordination plane from left to right.

- Group I – Medium to large woody shrubs

A group of medium-sized nanophanerophytes, microphanerophytes and frutescent chamaephytes with uncommon carbohydrate storage, but common belowground clonality. Ligneous shoots with intermediately spiny stems mostly had semi-circle shrub architecture, but the caespitose shrub type also occurred. Leaves were mostly spineless, consistently small (leptophyll to nanophyll), hairless and sclerophyllous. Plant occurred singly or uncommonly in loose groups. Diaspores consisted either of fleshy pulp fruit or had no attachments and were dispersed endozoochorously. Seed mass was mostly small to medium, although large seeds were also observed.

- Group II – Large woody shrubs and trees

No carbohydrate storage or clonality was observed in these large microphanerophytes, or sometimes nano- or microphanerophytes. Intermediately spiny, ligneous stems formed semi-circle shrub, caespitose shrub or hydra shoot architectures. Leaves were medium-sized, spineless, glabrous and mostly semi-sclerophyllous, although sclerophyllous also occurred. Resinous or aqueous exudates were uncommonly observed. The dominant social arrangement was loose groups (sometimes single). Large seeds were found in diaspores that generally did not have any attachments, although winged fruit were also found. Endozoochory was the principal dispersal mode, followed by anemochory.

- Group III – Large woody shrubs

This group was typified by large nano- or microphanerophytes with belowground clonality, but no carbohydrate storage. Ligneous stems were intermediately to very spiny and formed semi-circle shrub, caespitose shrub or rhizomatous shrub shoot architectures. Leaves were medium-sized and spineless, but sparsely to intermediately hairy. Leaf consistency was variable from malacophyllous to sclerophyllous. Aqueous exudates were common and sociability was either

single or in dense clumps or large herds. The diaspores of fleshy pulp or without attachments carried seeds of variable size, but the primary dispersal mode was endozoochory.

- Group IV – Medium to large woody shrubs

The medium to large nanophanerophytes (uncommonly microphanerophytes or suffrutescent chamaephytes) did not have carbohydrate storage but uncommonly showed belowground clonality or lying branches that root. Ligneous, but sometimes hemixylous, stems were mostly intermediately spiny and structured into caespitose shrub or semi-circle shrub shoot architectures. Leaves were spineless, ranged in consistency from malacophyllous to sclerophyllous and were generally medium-sized. Adaxial leaf hairiness was sparse to intermediate and abaxial leaf hairiness intermediate to dense. Sociability was variable but mostly loose groups. Small to medium seeds were carried in diaspores with fleshy pulp fruit or were without attachments, although winged seeds were uncommonly observed. Endozoochory was the dominant form of dispersal followed by anemochory and autochory.

- Group V – Small to medium woody shrubs and robust grass

Carbohydrate storage and clonality were absent in medium-sized plants with predominantly a suffrutescent chamaephyte life form, although nanophanerophytes and herbaceous chamaephytes were also present. The spineless stems were mostly hemixylous (occasionally ligneous) and formed semi-circle shrub architectures, or uncommonly caespitose shrub or broom architectures. Leaf size was variable, but mostly small and leaves were further glabrous and semi-sclerophyllous to sclerophyllous. Individuals occurred singly or in loose groups. Diaspores consisted of plumed seeds or had no attachments, but winged or glandular seeds were also uncommonly present. The small- to medium-sized seeds were dispersed primarily by anemochory or less frequently by epizoochory or autochory.

- Group VI – Small woody shrubs

In this group plants were of medium size and without carbohydrate storage or clonality. Raunkier life forms were variable but suffrutescent chamaephytes were dominant and nanophanerophytes and frutescent chamaephytes less common. Hemixylous stems (uncommonly ligneous) were spineless and structured into semi-circle shrub or caespitose shrub shoot architectures. The small leaves were spineless and sparsely to intermediately hairy, whereas leaf consistency ranged from semi-sclerophyllous to sclerophyllous (although malacophyllous also occurred). Loose groups were the most common social structure with single individuals being less common. Small to medium sized seeds were mostly dispersed by anemochory and less commonly by endozoochory or autochory in diaspores without any attachments. Fleshy pulp diaspores were uncommonly observed.

- Group VII – Perennial herbs and perennial creepers

Carbohydrate storage was uncommonly observed in this group, but no clonality. The herbaceous chamaephytes or rhizomatous geophytes (at times caespitose or reptant therophytes) were of small to medium size. The herbaceous, but infrequently hemixylous, stems were spineless and formed semi-circle shrub or scandent shoot architectures. The spineless, but intermediate to densely hairy leaves had consistencies ranging from malacophyllous to semi-sclerophyllous, and occasionally sclerophyllous. Leaves were of medium to large size. Loose groups were the most common sociability structure and large herds or single plants less common. Seed size was very variable, with diaspores either possessing fleshy pulp or no attachments, but also uncommonly being bristled seed. Anemochory and endozoochory were the primary modes of dispersal.

- Group VIII – Geophytes, perennial grasses, semi-woody shrubs, prostrate and erect annuals

The small- to medium-sized plants of the group were mostly without clonality but, carbohydrate storage was uncommonly observed. Caespitose hemicryptophytes and caespitose therophytes typified the group, and to a lesser extent bulbous geophytes. The spineless, herbaceous stems were structured into a variety of shoot architecture types. Sub-caespitose tuft or procumbent types were most common, with caespitose tuft, semi-circle shrub, liana or erect types less so. Leaves were mostly spineless, glabrous, malacophyllous to semi-sclerophyllous and of small to medium size. Wax, latex or aqueous exudates were noted, but rarely occurred. Single or loose groups were the primary social structure. Small to medium seeds were carried in diaspores without attachments, or occasionally had burred seeds, plumed seeds or fleshy pulp fruit. Anemochory was most dominant followed by epizoochory and autochory or there was no obvious dispersal agent.

- Group IX – Erect and prostrate annual herbs and annual grasses

Plant height in the group was small and carbohydrate storage and clonality was absent. Caespitose or reptant therophytes dominated the group, followed by reptant hemicryptophytes. The herbaceous, spineless stems mostly formed procumbent shoot architectures, but liana, caespitose shrub, erect and decumbent types also occurred. Leaves were spineless, generally of medium size and malacophyllous to semi-sclerophyllous (rarely semi-succulent). Adaxial leaf hairiness ranged from sparse to dense and abaxial hairiness from intermediate to dense. Uncommonly sticky or aqueous exudates were noted. Loose group sociability was most common followed by large herds or single plants. The small seeds of diaspores mostly had no attachments, but bristled, burred or plumed seeds were also present. Dispersal was primarily by anemochory and less frequently by epizoochory or autochory.

Stem density
Stem spinescence
Leaf consistency
Plant height



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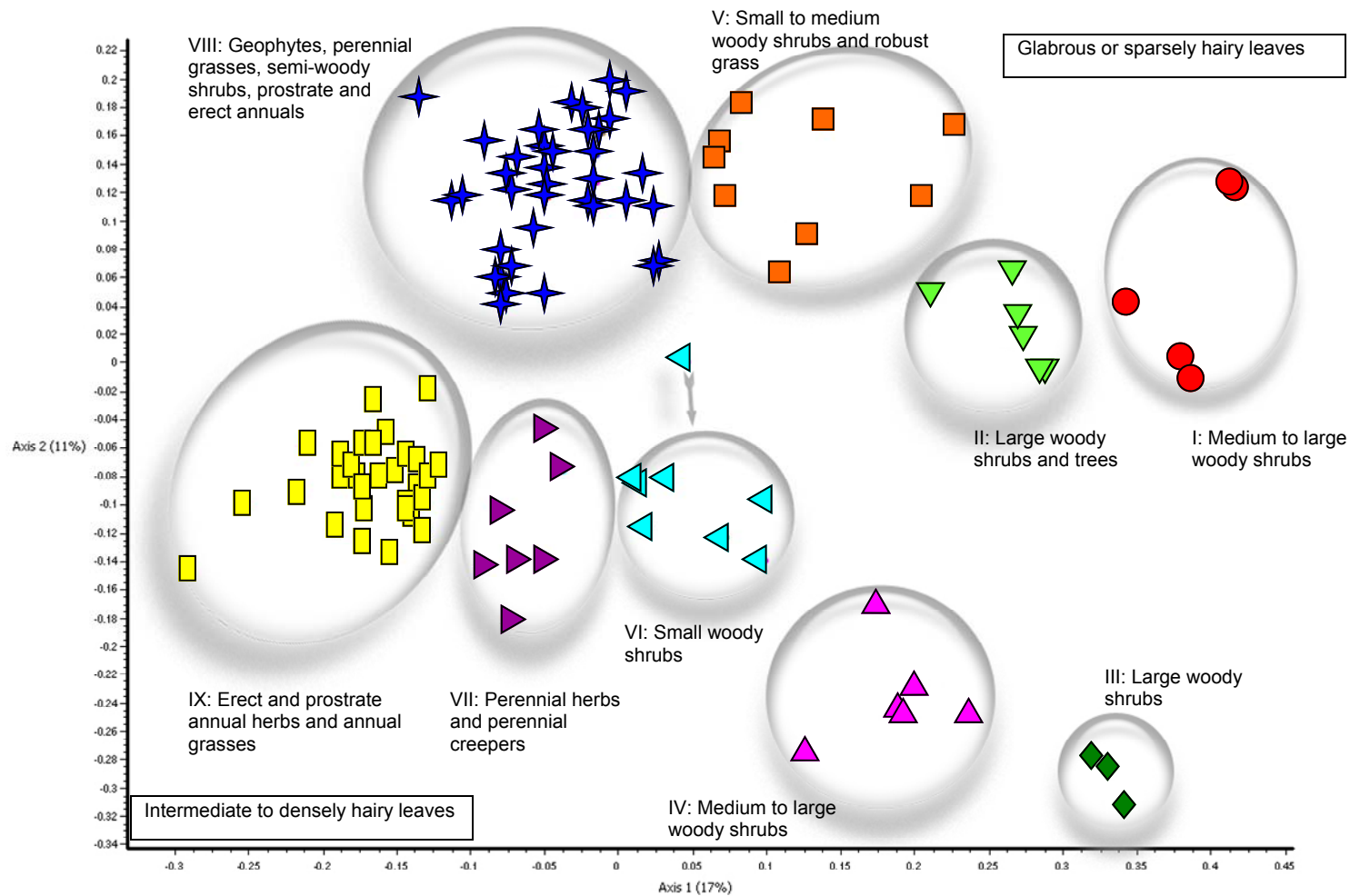


Figure 6.1 Principal Coordinates Analysis (PCoA) scatter diagram of 112 Kalahari plant species for a set of 17 grazing related plant traits and the subsequent groups identified. The percentage variance explained by axes is indicated in brackets after each axis label.

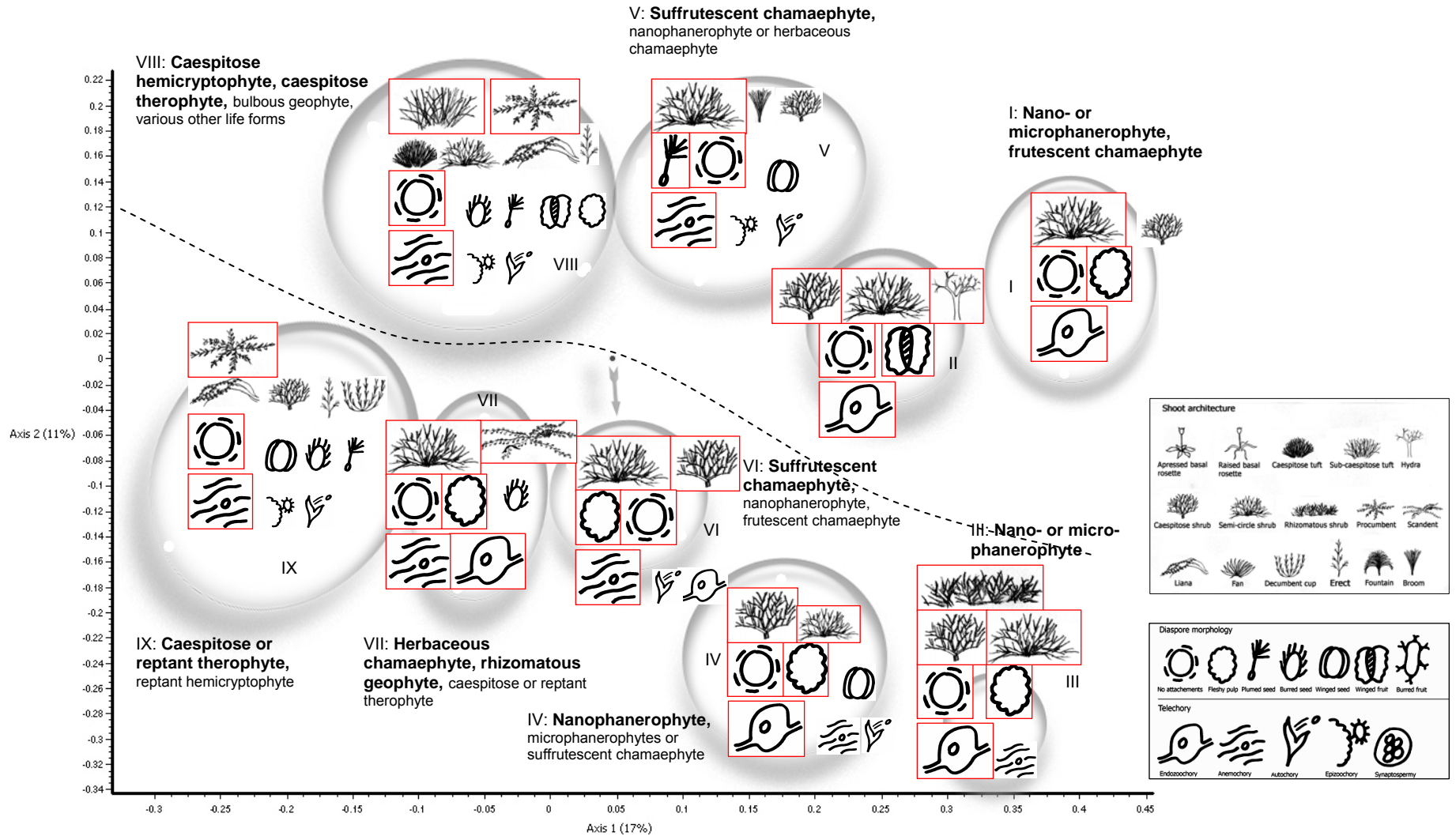


Figure 6.2 Principal Coordinates Analysis (PCoA) scatter diagram of 112 Kalahari plant species for a set of 17 grazing related plant traits and the subsequent groups identified. Raunkier life form, shoot architecture, diaspore morphology and telechory types per group are indicated, with large boxed icons and bold text denoting dominant types. The percentage variance explained by axes is indicated in brackets after each axis label.



Table 6.1 Detailed descriptions of functional groups identified by PCoA of 17 grazing related traits (Figures 6.1 & 6.2)

	Group I Medium to large shrubs	Group II Large woody shrubs and trees	Group III Large woody shrubs	Group IV Medium to large woody shrubs	Group V Small to medium woody shrubs and robust grass	Group VI Small woody shrubs	Group VII Perennial herbs and perennial creepers	Group VIII Geophytes, perennial grasses, semi- woody shrubs, prostrate and erect annuals	Group IX Erect and prostrate annual herbs and annual grasses
Number of species	5	6	3	6	9	7	7	39	30
Carbohydrate storage	Uncommon	No carbohydrate storage	No carbohydrate storage	No carbohydrate storage	Rare	No carbohydrate storage	Uncommon	Uncommon	Rare
Raunkier life form	Nano- or micro-phanerophyte, frutescent chamaephyte	Micro-phanerophyte, uncommonly nano- or meso-phanerophyte	Nano- or micro-phanerophyte	Nano-phanerophyte, uncommonly micro-phanerophyte or suffrutescent chamaephyte	Suffrutescent chamaephyte, uncommonly nano-phanerophyte, herbaceous chamaephyte	Suffrutescent chamaephyte, uncommonly nano-phanerophyte or frutescent chamaephyte	Herbaceous chamaephyte or rhizomatous geophyte, uncommonly caespitose or reptant therophyte	Caespitose hemicryptophyte or caespitose therophyte, uncommonly bulbous geophyte, rarely other	Caespitose or reptant therophyte, uncommonly reptant hemicryptophyte
Shoot architecture	Semi-circle shrub, uncommonly caespitose shrub	Semi-circle shrub, caespitose shrub or hydra	Semi-circle shrub, caespitose shrub or rhizomatous shrub	Caespitose shrub, uncommonly semi-circle shrub	Semi-circle shrub, uncommonly caespitose shrub or broom	Semi-circle shrub or caespitose shrub	Semi-circle shrub or scandent	Sub-caespitose tuft or procumbent, uncommonly caespitose tuft, semi-circle shrub, liana or erect	Procumbent, uncommonly liana, caespitose shrub, erect or decumbent
Plant height (m)	>50–150, uncommonly >150–200	>200, uncommonly 100–150	>100–300	>50–200, uncommonly >10–50 or >200–300	>10–100, uncommonly >100–200	>10–100, uncommonly >100–150	>10–50, rarely >3–10	>3–100, rarely ≤3	≤3–50; rarely 50–100
Stem density	Ligneous, uncommonly hemixylous	Ligneous	Ligneous	Ligneous, uncommonly hemixylous	Hemixylous, uncommonly ligneous	Hemixylous, uncommonly ligneous	Herbaceous, uncommonly hemixylous	Herbaceous	Herbaceous
Clonality	Belowground clonality, uncommonly none	No clonality	Belowground clonality	No clonality, uncommonly belowground or lying branches rooting	No clonality, rarely belowground clonality	No clonality	No clonality	None, rarely belowground or aboveground clonality	No clonality
Spinescence: Stem	Intermediately spiny, uncommonly slightly spiny	Intermediately spiny, rarely none	Intermediately or very spiny	Intermediately spiny, uncommonly none	None	None	None	None	None
Spinescence: Leaf	None, uncommonly intermediately spiny	None	None	None, rarely slightly spiny	None, uncommonly slightly to intermediately spiny	None, rarely slightly spiny	None	None, rarely slightly spiny	None
Leaf area (mm²)	Leptophyll to nanophyll	Nanophyll to microphyll	Nanophyll to microphyll	Nanophyll to microphyll, uncommonly leptophyll or mesophyll	Leptophyll to nanophyll, uncommonly microphyll to mesophyll	Leptophyll to nanophyll, uncommonly mesophyll	Microphyll to mesophyll, uncommonly leptophyll to nanophyll	Nanophyll to microphyll, uncommonly leptophyll, rarely mesophyll	Nanophyll to microphyll, rarely leptophyll or mesophyll
Leaf hairiness: adaxial	Glabrous	Glabrous	Sparse or dense	Sparse to intermediate, rarely dense	Glabrous	Sparse to dense	Intermediate to dense, rarely sparse	Glabrous	Sparse to dense
Leaf hairiness: abaxial	Glabrous	Glabrous	Sparse or dense	Intermediate to dense, rarely sparse	Glabrous	Sparse or dense	Intermediate to dense, rarely sparse	Glabrous, uncommonly sparse	Intermediate to dense, uncommonly sparse
Leaf consistency	Sclerophyllous	Semi-sclerophyllous, uncommonly sclerophyllous	Malacophyllous to sclerophyllous	Malacophyllous to sclerophyllous	Semi-sclerophyllous or sclerophyllous, rarely malacophyllous or semi-succulent	Semi-sclerophyllous to sclerophyllous, uncommonly malacophyllous	Malacophyllous to semi-sclerophyllous, uncommonly sclerophyllous	Malacophyllous to semi-sclerophyllous, rarely sclerophyllous	Malacophyllous to semi-sclerophyllous, rarely semi-succulent
Leaf/stem exudates	None	None, uncommonly resin or aqueous	Aqueous	None	None	None	None	None, rarely wax, latex or aqueous	None, uncommonly aqueous or sticky
Sociability	Single, uncommonly loose groups	Loose groups, uncommonly single	Single, dense clumps or large herds	Loose groups, uncommonly single, dense clumps or large herds	Single or loose groups, rarely dense clumps	Loose groups, uncommonly single	Loose groups, uncommonly single or large herds	Single or loose groups, rarely large herds	Loose groups, uncommonly single or large herds
Diaspore morphology	Fleshy pulp fruit or no attachments	No attachments, uncommonly winged fruit	Fleshy pulp fruit or no attachments	Fleshy pulp fruit or no attachments, uncommonly winged seeds	Plumed seeds or no attachments, uncommonly winged seeds or glandular seeds	No attachments, uncommonly fleshy pulp fruit	Fleshy pulp fruit or no attachments, uncommonly bristled seeds	No attachments, uncommonly burred seeds, plumed seeds or fleshy pulp fruit	No attachments, uncommonly, bristled seeds, plumed seeds or plumed seeds
Telechory	Endozoochory	Endozoochory, uncommonly anemochory	Endozoochory	Endozoochory, uncommonly anemochory or autochory	Anemochory, uncommonly epizoochory or autochory	Anemochory, uncommonly endozoochory or autochory	Anemochory or endozoochory, rarely no obvious agent	Anemochory, uncommonly epizoochory, autochory or no obvious agent	Anemochory, uncommonly epizoochory or autochory
Seed mass class (mg)	≤0.1 or >1–10, uncommonly >100–1000	>100–1000, uncommonly >1–10	>1–1000	>1–10, rarely >100–1000	>0–1–10, rarely >10–100	>0.1–10	≤0.1–1000	≤0.1–100	≤0.1–10

6.3.2 *Grazing related trait response to the range condition gradient*

Species encountered in the dune crest habitat that are part of the medium to large woody shrub functional groups (Groups I to IV), were mostly associated with a poor to medium range condition state (Figure 6.3). Small to medium woody shrubs and robust grass (Group V) was mostly associated with medium range condition. Groups VI to IX were associated with medium to good range condition, except for Group VIII, which was associated with a broad band of poor to good range condition.

In the dune slope habitat Groups I to IV were similarly associated with poor to medium range condition (Figure 6.4). Unlike the dune crest habitat, functional group IX which consist mainly of annuals, was also associated with poor to medium range condition. Groups VI to VIII were associated with medium to good range condition, as was Group V, although it also extend into poor range condition. No specific group was associated purely with good range condition.

In the dune street habitat Groups II and III large woody shrubs and trees was associated with poor to medium range condition (Figure 6.5). Group VI small woody shrubs, Group VII perennial herbs and creepers and Group I medium to large shrubs was associated with medium to good range condition. The Group I trend is contrary to the dune crest and dune slope habitats. Groups IV, V, VIII and IX were associated with a broad band of range condition from poor to good. The Group IX annual herbs and grasses thus did not show any strong relationship with either end of the range condition gradient, as observed in the dune crest and dune slope habitats.

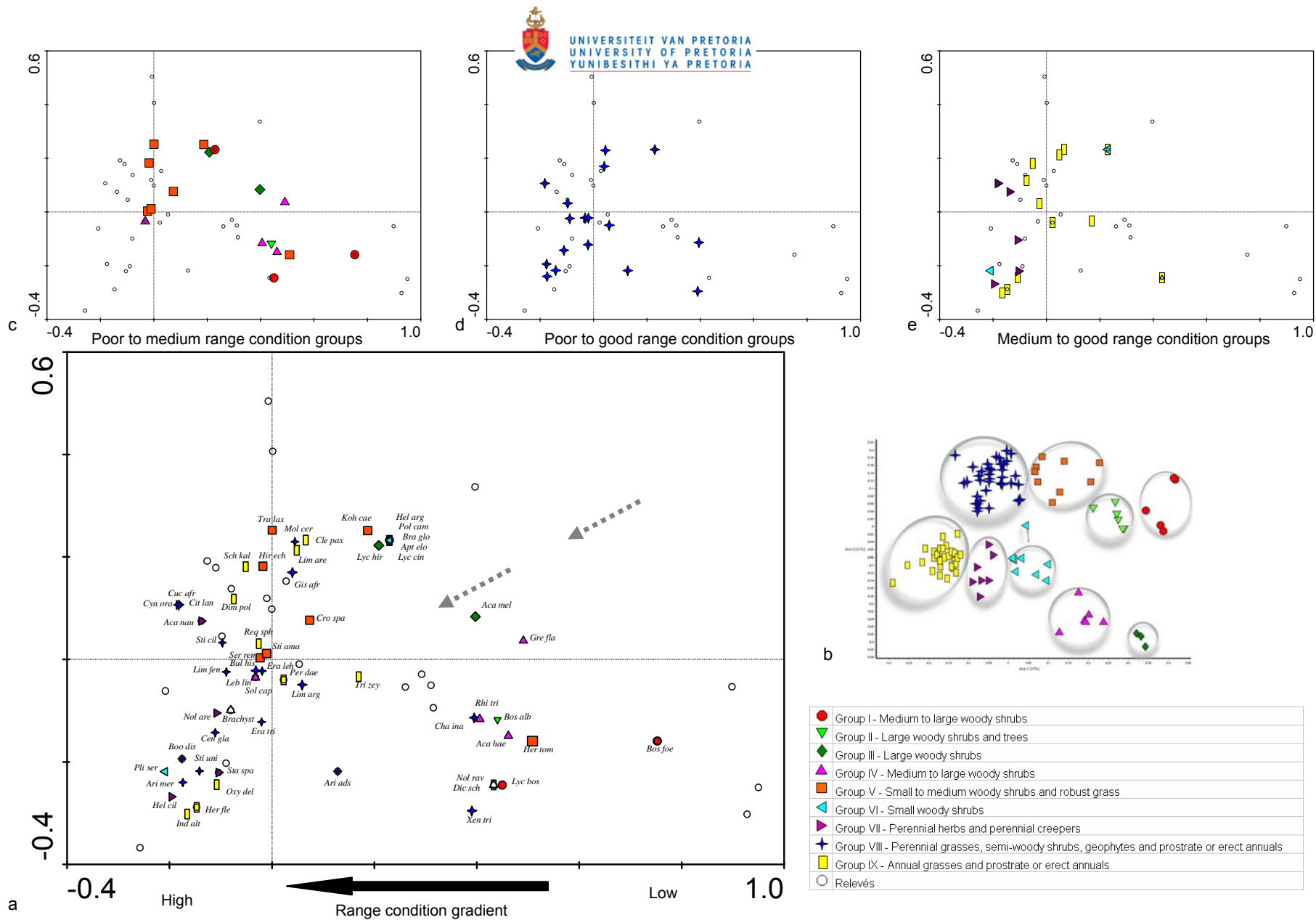


Figure 6.3 Correspondence Analysis (CA) of the dune crest habitat of 11 Kalahari farms showing species (coloured symbols) and relevé distributions (open circles) (a). Functional groupings of 112 common Kalahari species by principal coordinate analysis (PCoA) for 17 grazing related traits are shown in b. The distribution of functional groups in the CA analyses is depicted in c – e. Black arrow indicates increasing range condition.

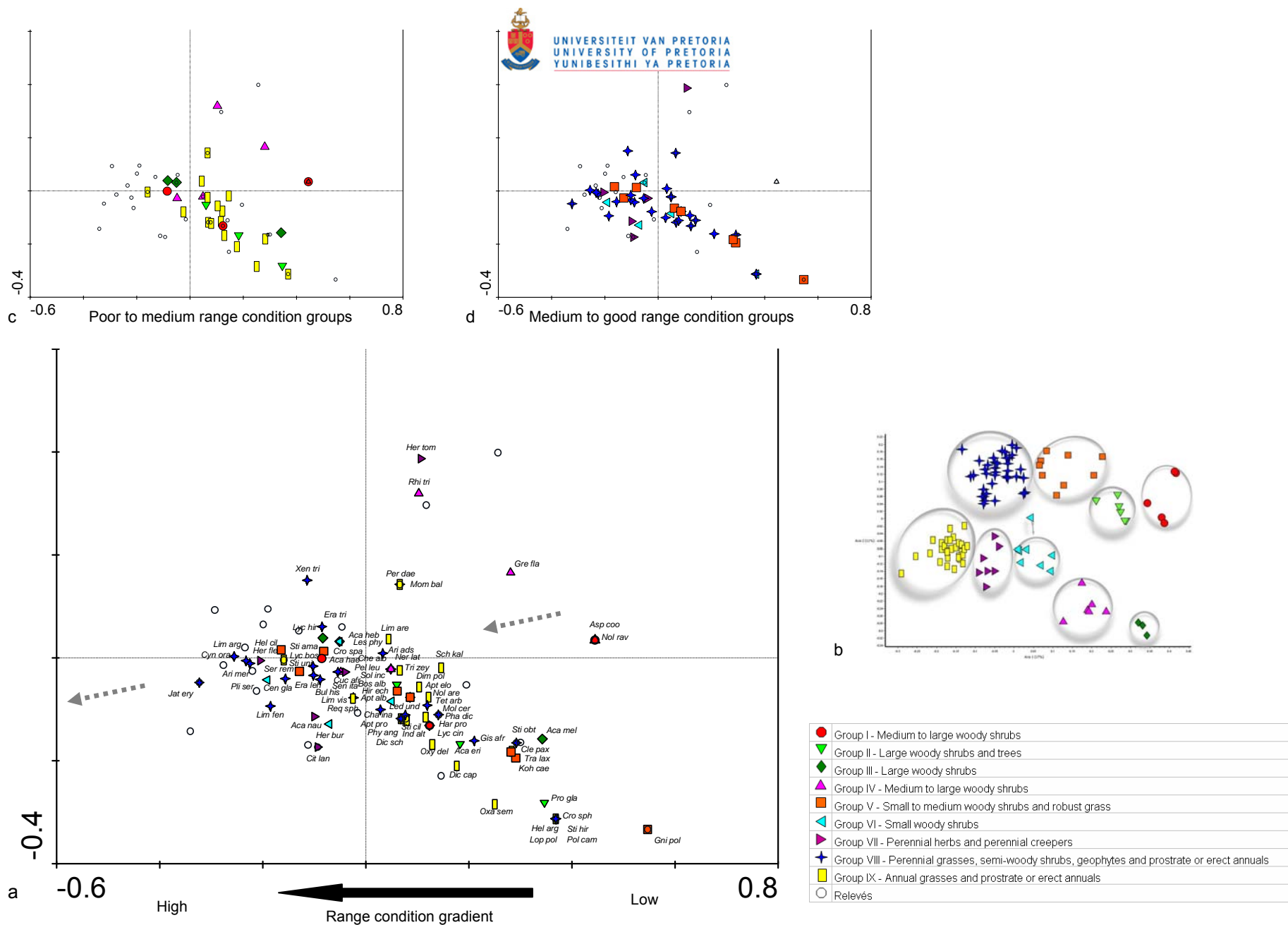


Figure 6.4 Correspondence Analysis (CA) of the dune slope habitat of 11 Kalahari farms showing species (coloured symbols) and relevé distributions (open circles) (a). Functional groupings of 112 common Kalahari species by principal coordinate analysis (PCoA) for 17 grazing related traits are shown in b. The distribution of functional groups in the CA analyses is depicted in c and d. Black arrow indicates increasing range condition.

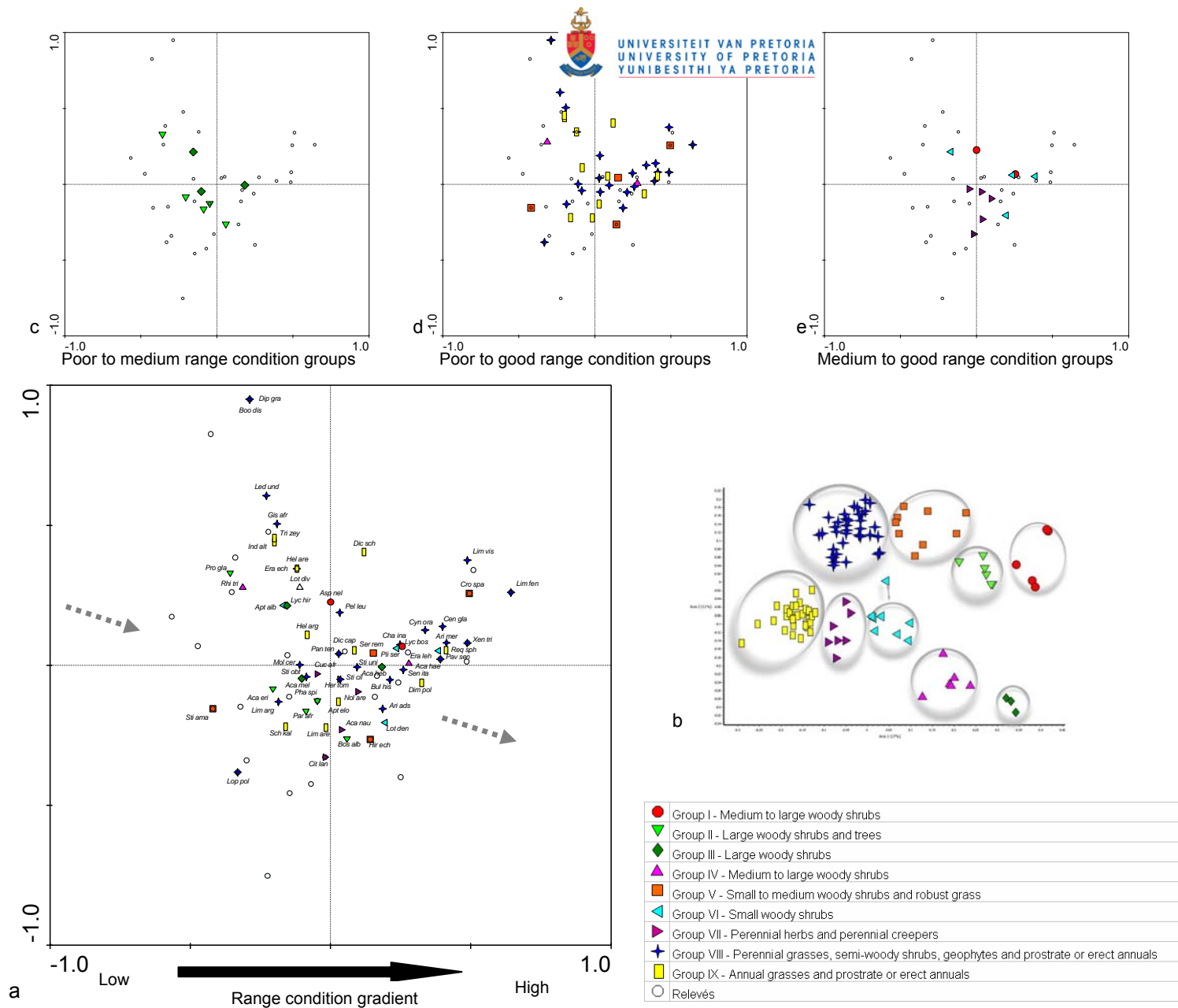


Figure 6.5 Correspondence Analysis (CA) of the dune street habitat of 11 Kalahari farms showing species (coloured symbols) and relevé distributions (open circles) (a). Functional groupings of 112 common Kalahari species by principal coordinate analysis (PCoA) for 17 grazing related traits are shown in b. The distribution of functional groups in the CA analyses is depicted in c – e. Black arrow indicates increasing range condition.

6.4 General discussion

The traits for each of the functional groups often exhibited a broad range of categories as was described in Chapter 5 (Tables 5.3 and 5.4). Between functional groups there were also significant overlaps in the trait categories. In nature species or vegetation assemblages and their natural histories can rarely be compartmentalized. The diversity of adaptations to environmental stresses, diverse environmental influences and the miscellaneous phylogenetic histories of species lead to a continuum of species responses to perturbations. The search for common species trait categories and functional groupings of species should therefore be expected to constitute sets of overlapping and often non-discreet entities.

Species or functional groups that defined the lower end of the degradation gradient (poor range condition) were not always more abundant in comparison with sites of lower degradation (good range condition). It is possible that the absence of certain species leads to the greater influence of a few resident species of degraded sites on the floristic character of those degraded sites.

Vegetative traits imparted a strong influence on species distributions in the PCoA analyses of the grazing trait data set, whereby broadly similar life forms could be identified as functional groups (Figure 6.1). This phenomenon was previously also observed in the analysis of a larger complete trait data set of 46 traits (Figure 5.1 in Chapter 5).

6.4.1 Response of woody dominated functional groups to range condition

All functional groups representing nano- to macrophanerophytes and herbaceous to frutescent chamaephytes were present in each of the three dunefield habitats. In both the dune crest and dune slope habitats it was observed that functional groups I to IV, constituted mainly of medium shrubs to trees, were associated with poor to medium range condition (Table 6.2). The dune crest habitat additionally had Group V, consisting of nanophanerophytes and suffrutescent or herbaceous chamaephytes associated with poor to medium range condition. The dune street habitat also had Groups II and III associated with poor to medium range condition, but Group IV was associated with poor to good range condition and Group I with good range condition. These findings are in line with published reports of bush encroachment as a result of utilization pressure. Skarpe (1990a, 1990b) reported increases in shrub cover with overgrazing in the Kalahari and attributed it mainly to increases in *Acacia mellifera* (Group III) and *Grewia flava* (Group IV) cover while no change in *Boscia albitrunca* (Group II) cover was observed.

Table 6.2 Summary table of the grazing trait set functional groups associated with each of the dune crest, dune slope and dune street habitats (highlighted).

Range condition		Poor to medium range condition	Poor to good range condition	Medium to good range condition
Functional groups per habitat	Dune crest	I	I	I
		II	II	II
		III	III	III
		IV	IV	IV
		V	V	V
		VI	VI	VI
		VII	VII	VII
		VIII	VIII	VIII
		IX	IX	IX
	Dune slope	I	I	I
		II	II	II
		III	III	III
		IV	IV	IV
		V	V	V
		VI	VI	VI
		VII	VII	VII
		VIII	VIII	VIII
		IX	IX	IX
	Dune street	I	I	I
		II	II	II
		III	III	III
		IV	IV	IV
		V	V	V
		VI	VI	VI
		VII	VII	VII
		VIII	VIII	VIII
		IX	IX	IX

●	Group I - Medium to large woody shrubs
▼	Group II - Large woody shrubs and trees
◆	Group III - Large woody shrubs
▲	Group IV - Medium to large woody shrubs
■	Group V - Small to medium woody shrubs and robust grass
◀	Group VI - Small woody shrubs
▶	Group VII - Perennial herbs and perennial creepers
+	Group VIII - Perennial grasses, semi-woody shrubs, geophytes and prostrate or erect annuals
■	Group IX - Annual grasses and prostrate or erect annuals

Perkins & Thomas (1993) observed increases in shrub cover with closer distance to boreholes in the eastern Kalahari and Brits *et al.* (2002) in the Kruger National Park tree savanna. Conversely Kalikawe (1990) anticipates that cover of *G. flava* (together with *B. albitrunca*) is likely to decrease with increased utilization pressure, but that *Acacia hebeclada* (Group III) cover would increase. Moore *et al.* (1988) and Du Toit (2002) identified *Rhigozum trichotomum* (Group IV) as a major bush encroaching shrub associated with increased grazing pressure in the Kalahari. Long-term studies by Van Rooyen *et al.* (1994) with the aid of line transects from watering points in Kgalagadi Transfrontier Park as well as work by Fourie *et al.* (1987) did not report increases in *R. trichotomum* cover with increased utilization. Shrub species with a similar preponderance or potential for encroachment under conditions of overutilisation or disturbance were not grouped into the same functional groups, e.g. *Rhigozum trichotomum*, *Grewia flava* (Group IV), *Acacia mellifera*, *Acacia hebeclada* and *Solanum incanum* (Group III). These species could however have been subjectively grouped as one group in the ordination. It is noteworthy that these encroaching species all grouped in the same vicinity in the ordination plane, except for *Prosopis glandulosa* in Group II. This species is however an alien invasive from Mexico and its spread is not linked solely to disturbance but also because of the lack of its natural regulatory agents.

The phanerophytes and chamaephytes of Groups I to IV were distinguished by tall plant height, high stem density, sclerophyllous or semi-sclerophyllous leaves, and prominent stem spinescence. Group V was similar with respect to these traits but differed by having almost no stem spinescence. It did however rank second highest for leaf spinescence after Group I.

An analysis of 56 species in this study showed that significant negative relationships exist between specific leaf area and the traits plant height ($p < 0.05$; $r = -0.42$), leaf consistency ($p < 0.05$; $r = -0.40$), stem density ($p < 0.05$; $r = -0.52$) and stem spinescence ($p < 0.05$; $r = -0.34$). SLA relates to the potential growth rate of a species and species with larger SLAs are often associated with resource rich environments while species with lower SLAs are associated with resource-poor environments (Cornelissen *et al.*, 2003; McIntyre, 2008). Leaves with low SLA are expected to have highly sclerophyllous leaves which imply higher construction “cost” per unit leaf area. The cost can only be recovered in the longer term through prolonged energy capture because of reduced production capability, although a reduction in water loss in the short term may also be beneficial (Skarpe, 1996). SLA and leaf dry matter content, which could be regarded as a proxy for leaf consistency, were also significantly negatively related ($p < 0.05$; $r = -0.60$). The close relationship between leaf consistency (sclerophylly), specific leaf area and leaf dry matter content was also reported by Skarpe (1996), Wilson *et al.* (1999), Diaz *et al.* (2001) and McIntyre (2008). High stem density relates to a longer lifespan and a concomitant investment in resources with resulting carbon storage structures, increased plant height (supporting structure) and reduced stem palatability (Weiher *et al.*, 1999). Spinescence, both in leaf and stem form, have as main function protection against large vertebrate herbivory (Hanley *et al.*, 2007), but may provide secondary advantages by providing protection for axillary meristems (Gowda, 1996) or reducing radiation flux (Nobel, 1988 quoted in Hanley *et al.* 2007).

In Argentinean and Israeli moist grasslands (rainfall > 500 mm p.a.), Diaz *et al.* (2001) observed that low plant height, higher SLA, large leaves (leaf area) and tender leaves (non sclerophyllous) react positively to grazing pressure, contradicting the results found here. It is postulated that this may be due to the moister, more nutrient rich conditions in comparison with the semi-arid, low nutrient southern Kalahari, where grazing avoidance rather than grazing tolerance would be preferable (Herms & Mattson, 1992). In this environment compensatory growth upon herbivory would not be feasible. In the high resource scenario it is possible that leaf area would be positively associated with grazing intensity. In the present study no strong relationship was observed between leaf area and range condition, further supporting the theory of cost-nutrient availability theory. Leaf size can however be linked with ecological stresses pertaining to nutrient availability and disturbances (Cornelissen *et al.* (2003). Leaf size plays an important role in light interception, heat balance, CO_2 diffusion and water balance and in phanerophytes particularly leaf

size reduces with a decrease in moisture availability (Orians & Solbrig, 1977; Skarpe, 1996). The generally small leaves of species found in arid savannas may also facilitate greater heat transfer, since evidence suggests that heat transfer in smaller objects can be significantly influenced by slight air movements (Roth-Nebelsick, 2001). Persistence within variable environmental conditions (moisture availability) through transpiration reduction and long leaf longevity necessitates defenses such as increased hairiness, leaf spinescence or stem spinescence, tannins or other secondary compounds, and tough leaves to reduce leaf accessibility and palatability to herbivores.

Once woody phanerophytes have grown to a critical height they may escape attack from herbivores on their leaf crowns. This has been observed in greater density of thorns of *Acacia* species at the browse line, in comparison with branches in the canopy center or at the top (Young *et al.*, 2003). A term coined “divaricate branching” by Hanley *et al.* (1996) has been proposed as an additional structural defence trait whereby shoots with wiry, dense, interweaving stems cause greater difficulty for browsers to access forage while also reducing water loss within the dense crown. The dominance of phanerophytes and chamaephytes with rigid, tangled and often inaccessible caespitose shrub, semi-circle shrub and rhizomatous shrub shoot architectures would confer an advantage to large herbivore defence.

Seedlings of palatable species without sufficient browse deterring traits such as thorns (e.g. *Boscia albitrunca* and *Phaeoptilum spinosum*) may however have poor recruitment which could lead to degeneration of populations over the long-term. Groups II, III and IV should benefit from nitrogen fixing ability. This is due to the nutrient poor soils of the Kalahari (Buckley *et al.*, 1987a; Buckley *et al.*, 1987b; Skarpe, 1991a; Van Rooyen & Van Rooyen, 1998). The loss of grasses (and their nutrient carrying biomass) between canopies may result in “islands of fertility” under woody plant canopies, which is promoted by leaf and fruit litter as well as animal dung under the plants (Feral *et al.*, 2003).

A reduction in perennial grass cover with decreasing range condition (see Chapter 5, $p=-0.000$, $r=0.9169$) will lead to a reduction in the available standing herbaceous biomass that would fuel fires of sufficient intensity to affect woody species survival (Skarpe, 1980). In the southern Kalahari fires occur at large intervals but nonetheless have an important effect on vegetation by killing tree and shrub seedlings (Lloyd & Fairall, 1994; Jeltsch *et al.*, 1996, 1997). The prominence of Groups I to V at the poorer end of the degradation gradient may be promoted by the absence of perennial grass cover (and biomass build-up) which leads to the absence of fire events that would otherwise control woody phanerophyte and chamaephyte proliferation.

In this study it was found that reproductive characteristics supplied a link with zoochorous dispersal under greater grazing pressure. Species or functional groups with adaptations to zoochorous dispersal can be expected to benefit from higher utilization pressures, because of the greater abundance of dispersal agents. In pine forests of southern France logging favoured the establishment of plants that were wind dispersed rather than animal dispersed (Gondard *et al.* 2003), but in such circumstances the disturbance is not facilitated through herbivores but by human intervention. Groups I to IV are characterized by fleshy, or large weakly winged diaspores that are utilized by livestock and wildlife and would be actively dispersed by these agents. This benefit is however counteracted if species are relatively palatable in the juvenile phase and intensely utilized, which would cause high mortality in the young cohorts. Species which do not produce long-term persistent seed banks, as is common in functional groups Groups I to V, would also suffer from grazing pressure on seedlings. *Acacia mellifera* and *R. trichotomum* have however been implicated in bush encroachment due to overgrazing. Possible explanations for their proliferation are:

- Many commercial farms in the southern Kalahari are sheep or cattle farms which lead to a lack of herbivores that are predominantly browsers to curtail establishment.
- Selective utilization of grasses would provide a foothold for woody species expansions. The superior ability of these woody species to access the upper soil strata moisture through their expansive shallow root systems has been documented and stated previously (Skarpe, 1990a; Skarpe, 1990b; Du Toit, 2002; Hipondonka *et al.*, 2003).
- *Rhigozum trichotomum* seeds are winged, which makes the alternative option of anemochory available as dispersal method.
- *Rhigozum trichotomum* does not produce significant amounts of forage (Du Toit, 2002) although flowers and fruit may be utilized and it is therefore not an important browse species.
- *Rhigozum trichotomum* has belowground clonality which provides an additional mode of proliferation.
- With respect to their sociology the very spinescent *R. trichotomum* and *A. mellifera* often occur in dense stands which limit browser access to central plant individuals in the population stands and there is reduced grass cover within these clumps to act as fuel for fire events (Skarpe, 1991a).
- Although *A. mellifera* is also dispersed by livestock, any possible lack of dispersal agents could be irrelevant for these species, since their habit of excluding microhabitats for other species supplies potential establishment niches for their own seedlings in the event of adult mortality. The ability of these species to optimally utilize available soil resources is

often evident from the dense, uniformly sized individuals across sections of land with even distributions of soil resources (Skarpe, 1991a).

It has been shown that savanna woody cover is linked to mean annual precipitation and that savannas are primarily climate driven (woody cover restricted) in regions with less than ca. 650 mm per year (Sankaran *et al.* 2005). Accordingly, the role that herbivory and fire play in woody cover dynamics becomes less, especially below ca. 350 mm per year, unless the soils are sandy, as is found in the Kalahari, with superior moisture retention capability (Sankaran *et al.*, 2005). Rainfall and nutrients are therefore primary determinants of savanna structure, and fire and herbivory are secondary determinants because the latter affects nutrient cycling and biomass fuel load, but both sets of attributes affect grass-shrub dynamics (Scholes & Archer, 1997; Wiegand *et al.*, 2006).

The greatest incidences of clonality were observed in Groups I to IV, which supports the expectation that clonality may be favoured under intensive grazing pressure (Navarro *et al.*, 2006; McIntyre & Lavorel, 2007).

Groups VI and VII of the grazing trait data set was composed of small woody or semi-woody shrubs and erect perennial herbs or geophytic perennial creepers respectively. These species were associated with medium to good range condition in the dune crest and dune street habitats, which may be attributed to a number of features, notably a reduction in spinescence, stem density, leaf toughness and plant height. These attributes make these functional groups more vulnerable to herbivores. Group VII includes the species *Acanthosicyos naudinianus*, *Citrillus lanatus* and *Cucumis africanus* that produce some of the largest fruiting bodies of the region resembling cucumbers and melons and are almost certainly mainly distributed by large herbivores as well as small mammals (Mills & Mills, 2010). The production of large fruit or seeds require a long maturation time for the fruit, great resource expense from the plant, overlap in fruit production and vegetative growth periods and sufficient time for resource acquisition for the following growth period (Castro-Diez *et al.*, 2003). The benefit that these species may enjoy from greater dispersal agent density would be counteracted by sustained herbivory on the foliage and if the seed bank was not persistent. These species are less dense and protected from attack in comparison with thorny dense or rigid shrub forms. It has been observed that *Citrillus lanatus* can occur in extremely high densities during favourable environmental conditions (>15 000 fruit per hectare, van Rooyen, 2001). The large numbers of plants would counter a lack of morphological or physiological defense strategies against herbivory.

The combination of traits observed in Groups I to V in the grazing trait set analysis that leads to the ability of these groups to persist under greater utilization pressures are therefore:

- Greater plant height to escape vertical strata of herbivory,
- Greater levels of spinescence to protect high production cost leaves that possess low SLA, high LDMC, greater sclerophylly and greater stem density,
- Densely structured stem architectures that impede access to fodder.
- Sociologies within populations that restrict penetration of the stand and reduce the herbivore impact on the population,
- Zoochorous diaspore dispersal mechanisms that would benefit from increased herbivore densities, but also the additional potential to disperse anemochorously.

6.4.2 Response of herbaceous dominated functional groups to range condition

Hemicryptophytic grasses that were characteristic of specific habitats were *Aristida meridionalis* and *Centropodia glauca* in the dune slope habitat and *Stipagrostis amabilis* and *Eragrostis trichophora* in the dune crest habitat (Fourie *et al.*, 1987; Van Rooyen, 2001). *Stipagrostis obtusa* is characteristic of the dune street habitat and *S. ciliata* of the dune street and dune slope habitats (Fourie *et al.*, 1987). It was previously shown that perennial grass cover as a whole decreased with grazing intensity in all habitats (Figure 4.11). *Stipagrostis amabilis* and *Eragrostis trichophora* cover abundance decreased with increasing grazing intensity in the dune crest habitat (Figure 4.12). A similar response was shown by *Aristida meridionalis*, *Centropodia glauca* and *Eragrostis lehmanniana* in the dune slope habitat as well as *S. ciliata* and to a lesser extent *S. obtusa* in the dune street habitat (Figure 4.12). *Centropodia glauca* is considered an important indicator species for detecting veld degradation (Du Toit, 2002). Perennial grasses are known to vary in their response to grazing whereby some species are impacted under low utilisation pressure (e.g. *Centropodia glauca*), whereas others may benefit from more intense utilisation pressure (e.g. *Aristida meridionalis*). Similar perennial grass cover may therefore be present under different land use intensities, but species composition will change. Under conditions of intensive grazing pressure total cover will decrease more due to the increased utilisation of less preferred grass species.

Graminoid hemicryptophytes (perennial grasses) were grouped among a diverse assemblage of other plant growth and life forms in Group VIII in the grazing trait analysis, but the grass species were nonetheless in the same group (except for *S. amabilis*). Known differences in the response of different perennial grass species to grazing pressure was therefore not reflected in the grazing trait set ordination. This group was associated with poor to good range or medium to good range condition, but the association with good range condition was stronger in the dune street habitat

than in the dune crest or dune slope habitats. This is in line with the observation that the dune street habitat is utilized by livestock first, before the less accessible dune slope and dune crest habitats (Chapter 4). Perennial grass cover would therefore decline first in the dune street habitat. This group is transitional between the robust perennial groups (I to VI) and the purely herbaceous ephemerals of Group IX. The Group VIII assemblage was distinct from the erect or prostrate annuals of Group IX by exhibiting less leaf hairiness, increased plant height and more sclerophyllous leaf consistency. Groups VIII and IX furthermore had low seed mass in comparison with other groups with diaspores either having no seed appendages or plumes, burrs or wings, indicating a preponderance for anemochorous dispersal mechanisms.

The decrease in perennial grass cover in response to increased grazing pressure is supported by the previous identification of a significant negative relationship between perennial grass cover and range condition ($p=0.000$; $r=-0.9169$). The robust grass *Stipagrostis amabilis*, typical of the dune crests and regarded in this study as a hemicryptophyte, is a robust grass species and was unique due to its alliance with Group V shrubs in the grazing set analysis. The species could conceivably also be classified as a chamaephyte, with leaf clusters occurring at nodes which are carried aerially on shoots. The perennial grasses represent a collection of species with different responses to grazing pressure, with the dune street habitat harboring mainly Category 1 (Decreaser) species (apart from *S. uniplumis* which is a Category 3 species) and the dune slope and dune crest habitats harboring Category 1 to Category 3 species. The response of the group as a whole to range condition is therefore not expected to be clearly defined. Grasses do however possess evolutionary derived adaptations that enable the co-existence with grazers for example, (a) the presence of intercalary meristems that theoretically facilitate perpetual growth, (b) the presence of abrasive silica cells in the epidermis and (c) apical meristems of shoots that are carried at or below ground level away from grazers (and fire) (Gibbs Russell *et al.*, 1990).

The Group VIII diverse species assemblage in the grazing trait analysis is more susceptible to grazing pressure than the perennial shrub groups because of (a) less protection in the form of spines or hairs than groups to the right of the ordination plane, (b) less protection in the form of dense, robust shoot architectures and (c) lower overall height to escape the browse line. Group VIII would also be more susceptible to grazing pressure than the herbaceous annual dominated Group IX due to (a) generally greater plant height implying exposure to herbivory, (b) more leaf dry matter content (higher leaf consistency), making them more valuable to grazers, but also suffering greater losses due to leaf construction cost and (c) year round availability to herbivores as grazing. It should however be noted that Group VIII contained a number of species that are regarded as unpalatable and even poisonous to livestock such as *Crotalaria sphaerocarpa*, *Boophane disticha*, *Pancratium tenuifolium* and *Nerine laticoma*, where chemical defence

strategies are employed to counter predation. Group VIII therefore represent a group with a combination of avoidance and tolerance strategies against environmental stresses (abiotic and biotic), whereas the Group IX herbaceous annuals consist almost exclusively of species employing the avoidance strategy.

Bekker *et al.* (1998) found that small seeds penetrate deeper into the soil and had greater longevity than large seeds. This is supported by Guo *et al.* (2000) from studies of Arizona Desert plants who further reported that small seeds are distributed more widely and more abundantly than large seeds. In general seedlings emanating from large seeds are initially larger than seedlings from small seeds, but seedlings originating from small seeds have faster relative growth rates than seedlings originating from large seeds (Swanborough & Westoby, 1996; Milberg *et al.*, 1998). The grass species dominated groups as well as groups containing herbaceous annuals have small seeds (low seed mass), although no clear difference was observed in seed mass between these groups. This traits links with the short-lived nature of favourable environmental conditions for germination and growth, when seedlings have to grow quickly during periods of moisture availability. Upon seed release seed distribute quickly and deeply into permanent seed banks. The distribution of seeds through a broad soil depth profile furthermore ensures only partial germination because seeds located too deep in the profile (without adequate light requirements) do not germinate readily (Schütz *et al.*, 2002). In Mediterranean grassland it was observed that a larger fraction of perennial and annual grass seed banks germinated during watering in comparison with annual legumes, crucifers, thistles and forbs (Sternberg *et al.*, 2003). This could further explain the reduction in grass cover observed on severely utilised farms.

Of special interest was the observation that the functional group representing annuals in the grazing trait set (Group IX), was not necessarily associated with poor range condition. In the dune crest habitat these groups were often associated with medium to good range condition, possibly indicating the value of dune stability and protection provided by *Stipagrostis amabilis* whereby seeds are captured and held in this habitat and are not lost due to wind activity. This would promote species richness and higher species richness was indeed observed on farms with good range condition (Figure 4.14). Livestock is also only expected to utilize the dune crest habitat frequently once available fodder in the more accessible dune streets and slopes has been depleted. The herbaceous annual groups were also not consistently associated with poor range condition in the dune street and dune slope habitats. This could potentially be attributed to the lesser role that herbivory plays in the dominance of ephemerals in the duneveld habitat and the greater influence of climate in seedling emergence. Only under conditions of extreme and continuous grazing pressure, as was observed on the farm Ballater (Figure 2.19) will the seed

bank of annuals be depleted due to a combination of substrate removal due to wind and the lack of reproduction opportunity for emerging plants.

Schmidtia kalahariensis is a ubiquitous grass species of the Kalahari that is known to respond vigorously to favourable environmental conditions by occurring in vast stands in the dunefield habitat (Van Rooyen, 2001). In the grazing traits analysis this species falls within the herbaceous annuals of Group IX, pointing towards a weedy character. It is relatively tall, wide and fast growing in comparison with other Kalahari grass species. It has a unique decumbent cup growth form, leaves that are strap-shaped rather than linear, have greater leaf area and specific leaf area than most grass species and leaves that are hairy, sticky and with serrated edges. The grass is unpalatable during the growth stages (Du Toit, 2002). The hairy and sticky leaves with serrated edges causes irritation that contributes to its low palatability during active growth. Large leaf area and specific leaf area is associated with growth vigour and low investments in leaf defences (Cornelissen *et al.*, 2003). Large SLA is also associated with high productivity (photosynthetic activity) and is often found in resource-rich environments, but such leaves are also short-lived and vulnerable to herbivory (Wilson *et al.* 1999). As a therophyte *S. kalahariensis* is highly productive in its growth stages due to the high SLA, but to counteract the associated increased vulnerability to herbivory the species has several vegetative adaptations to deter grazers. The species is only grazed in its senescent stage when the acids have been removed from the plant. At this stage the plant has already seeded and the effect on reproduction is minimal. *Schmidtia kalahariensis* counters the general argument that high SLA is associated with low leaf defences by utilizing such deterrence mechanisms, although the exact cost involved in such as strategy could only be established if a more thorough analysis of the biological manufacturing cost in proportion to photosynthetic activity is conducted. This species also has burred seed that facilitates dual dispersal mechanisms of epizoochory as well as anemochory.

6.5 Conclusion

In the semi-arid Kalahari savanna the primary driving force for plant community dynamics is climate (moisture), although secondary forces such as fire and herbivory do influence the structure of the vegetation as was proven here by the different range conditions observed across a series of farms with different management histories. Differences in the plant community in response to utilization pressure do not only manifest in species composition, but also in the functional traits as represented by the different functional groups identified.

The sets of traits and trait categories that would filter through for appropriate species surviving in the Kalahari dunefield differ, depending on the balance between the natural climatic filters (rainfall

amount, seasonality and reliability) and artificial filters that operate through the provision of artificial watering points for livestock and/or wildlife. Such infrastructure can be seen as an artificial filter due to the abnormally severe and sustained utilization pressures that high livestock numbers exert on plant communities. Similar pressures would have been unlikely prior to the colonization, fencing and associated commercial infrastructure development of the region.

Syndromes of traits are identifiable that respond to specific land use practices and in the Kalahari the syndromes of trait categories associated with land use intensity often manifest in clear structural or life and growth form specific functional groups. Most of the species evaluated in this study are common Kalahari species and are “inherently” adapted to survive and proliferate within an arid environment where resource availability is a limiting factor. Within niche specific and heterogeneous environments where resources are distributed patchily the change over in functional groups with respect to external influences such as grazing intensity may be more distinct. The period over which such pressures have been exerted on plant communities in the Kalahari would also be important, because many of the species are intrinsically adapted to disturbance.

Sets of traits that are known to be correlated with grazing intensity may be used as indicators for utilization pressure. The traits identified here may be incorporated into a database system to establish a reference system for trait-environment linkages. The strength of the associations must however be further semented through investigations into possible seasonal changes in trait attributes, the applicability of traits in different landscapes and the identification of traits that are directly associated with grazing intensity and are not potential evolutionary relics of historic environmental regimes. The array of influences acting on plant species assemblages such as fire, nutrients, grazing, climate and human activity means that circumspection is required in determining the extent to which specific environmental factors are responsible for observed trait responses.

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Chapter 7

Synthesis

7.1 Savanna ecosystem dynamics

The starting objective of identifying a range of commercial farms in the southwestern Kalahari dune vegetation that represented a series of farms with range condition from poor to good was achieved. The subjective selection of farms through expert local knowledge combined with known satellite data of the land degradation index and Normalized Difference Vegetation Index was supported by field analysis to determine range condition for farms. The arid savannas are typified by sporadic and localized rainfall events, the main driver of vegetation change (Scholes *et al.*, 1997; Wiegand *et al.*, 2006), which may lead to differences in perceived range condition and species composition in areas that are geographically close to each other. Such observed differences could however be attributed to ephemerals, and total plant cover may mask a true reflection of the range condition (i.e. total perennial cover or cover of valuable fodder species).

Although rainfall (together with soil nutrients) can be regarded as a primary determinant of biomass production in arid or semi-arid systems (Scholes, 1997), the link between vegetation condition and herbivore numbers can not be decoupled completely, with herbivores influencing range condition under certain conditions (Illius & O'Connor, 1999). Over the last two decades, savanna rangeland dynamics have been intensely debated around different opinions on the strength of the coupling between primary resources, their users (herbivores) and climate. The equilibrium theory proposes that where climate stability is high, the levels of primary production will be fairly constant, and a balance can be achieved between herbivore numbers and the ability of plants to regenerate after herbivory. A direct link is therefore made between the herbivores and the existing plant biomass, with stocking densities affecting range condition and possible range degradation. Assigning fixed stocking densities to rangeland only makes sense in equilibrium systems.

Nonequilibrium theory for savannas disregards such a stable state and predicts changes in the tree and grass components of a savanna system over time and space. Variation in annual precipitation, fire, disturbance, long-term climate cycles and environmental stochasticity precludes the existence of a stable equilibrium state. In essence, the nonequilibrium theory downplays the effect that herbivores have on plant populations by proposing that during drought, animal numbers are reduced before they have an effect on the plants and that after droughts, the

recovery of herbivore populations from a low base count is so slow, that herbivores effectively do not have a negative impact on range condition (Scoones, 1995). The continuous “crash and growth” cycles therefore have herbivore populations continuously recovering from periods of decimation, with accordingly low resource impacts. It follows from this theory that range degradation from overgrazing in arid or semi-arid systems is not possible or not likely. This model is especially relevant in areas that experience great variation in annual rainfall (Fernandez-Gimenez and Allen-Diaz, 1999) with a coefficient of variation of 33% or more (Vetter, 2005). A 30 year rainfall period from 1977 to 2006 for Upington shows a CV of 39.4% (South African Weather Service, 2007) and nonequilibrium dynamics can therefore be assumed to prevail in the study area. Nonequilibrium models for savannas can be divided into three types (Gillson, 2004): (a) Cyclical models predict periodic oscillations or a state of flux between woodland and grassland (never reaching equilibrium), and is driven by tree senescence, climate cycles, fire, herbivory, competition and recruitment; (b) phase and transition models assume a tendency for reverting to one of two stable phases, grassland or woodland, with the transition to either two occurring rapidly once a threshold that exceeds the critical level of resilience has been reached. The two phases could be regarded as “domains of attraction” rather than equilibrium states which do not occur at regular intervals and is driven by *inter alia* fire, herbivory, recruitment, rainfall (or drought) or combinations of these factors; and (c) stochastic models do not predict a tendency to revert to any particular state, but rather focus on the existence of small scale resource heterogeneities such as patchiness of soil nutrients, moisture, fire and animal disturbance (the latter due to the existence of key resource areas). Disequilibrium theory is a subtype of stochastic models pertinent to larger spatial scales, which describe large floods or fires and drought as primary drivers of savanna ecosystem processes. Disequilibrium theory does not allow for tree-grass co-existence, with a tendency for a system to converge to either state in the absence of controlling factors (Gil-Romera *et al.*, 2010).

It has been shown that under certain conditions a system will change markedly from a state of density-independence to density-dependence through environmental disruptions that cause above normal and sustained pressures on vegetation, resulting in degradation, for example (a) increased pressure on available browse during drought; (b) herbivore focus on high resource patches such as drainage lines; (c) the supply of artificial watering points and/or feed with associated high stocking densities; (d), fire-induced range selection by herbivores; and (e) closed camped systems that preclude migration of herbivores from resource poor to resource rich environments (Illius & O’Connor, 1999 and references therein). Although rainfall would certainly influence plant production, range condition would be impacted by long-term sustained land use practices and stocking densities due to equilibrium disrupting environmental pressures. Potential rainfall heterogeneity across the area of investigation in this study could therefore contribute to

difference in biomass production, but other indicators of range condition deterioration would arise, and manifest in perennial and annual grass production disparities, bare surface cover dissimilarities and bush encroachment. Range degradation in the arid savannas has been extensively documented (Kalikawe, 1990; Skarpe, 1990a and b; Perkins & Thomas, 1993; Jeltsch *et al.*, 1997; Parker & Witkowski, 1999; Jeltsch *et al.*, 2000; Tews *et al.*, 2006; Rutherford & Powrie, 2009; Scholes, 2009).

Long-term cycles between predominantly wooded and grassy states for savannas have been documented through pollen analysis of soil cores (Gillson, 2004) and hyrax middens (Gil-Romera *et al.*, 2010) and have been largely attributed to long-term rainfall cycles (Gillson, 2004; Vazquez, 2010; Gil-Romera *et al.*, 2010) with fire playing a secondary role only as a possible effect of increased grass cover and not necessarily a cause of transition to a grassy state. These investigations refer to very large spatial and temporal scales. Disturbances such as fire and herbivory can however on smaller scales at least have an effect on the grass-tree co-existence dynamics, whereby reduced grass biomass lowers fire frequency and intensity, promoting tree seedling establishment and survival (Bond & Keely, 2004; Sankaran *et al.*, 2004), although Bond & Keely (2004) also invoke the importance of fire on ecosystem formation at the biome level. Savanna trees also have the ability to survive fire once sufficient fire resistance (size) has been achieved from the seedling stage (Shackleton, 2007). Fire could therefore be considered as a contributing variable that maintains ecosystem structure in a particular state (Gil-Romera, 2010). Scale reference is thus an important consideration, as large scale dynamics may mask small scale heterogeneities that can be attributed either to natural or anthropogenic variables or combinations of both.

Competitive effects alone between the woody and grass swards may not be as crucial as previously thought, and an existing well-developed grass component does not necessarily prevent the establishment of woody saplings (Kraaij & Ward, 2006; Joubert *et al.*, 2008). Instead, interaction between grass biomass, herbivory and above average successive rainfall years or drought, all influence the grass-tree co-existence dynamic to facilitate a possible state and transition model of savanna ecology (Joubert *et al.*, 2008). Attributing either equilibrium or nonequilibrium dynamics outright to savanna systems may be inaccurate and it may well be that the existence of either type of dynamic may be dependent on factors such as rainfall or drought (Vetter, 2005) or scale (Derry & Boon, 2010).

7.2 Plant species composition change over a range condition gradient

The dune crest, dune slope and dune street habitats of the Kalahari dune vegetation were distinct from each other in terms of the substrate characteristics, abiotic influences acting on the habitats (e.g. wind) and the plant communities. Floristically, dune crests were most distinct, whereas the floristic composition of dune slopes and dune streets graded into each other with the level of similarity depending on the grazing pressure. Perennial grass cover reduced with increased grazing intensity in all habitats. In the dune crest and dune slope habitats however, a reduction in cumulative cover and an increase in bare surface cover were indicative of greater grazing intensity. In the dune street shrub cover and annual grass cover increased when veld was overgrazed which did not lead to a reduction in total cover as was observed in the dune street and dune slope habitats.

Degradation of dune veld proceeds sequentially across the three dune vegetation habitats. The dune street habitat is impacted first, because (a) it is an easy corridor for movement for especially livestock; (b) watering points are positioned in dune streets; (c) most of the palatable grass species are found in the dune streets; and (d) most of the prominent perennial grass species in this habitat are Category 1 grasses. Overgrazing leads to the loss of perennial grasses and an increase in shrub cover (bush encroachment) and annual grass cover in the dune street. With persistent overgrazing these pressures extend to the dune slopes, where bare surface patches also start to emerge. As dune streets and slopes become severely depleted livestock move to the dune crests and start to graze the tough *Stipagrostis amabilis* which is normally avoided when other fodder is available. This species is essential to stabilize and protect the dune crest. Dune crests are inherently unstable due to the deep sand substrate and seedling emergence and persistence in the absence of the sheltering *S. amabilis* plants would be difficult. The species is unlike other grasses in that leaves also emerge from intercalary meristems at nodes that are borne aerially, which may increase the vulnerability of the species to grazing, despite its very sclerophyllous leaves and shoots. Overutilisation of this grass species leads to bare dune crests and under extreme grazing pressures cause flattening of dune crests.

Schmidtia kalahariensis is similarly a unique grass species, but rather for its widespread utilisation of habitats than restricted niche occupation as observed for *S. amabilis* in dune crests. The species has unique morphological and physiological adaptations and displays similarities with ephemeral herbs that enable it to rapidly exploit favourable environmental conditions, but with effective deterrents against herbivory. The sheer number of plants emerging after good rains also provides a buffer against any possible herbivore attack during the seedling phase.

Total shrub cover, which was mainly attributed to *Acacia mellifera* and *Rhigozum trichotomum*, was only significantly correlated with range condition in the dune street habitat. *Rhigozum trichotomum* is able to exploit available niches from reduced perennial grass cover after overgrazing which leads to a stronger association of shrub cover with range condition. Moisture availability is an important determining factor in shrub cover in savannas and therefore contribute to observed changes in shrub cover (Skarpe, 1990b; Sankaran *et al.*, 2005), but the current study the correlation of shrub cover with range condition over a whole series of farms supported other observations of shrub encroachment when rangeland is overutilised (Skarpe, 1990; Weber & Jeltsch, 2000; Tews *et al.*, 2006).

A particularly relevant recent study by Rutherford and Powrie (2009) compared plant attributes and diversity between the farms Ballater (regarded as high utilisation pressure in their study) and Avond Schijn (regarded as low utilisation pressure in their study), which represented a good fence line contrast. These two farms also formed part of current study, but when viewing their position on the range condition gradient, both were found to be at the poor end of the range condition. The extreme degradation on Ballater does however produce a perceived fenceline contrast between poor and good range condition areas (pers. obs.). Rutherford and Powrie (2009) found that annuals and stoloniferous plants declined and prostrate plants and shrubs increased with higher degradation. This was found to be in contrast to a global synthesis of expected grazing responses for these traits compiled by Diaz *et al.* (2007). Across the entire range condition gradient of 11 farms in the current study no specific trend was found with regard to cover by either annuals, or stoloniferous plants. However, *Rhigozum trichotomum* was a common stoloniferous shrub species that proliferated with increased utilisation pressure, as did overall shrub cover. In the dune street habitat there was a significant increase in annual grass cover with poorer range condition. Prostrate plants (and the closely related trait low plant height) were not associated with high grazing pressure, in agreement as was reported by Rutherford and Powrie (2009). Poor range condition in the current study was rather associated with increased plant height and more dense shoot architecture, and not with prostrate growth. Ballater was a farm on which biodiversity had been greatly depleted resulting in few resident plant species and low species evenness (Rutherford and Powrie, 2009). In their study this may have produced a distorted representation of the impact of grazing on biodiversity and plant attributes, with patterns emerging more clearly in a diversified range condition data set.

Diaz *et al.* (2007) stated that globally, forbs and woody growth forms exhibited neutral responses to grazing, with woody growth form being least consistent, whereas graminoids exhibited negative response. In the current study, woody growth forms responded positively to increased grazing pressure, and perennial grasses declined. Annual grasses did not however respond consistently

to grazing pressure. In arid climates with a long history of herbivory perennial plant cover and annual plant cover have been observed to not change markedly with increased grazing pressure, in contrast to mesic climates where these two life forms decreased with increased grazing pressure (Jauffret & Lavorel, 2003; Adler *et al.*, 2004; Diaz *et al.*, 2007). Kalahari vegetation also has a long history of herbivory and total perennial cover and total annual cover did not exhibit a strong relationship with each other (Figure 7.1a). This relationship was however not consistent across habitats.

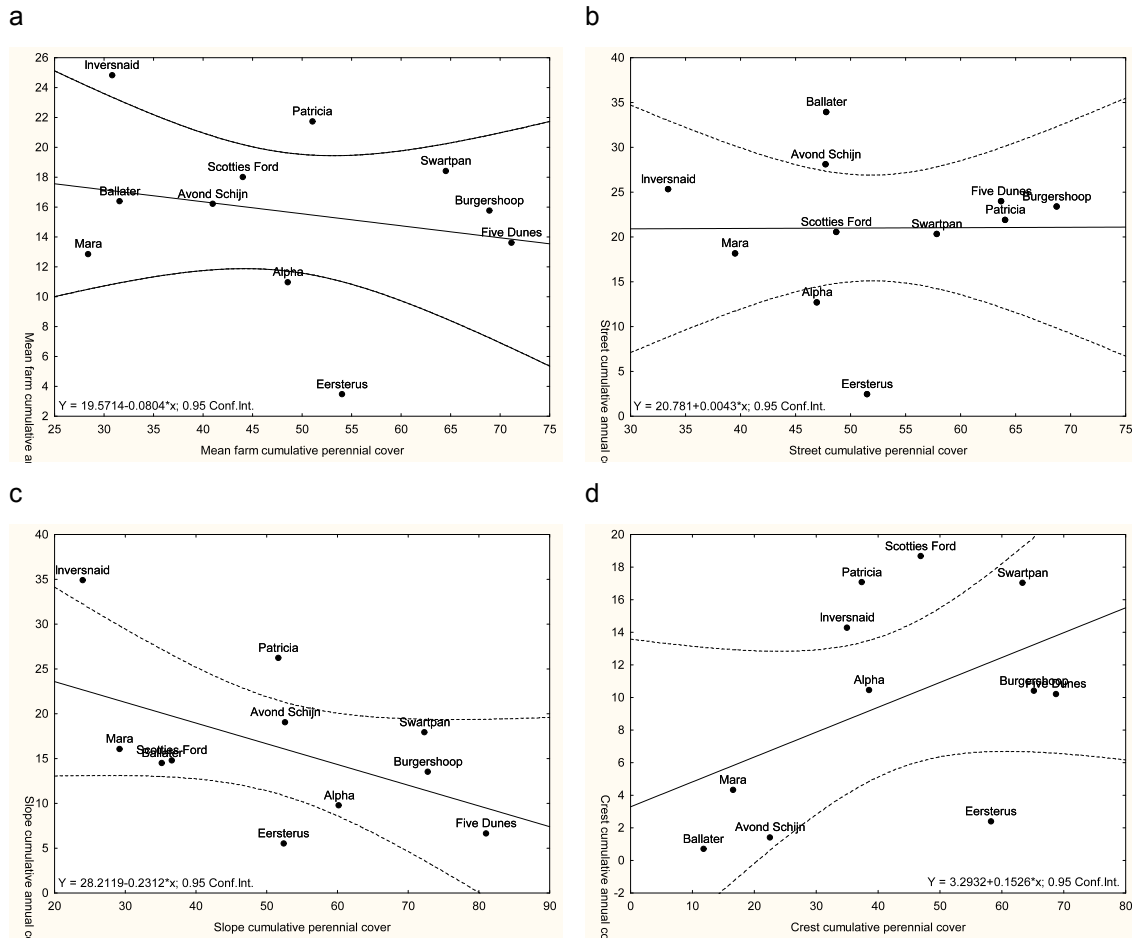


Figure 7.1 The relationship between total (cumulative) perennial cover and total (cumulative) annual cover across a range condition gradient for (a) all dune habitats combined, (b) the dune street habitat, (c) the dune slope habitat and (d) the dune crest habitat. The five farms with the highest range condition scores were Swartpan, Eersterus, Five Dunes, Alpha and Burgershoop. Dotted lines indicate 95% confidence levels.

In the dune slope habitat annual cover decreased when perennial cover increased (Figure 7.1c), whereas the opposite relationship was observed in the dune crest habitat (Figure 7.1d). One

could argue that the dune streets, as most favoured habitat by herbivores, have the longest exposure to or “history” of grazing and the argument of limited cover change with grazing pressure holds true. The dune slopes, as second most favoured habitat, experience less grazing pressure than the dune streets and also harbour some dune crest species with reduced grazing tolerance. Perennial plant cover decline may therefore be observed with overutilisation, concomitant with a reduction in annual cover (Figure 7.1c and Figure 4.11b). The dune crests were not historically exposed to intensive grazing pressure and experience total cover decline only under sustained utilisation pressure. Together with the necessity of stabilizing and protective plant species on the dune crests, this implies that both perennial and annual cover would decline under intensive utilisation pressure (Figure 7.1d and Figure 4.11a).

7.3 Species richness and Shannon-Wiener index of diversity change over a range condition gradient

A link was observed between range condition and both species richness and Shannon-Wiener index of diversity. The significance of the association was however variable (generally fairly high “r” values, but marginal or nonsignificant “p” values). Species richness did not change significantly with range condition when viewed across all habitats on farms, but the Shannon-Wiener index of diversity did. Species richness increased when veld condition improved in the dune crest and dune street habitats. The association of lower species richness with higher grazing pressure was also recorded by Rutherford and Powrie (2009) in a comparison of the total species richness between Ballater and Avond Schijn. The report of a decrease in species richness from the dune crests to the dune valleys (streets) by Leistner and Werger (1973) was not recorded in this study. The Shannon-Wiener index of diversity also increased when veld condition improved in the dune street and dune slope habitats as well as across all habitats. This relationship was not however repeated in the dune crest habitat. In the present study, dune slopes had the highest species richness, with the observation that nine of the 11 farms had the highest mean species richness on the dune slopes, regardless of range condition. The exceptions were Inversnaid (dune street highest, medium range condition farm) and Eersterus (dune street highest, good range condition farm). Shannon-Wiener Index of diversity was also highest in the dune slope on all but two farms, namely Inversnaid (dune street highest, medium range condition farm) and Ballater (dune crest highest, poor range condition farm). Although the dune slope habitat was classified as a distinct habitat type, it can also be regarded as an ecotone between the dune street and dune slope habitats, potentially harbouring species occurring in these habitats, as well as dune slope specific species.

7.4 Change in plant trait categories over a range condition gradient and emerging Plant Functional Types

Before the investigation into the response of individual trait categories or PFTs across a range condition gradient, different traits sets (vegetative, reproductive and complete sets) were subjected to exploratory analysis. During this exploratory analysis it was established that vegetative traits imparted a strong influence on plant functional group composition. Navarro *et al.* (2006) found that vegetative traits correlated more strongly with each other than regenerative traits, which was also observed in the present study. Distinct macrocharacteristics represented by the Raunkier Life Form type, shoot architecture or plant height for example, typified different groups. Readily identifiable life forms such as herbaceous annuals, perennial grasses or large woody shrubs and trees emerged. These groups represent different strategies, such as avoidance versus persistence or K-selection versus *r*-selection, for persisting and proliferating in a challenging arid habitat. In the Kalahari environment various filters act on species selection such as response to herbivory, fire, moisture availability and resource acquisition strategies (Diaz *et al.*, 199a). These functional groups were therefore identified from a set of traits that were not necessarily relevant in elucidating grazing response adaptations *per se*. Accordingly a reduced set of 17 traits were selected to identify functional groups that may have specific relevance in grazing response.

Functional groups emerged in the grazing trait analysis that could also be described according to prominent life or growth forms, with leaf hairiness a strong divisive trait. Medium to large woody shrubs and trees were separated into a number of groups. Perennial herbs and creepers as well as annual herbs and grasses formed separate groups. A functional group was also identified that consisted of a broad spectrum of life forms, including the perennial grasses, semi-woody shrubs, geophytes and annuals. The grazing response trait categories did not translate into a clear separation of plant functional groups that were specific to either end of the range condition gradient. PFTs based on these grazing response traits were mostly spread over a broad band of the range condition gradient, for example in the poor to medium, medium to good, or broader poor to good range condition region. Large woody shrubs were consistently associated with poor to medium range condition in all habitats. The functional group that contained all the perennial grasses together with other life forms, did not exhibit a relationship with the range condition gradient. In all habitats it occurred from poor to good range condition. This was not surprising as different grass species respond differently to disturbance and may be negatively or positively influenced by disturbance pressure. It was noteworthy that this variance in response did not emerge in the functional group classification, but perennial grass cover as a whole and species composition did reflect range condition state. Small woody shrubs and perennial herbs and

creepers were furthermore also indicative of medium to good range condition, but annual grasses and herbs mostly did not exhibit any consistent trend across habitats.

Based on the distribution of PFTs across the range condition gradient in the different habitats, a number of traits were identified in this study that may have relevance for plant species response or persistence under grazing pressure:

- Increased plant height facilitates an escape to higher vertical strata where herbivores cannot access plant material. Plant height correlation with grazing or land use intensity has been commonly recorded (Hadar *et al.*, 1999; Landsberg *et al.*, 1999; Lavorel *et al.*, 1999; Diaz *et al.*, 2001; Jauffret & Lavorel, 2003).
- Spinescence increases to protect high production cost leaves.
- Such high production cost leaves possess low SLA, high LDMC, greater sclerophylly and greater stem density (also confirmed by Diaz *et al.*, 2001; McIntyre, 2008).
- Densely structured stem architectures impede access to fodder.
- Sociologies within populations that restrict penetration of the stand and reduce the herbivore impact on the population,
- Zoochorous diaspore dispersal mechanisms that would benefit from increased herbivore densities, but also the additional potential to disperse anemochorously.

7.5 Value of the grazing Plant Functional Type approach

In this study a PFT was regarded as “a set of species that respond in unison to changes in the environment or have similar effects on the environment”. This PFT term definition reflects both effect and response types. In this study the focus was however on functional response types, and more specifically the response to grazing disturbance. Functional types do not assume any taxonomic linkages between the plant species within a functional type and this attribute was not included in any analysis. The functional groups that were identified in the various permutations of trait data sets showed that species within groups were not taxonomically affiliated.

Plant functional types are a simplified way of studying plant survival strategies. The local conditions that filter for specific plant traits (Diaz *et al.*, 1999a) promote establishment, persistence and reproduction. If sets of traits or syndromes are repeated in predictable patterns, changes that vegetation will undergo under external influences could be anticipated (Diaz *et al.*, 1999a). McIntyre *et al.* (1999a) emphasized the importance of finding such syndromes that are repeated in the flora rather than investigating isolated trait responses. Traits that may be evolutionary relics of which the functional significance is not relevant anymore, illustrates the

danger of assigning species response or effect to individual traits or, the capacity of a plant to resprout could be advantageous as both a fire response and a grazing response. It is not the trait in isolation that should be considered but rather an assembly of different traits with specific scores that define a specific adaptation (Diaz *et al.*, 1999a). In this study traits were selected that were thought to be relevant to grazing response and the aim was to, if possible, identify PFTs based on this syndrome of grazing traits. The broad PFT distribution across the range condition gradient in the three different habitats made the identification of grazing response syndromes difficult. Ideally, the syndromes of 17 traits should repeatedly result in an association of PFTs with poor to medium or medium to good range condition. Stated differently, PFTs should have emerged that aligned with low grazing pressure or high grazing pressure. The trait list corresponded well with published sets of checklist that should be considered when testing grazing or disturbance response (McIntyre *et al.*, 1999b; Vesk *et al.*, 2004). However, such global trait lists may not be applicable across different ecosystems and scales (Diaz *et al.*, 2002). Even across the three different habitat types identified in this study, consistent responses of PFTs to grazing intensity were difficult to achieve (Table 7.1), with only large shrubs and trees showing consistent response to range condition across all habitats. This inconsistency in response was however not only restricted to the PFT analysis. The cover abundance of different growth forms based on the “traditional” Braun-Blanquet survey also yielded different responses of growth forms across range condition (Table 7.1). Only perennial grasses were consistently linked with range condition across all habitats.

In central-western Argentina Diaz *et al.* (1999b) reported similar variation in plant functional trait responses to disturbance (grazing and logging) in different habitats. Variation was discernible in xerophytic woodlands, but not in xerophytic open shrublands and montane grasslands. The low variation in the latter habitats was attributed to the stronger filtering effect of climate, rather than disturbance. Sites across different disturbance regimes also had dominant species in common. In the Argentina study, sites were identified across the disturbance regimes and local vegetation investigated for a set of traits. That approach is in contrast to this study where an *a priori* identification of functional groups was conducted. The direct functional analysis of vegetation across the range condition gradient may have produced more defined response types.

From a rangeland management point of view, the traditional assessment of range condition from cover values of plant growth forms is still relevant. In this study perennial grass cover (a widely documented indicator of range condition) for example was found to be strongly linked to range condition, but the functional group that contained many perennial grasses in the functional trait analysis, only exhibited weak coupling with range condition (Table 7.1). Perennial grass cover as

a single variable does however have scope for refinement, since this parameter does not consider the response type of different perennial grass species to grazing intensity.

Table 7.1 Comparative strength of the association between range condition and plant growth forms identified in the *in situ* species cover abundance survey, and growth form groups derived from the Plant Functional Trait Analysis. Shaded blocks show similar habitat specific responses

	Strength of growth form association with range condition					
	Growth form groups derived from habitat cover abundance survey			Growth form groups derived from grazing trait specific Plant Functional Trait analysis		
	Dune crest	Dune slope	Dune Street	Dune crest	Dune slope	Dune Street
Large woody shrubs and trees	Moderate	Weak	Weak	Strong	Strong	Strong
Medium to large woody shrubs	Weak	Moderate	Strong	Strong	Strong	Weak
Small to medium woody shrubs	Weak	Weak	Weak	Moderate	Weak	Weak
Perennial herbs and creepers	Weak	Moderate	Moderate	Strong	Weak	Strong
Perennial grasses	Strong	Strong	Strong	Weak*	Weak*	Weak*
Annual herbs and creepers	Moderate	Weak	Weak	Weak	Strong	Strong
Annual grasses	Weak	Moderate	Strong			
Total cover	Weak	Strong	Strong		-----	
Bare surface cover	Weak	Strong	Strong		-----	

* Perennial grasses were grouped under a diverse group of growth forms in the grazing trait PFT analysis. The response to range condition of the group as a whole was weak in all habitats.

The *a priori* classification of local flora into subjective functional groups based on traits that are perceived to be relevant for divergent responses to grazing pressures can be problematic in heterogeneous habitats. Response to disturbance could be masked by differences in environmental parameters between the dune street, slope and crest habitats, such as soil texture and soil moisture, fire or wind abrasion. A trait group set for annual grasses that shows strong grazing response in the dune street habitat, may not be relevant in the dune crest habitat (Table 7.1). Assessing range condition in the southern Kalahari with the aid of plant functional analysis must therefore be done with consideration of what trait sets would be most suitable for a specific habitat, and a good understanding of what environmental filters other than grazing may be relevant to specific traits.

Stochasticity and fluctuations of rainfall, fire and nutrient resources can over evolutionary time scales lead to the prevalence of nonequilibrium savanna dynamics in the southern Kalahari. This would lead to a perceived weak coupling between plant population dynamics and structure, and herbivore densities. The existence of wildlife and livestock farming in enclosed, spatially restricted islands, with the addition of supplementary food and water, will inevitably lead to a more direct coupling (equilibrium) system at the local scale, with the risk of range degradation. Although models have been produced that illustrate fluctuation between predominantly woodland or grassland landscapes (whether state and transition, cyclical or stochastic), these are often

applied at the landscape level and over time scales of thousands of years, assuming “open” systems that facilitate migration capability. Anthropogenic alterations have however lead to concentrated, out of the ordinary pressures on vegetation, resulting in a need for awareness of detrimental impacts of this intensive utilisation on available resources.

Chapter 8

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Appendix A: List of species abbreviations (Germishuizen *et al.*, 2006; Klopper *et al.*, 2006)

Aca eri	<i>Acacia erioloba</i> E.Mey.
Aca hae	<i>Acacia haematoxylon</i> Willd.
Aca heb	<i>Acacia hebeclada</i> DC. subsp. <i>hebeclada</i>
Aca mel	<i>Acacia mellifera</i> (Vahl) Benth. subsp. <i>detinens</i> (Burch.) Brenan
Aca nau	<i>Acanthosicyos naudinianus</i> (Sond.) C.Jeffrey
Aca ref	<i>Acacia luederitzii</i> Engl. var. <i>luederitzii</i>
Acr inf	<i>Acrotome inflata</i> Benth.
Apt alb	<i>Aptosimum albomarginatum</i> Marloth & Engl.
Apt dec	<i>Aptosimum decumbens</i> Schinz
Apt elo	<i>Aptosimum elongatum</i> Engl.
Ari ads	<i>Aristida adscensionis</i> L.
Ari con	<i>Aristida congesta</i> Roem. & Schult. subsp. <i>congesta</i>
Ari mer	<i>Aristida meridionalis</i> Henrard
Asp coo	<i>Asparagus cooperi</i> Baker
Asp nel	<i>Asparagus nelsii</i> Schinz
Boo dis	<i>Boophane disticha</i> (L.f.) Herb.
Bos alb	<i>Boscia albitrunca</i> (Burch.) Gilg & Gilg-Ben.
Bos foe	<i>Boscia foetida</i> Schinz subsp. <i>foetida</i>
Brachyst	<i>Brachystelma</i> sp.
Bra glo	<i>Brachiaria glomerata</i> (Hack.) A.Camus
Bul his	<i>Bulbostylis hispidula</i> (Vahl) R.W.Haines
Cen gla	<i>Centropodia glauca</i> (Nees) Cope
Cha ina	<i>Chamaesyce inaequilatera</i> Sond. var. <i>inaequilatera</i>
Cha pum	<i>Chascanum pumilum</i> E.Mey.
Che alb	<i>Chenopodium album</i> L.
Cit lan	<i>Citrullus lanatus</i> (Thunb.) Matsum. & Nakai
Cle pax	<i>Cleome paxii</i> (Schinz) Gilg. & Gilg-Ben.
Cro pod	<i>Crotalaria podocarpa</i> DC.
Cro spa	<i>Crotalaria spartioides</i> DC.
Cro sph	<i>Crotalaria sphaerocarpa</i> Perr. ex DC.
Cuc afr	<i>Cucumis africanus</i> L.f.
Cya ser	<i>Cyamopsis serrata</i> Schinz
Cyn ora	<i>Cynanchum orangeanum</i> (Schltr.) N.E.Br.
Dic cap	<i>Dicoma capensis</i> Less.
Dic sch	<i>Dicoma schinzii</i> O.Hoffm.

Dim pol	<i>Dimorphotheca polyptera</i> DC.
Dip gra	<i>Dipcadi gracillimum</i> Baker
Era ech	<i>Eragrostis echinocloidea</i> Stapf.
Era leh	<i>Eragrostis lehmanniana</i> Nees
Era tri	<i>Eragrostis trichophora</i> Coss. & Durieu
Gis afr	<i>Gisekia africana</i> (Lour.) Kuntze var. <i>africana</i>
Gni pol	<i>Gnidia polycephala</i> (C.A.Mey.) Gilg.
Gre fla	<i>Grewia flava</i> DC.
Har pro	<i>Harpagophytum procumbens</i> (Burch.) DC. ex Meisn. subsp. <i>procumbens</i>
Hel are	<i>Helichrysum arenicola</i> M.D.Hend.
Hel arg	<i>Helichrysum argyrosphaerum</i> DC.
Hel cil	<i>Heliotropium ciliatum</i> Kaplan
Her bur	<i>Hermannia burchelli</i> (Sweet) I.Verd.
Her mod	<i>Hermannia modesta</i> (Ehrenb.) Mast.
Her tom	<i>Hermannia tomentosa</i> (Turcz.) Schinz ex Engl.
Her fle	<i>Hermbstaedtia fleckii</i> (Schinz) Baker & C.B.Clarke
Hir ech	<i>Hirpicium echinus</i> Less.
Ind alt	<i>Indigofera alternans</i> DC. var. <i>alternans</i>
Ipo hac	<i>Ipomoea hackeliana</i> (Schinz) Hallier f.
Jat ery	<i>Jatropha erythropoda</i> Pax & K.Hoffm.
Koh cae	<i>Kohautia caespitosa</i> Schinz subsp. <i>brachyloba</i> (Sond.) D.Mantell
Leb lin	<i>Calobota linearifolia</i> E.Mey. = <i>Lebeckia linearifolia</i> E.Mey.
Led und	<i>Ledebouria undulata</i> (Jacq.) Jessop
Les phy	<i>Lessertia physodes</i> Eckl. & Zeyh.
Lim are	<i>Limeum arenicolum</i> G.Schellenb.
Lim arg	<i>Limeum argute-carinatum</i> Wawra ex Wawra & Peyr. var. <i>argute-carinatum</i>
Lim fen	<i>Limeum fenestratum</i> (Fenzl) Heimerl
Lim myo	<i>Limeum myosotis</i> H.Walter var. <i>myosotis</i>
Lim vis	<i>Limeum viscosum</i> (J.Gay) Fenzl subsp. <i>viscosum</i>
Lop pol	<i>Lophiocarpus polystachyus</i> Turcz.
Lot den	<i>Lotononis densa</i> (Thunb.) Harv. subsp. <i>gracillis</i> (E.Mey.) B.-E.van Wyk
Lot pla	<i>Lotononis platycarpa</i> (Viv.) Pic.Serm.
Lot div	<i>Lotononis divaricata</i> (Eckl. & Zeyh.) Benth.
Lyc bos	<i>Lycium bosciifolium</i> Schinz
Lyc cin	<i>Lycium cinereum</i> Thunb.
Lyc hir	<i>Lycium hirsutum</i> Dunal

Mer ver	<i>Merremia verecunda</i> Rendle
Mol cer	<i>Mollugo cerviana</i> (L.) Ser. ex DC.
Mom bal	<i>Momordica balsamina</i> L.
Ner lat	<i>Nerine laticoma</i> (Ker Gawl.) T.Durand & Schinz
Neu aus	<i>Neuradopsis austro-africana</i> (Schinz) Bremek. & Oberm.
Nol are	<i>Nolletia arenosa</i> O.Hoffm.
Nol rar	<i>Nolletia rarifolia</i> (Turcz.) Steetz
Oxa sem	<i>Oxalis semiloba</i> Sond. subsp. <i>semiloba</i>
Oxy del	<i>Oxygonum delagoense</i> Kuntze
Pan ten	<i>Pancratium tenuifolium</i> Hochst. ex A.Rich.
Par afr	<i>Parkinsonia africana</i> Sond.
Pav sen	<i>Pavonia senegalensis</i> (Cav.) Leistner
Pel leu	<i>Peliostomum leucorrhizum</i> E.Mey. ex Benth.
Per dae	<i>Pergularia daemia</i> (Forssk.) Chiov.
Pha spi	<i>Phaeoptilum spinosum</i> Radlk.
Pharnaci	<i>Pharnaceum</i> sp.
Phy ang	<i>Phyllanthus angolensis</i> Müll.Arg.
Pli kar	<i>Plinthus karooicus</i> I.Verd.
Pli ser	<i>Plinthus sericeus</i> Pax
Pol cam	<i>Pollichia campestris</i> Aiton
Pro gla	<i>Prosopis glandulosa</i> Torr. var. <i>glandulosa</i>
Pty bif	<i>Ptychlobium biflorum</i> (E.Mey.) Brummitt subsp. <i>biflorum</i>
Req sph	<i>Requienia sphaerosperma</i> DC.
Rhi tri	<i>Rhigozum trichotomum</i> Burch.
Sal kal	<i>Salsola kali</i> L.
Sch kal	<i>Schmidtia kalahariensis</i> Stent
Ser rem	<i>Sericorema remotiflora</i> (Hook.) Lopr.
Ses tri	<i>Sesamum triphyllum</i> Welw. ex Asch. var. <i>triphyllum</i>
Sen ita	<i>Senna italica</i> Mill. subsp. <i>arachoides</i> (Burch.) Lock
Sol cap	<i>Solanum capense</i> L.
Sol inc	<i>Solanum incanum</i> L.
Sta spa	<i>Stachys spathulata</i> Burch. ex Benth.
Sti ama	<i>Stipagrostis amabilis</i> (Schweick.) De Winter
Sti cil	<i>Stipagrostis ciliata</i> (Desf.) De Winter
Sti hir	<i>Stipagrostis hirtigluma</i> (Steud. ex Trin. & Rupr.) De Winter
Sti obt	<i>Stipagrostis obtusa</i> (Delile) Nees
Sti uni	<i>Stipagrostis uniplumis</i> (Licht.) De Winter



Tal caf	<i>Talinum caffrum</i> (Thunb.) Eckl. & Zeyh.
Tal cri	<i>Talinum crispatum</i> Dinter
Tet arb	<i>Tetragonia arbuscula</i> Fenzl
Tra lax	<i>Trachyandra laxa</i> (N.E.Br.) Oberm. var. <i>laxa</i>
Tri zey	<i>Tribulus zeyheri</i> Sond. subsp. <i>zeyheri</i>
Xen tri	<i>Xenostegia tridentata</i> (L.) D.F.Austin & Staples subsp. <i>angustifolia</i> (Jacq.) Lejoly & Lisowski



Appendix B: Farm relevé numbers

- 1-9 Alpha
- 10-18 Inversnaid
- 19-27 Avonds Schijn
- 28-36 Ballater
- 37-45 Eersterus
- 46-54 Mara
- 55-63 Patricia
- 64-72 Burgershoop
- 73-81 Swartpan
- 82-90 Five Dunes
- 91-99 Scotties Ford



Appendix C: Field survey sheet

Date:		GPS:			
Location:		Habitat:		Plot no.:	
Photo number:		Aspect:			
Slope:	Level (0-2)	Gentle (3-10)	Moder. (11-45)	Steep (>45)	
Rockiness:	0 (0-2%)	1 (3-15%)	2 (16-30%)	3 (30-50%)	4 (>50)
Soil:	0 (loose sand)	1 (semi-comp.)	2 (compacted)	3 (gravel)	5 (clay/sand)
Dominant veget. descr.:					
Fire evidence:			Distance from watering point:		
	Bush encroach.	Grazing	Browsing	Wood cutting	Trampling
Slight					
Moderate					
Severe					
Species	Br-BI cover	* - (<1%)	N Individuals	1 - one	
1		1 - (1-5%)		2 - (2-5)	
2		2a - (6-15%)		3 - (6-15)	
3		2b - (16-25%)		4 - (15-50)	
4		3 - (26-50%)		5 - (>50)	
5		4 - (51-75%)			
6		5 - (76-100%)			
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Appendix C: Continued

No.	Annual	Stri	Near	Perennial	Stri	Near	Wheel point		
1							Notes:		
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15							Spec		Freq
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44									
45									
46							Grass		Freq
47							Decr.		
48							Incr1		
49							Incr2		
50							Incr3		



Appendix D: Functional trait list

Plant species:					
Plant height (m)					
Canopy diam 1 (m)					
Canopy diam 2 (m)					
Canopy density	<25%	>25-50%	>50-75%	>75%	
Life form	Phanerophyte	Chamaephyte	Hemicryptophyte	Geophyte	Therophyte
Life span (years)	<1y	1-2y	2-5y	5-25y	25-50y
Organs shed	Plant	Shoot	Branch	Leaf	>50y
Shoot architecture	Compact	Lying	Shrub	Tree	Scapose
	Caespitose	Sub-caespitose	Pulvinate	Reptant	Twining
Growth form	Palm	Columnar	Funnel	Broom	Fountain
	Basal rosette	Semi-rosette	Round	Half-round	Upright broad
	Fan	Flat	Tendril	Upright long	Conical
Stem density	Herbaceous	Hemixylous	Ligneous	Succulent & green cortex	
	Succulent & bark	Spongy/manoxylous	Rigid, lekkerbreek	Rigid, not breaking	
Trophic type	N-fixing	Not			
Photosynth pathway	C4	C3	CAM		
Clonality	None	Aboveground	Belowground	Lying branches sometimes rooting	
Spinescence: Stem	None	Slightly spiny	Interm spiny	Very spiny	
Leaf	None	Slightly spiny	Interm spiny	Very spiny	
Leaf area	<1cm ²	>1cm ² - 4cm ²	>4cm ² - 16cm ²	>16cm ² - 64cm ²	>64cm ² - 256cm ²
Specific leaf area					
Leaf dry matter content					
Leaf colour	All green	All glaucous	All white	Green and white	
Leaf angle	Vertical up	Oblique	Horizontal	Hanging	Folded
Leaf hairiness: Adaxial	None	Sparse	Intermediate	Dense	
Abaxial	None	Sparse	Intermediate	Dense	
Leaf consistency	Mesomorph	Semi-sclerophyll	Sclerophyll	Semi-succulent	Succulent
Surface exudates	Wax	Resin	Aqueous		
Leaf longevity	<3 months	>3-6 months	>6-12 months	>12 months	
Leaf type	Simple	Pinnate	Bipinnate	Palmate or trifoliolate	



Appendix D: Continued












Leaf shape	Linear	Strap-shaped	Oblong	Sickle-shaped	Lance-shaped	Inverse lance
	Spoon-shaped	Oval	Elliptic	Ovate	Rounded	
	Heart-shaped	Kidney-shaped	Inverse heart	Obovate	Diamond-shaped	Triangular
Spear-shaped	Arrow-shaped	Fan-shaped	Peltate			
Leaf margin	Entire	Dentate	Denticulate	Serrate	Serrulate	Crenate
	Sinate	Lobed	Pinnatifid	Palmatifid	Undulate	Revolute
Carbohydrate storage	Specialized organs	No storage organs				
Response to fire	Killed	Resprout from aboveground buds	Resprouts from belowground buds			
Palatability	Toxic	Unknown	Limited palatability	Palatable	Very palatable	
Pyrogenic flowering	Yes	No				
Growth phenology	Spring	Summer	Autumn	Winter	Any time	
Flowering phenology	Spring	Summer	Autumn	Winter	Any time	
Fruiting phenology	Spring	Summer	Autumn	Winter	Any time	
Germination phenology	Spring	Summer	Autumn	Winter	Any time	
Sociability	Single	Loose groups	Dense clumps	Large herds		
Pollination mode	Self	Wind	Specialized zoo	Unspecialized zoo		
Inflor. prominence	Exposed	Indeterminate				








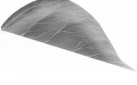








Appendix D: Continued

Inflorescence type	Solitary	Cluster	Head (capitulum)	Umbel	Cyme	
	Spike	Raceme	Corymb	Panicle		
Flower shape	Bell-funnel	Bowl-dish	Trumpet	Brush		
	Tube	Flag	Trap	Gullet		
Flower colour	White	Cream	Yellow	Orange	Red	Pink
	Purple	Blue	Green	Brown		
N seed per fruit						
Seed mass (mg)						
Seed mass class	0.01 - 0.1mg	>0.1 - 1mg	>1 - 10mg	>10 - 100mg	>100 - 1000mg	
Seed attachments	None	Burrs	Plumes	Wings		
Seed dispersal type	No obvious agent	Anemochory	External zoochory	Internal zoochory	Hydrochory	Ballistic
Diaspore morphology	Capsule	Nut	Berry	Drupe	Caryopsis	Tumbleweed
	Winged	Plumed	Wooley	Balloon	Dust	
Antitelechory	Myxospermy	Hygrochasy	Heterodiaspory	Synaptospermy		
Fecundity (per plant)	<200 seeds	>200 - 500 seeds	>500 - 1000 seeds	>1000 - 5000 seeds	>5000 seeds	
Seed dormancy	None	Moderate	Strong			
Seed bank type	None	Transient	Permanent			
Status	Indigenous	Naturalized	Exotic	Exotic invader		
















Appendix E: Glossary

Term	Definitions used in this study	Information source	Illustration
Adpressed	See adpressed		
Adpressed	(= adpressed) Lying close to and flat along the surface.	Leistner (2000); Retief & Hermann (1997)	
Adpressed basal rosette	Leaves emanating basally and spreading horizontally from a central, lateral stem, close to or on the substrate, around a central axis from which a scape often emanates.	None	
Bell/funnel flower shape	Bell-shaped: Used to describe a flower with a broad tube terminating in flared lobes. Funnel-shaped: Used to describe a flower in which the perianth widens gradually from the base into a spreading, often lobed mouth, like a funnel.	Brickell (2003)	
Bowl/dish flower shape	Bowl-shaped: Used to describe a flower that is hemispherical with the sides straight or very slightly spreading at the tips	Brickell (2003)	
Broom	Shoots spread centrally and laterally from a short main stem, or at substrate level, with the shoots straight or slightly curved.	None	
Brush flower shape	Usually an inflorescence where the individual flowers are carried terminally on a shortened peduncle without partial or entire encapsulation by calyx or corolla segments (e.g. Asteraceae)	None	
Caespitose	Branched from near the base with shoots in dense tufts.	Ellenberg & Mueller-Dombois (1974); Allaby (1992)	
Caespitose shrub	Shoots emanate close to substrate level from one to several main stems, at lateral to oblique angles with ramification of several orders. Shoots are plus minus randomly packed to form a dense aggregation.	None	
Caespitose tuft	Shoots are tightly packed together basally, often unidirectionally, to form a dense tuft with growth points at the substrate level. Shoots do not emanate from a central point	None	
Chamaephyte	Plants whose mature branch or shoot system remains perennially within 50 cm above ground surface, or plants that grow taller than 50 cm, but whose shoots die back periodically to that height limit.	Ellenberg & Mueller-Dombois (1974)	
Climber	Plants that climb or cling by means of modified stems, roots, leaves or leaf stalks, using other plants or objects as support.	Brickell (2003)	
Cluster inflorescence type	Arrangement of several inflorescences leaves, stems, roots or flowers that arise from a single point, or appear to do so.	Brickell (2003)	
Crenate leaf margin	Leaf margins with scalloped, or with broadly rounded teeth separated by shallow indentations.	Barnard <i>et al.</i> (2004); Brickell (2003)	
Cyathium inflorescence type	Inflorescence of <i>Euphorbia</i> , in which a cup-like involucre surrounds a single pistil and several male flowers, each with a single stamen; flowers are sometimes bisexual	Brickell (2003)	
Cyme inflorescence type	Flat or round-topped, branched inflorescence with each axis ending in a flower, the oldest at the centre, and the youngest arising in succession from the axils of bracteoles.	Brickell (2003)	
Decumbent	Spreading horizontally at first but then growing upwards	Leistner (2000)	








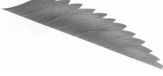



Decumbent cup	Shoots emanate horizontally and/or at an oblique angle from a central axis at first but then curve upwards at an oblique or right angle. Inflorescences and flowers are borne on individual shoots.	None	
Dentate leaf margin	Leaf margins with a row of more or less triangular teeth, their point directed outward, rather than inward	Barnard <i>et al.</i> (2004)	
Denticulate leaf margin	Leaf margins that are finely dentate, that is, with smaller and more closely spaced teeth	Barnard <i>et al.</i> (2004)	
Diamond-shaped leaf	Leaves that are roughly oval but with acute angles at the base and tip, and obtuse angles midway down both sides.	Brickell (2003)	
Elliptic leaf shape	Used to describe a leaf broadest at the centre, tapering towards each end; length is two times the width.	Brickell (2003)	
Entire leaf margin	Smooth leaf margins, without indentations or projections such as teeth or lobes.	Barnard <i>et al.</i> (2004)	
Erect	Shoots emanate at intervals along a main stem with each shoot ramifying few to several orders resulting in an upright overall growth form.	None	
Fan	Shoots or leaves radiate horizontally to laterally from a central axis, but in a dorsiventral manner.	None	
Flag flower shape	As for example in the pea flowers; a zygomorphic flower with perianth consisting of a well developed flag partially enveloping two wings which in turn partially envelop a keel.	None	
Floret flower shape	Tiny, individual flower within a dense inflorescence, such as a grass flower in a spikelet, or a disc or ray floret in a (Asteraceae) flowerhead.	Brickell (2003)	
Fountain	Shoots spread centrally and laterally from a short main stem or central point close to substrate level, with the shoots recurving and either carried aurally or touching the substrate.	None	
Fruticose	Shrubby in habit, as in the thalli of certain lichens (e.g. <i>Usnea</i> species)	Allaby (1992)	
Frutescent	Having the characters of a shrub.	Retief & Hermann (1997)	
Geophyte	Perennial (including biennial) herbaceous plants with periodic shoot reduction; Periodic reduction of the complete shoot system to storage organs that are imbedded in the soil.	Ellenberg & Mueller-Dombois (1974)	
Gullet flower shape	As is common in the Scrophulariaceae; a zygomorphic, tubular flower with perianth segments of unequal length and recurved at the apex, producing a "lipped" form.	None	
Head (capitulum) inflorescence type	Inflorescence consisting of a central group of tiny disc-florets, usually ringed by ray-florets, borne on a compressed axis or stem.	Brickell (2003)	
Heart-shaped leaf	Roughly ovate leaves, pointed at the tip, and with a deep cleft at the centre of a rounded base	Brickell (2003)	
Hemicryptophyte	Perennial (including biennial) herbaceous plants with periodic shoot reduction; periodic shoot reduction to a remnant shoot system that lies relatively flat on the ground surface.	Ellenberg & Mueller-Dombois (1974)	
Herbaceous	Like a herb; non-woody, soft and leafy, with a stem that dies back to the ground each year.	Van Wyk & Malan (1998)	












Hydra	Shoots are always carried above substrate level by a prominent main stem that ramifies to several orders. First order ramification usually occurs from a central point at the top of the main stem.	None	
Inverse lance-shaped leaf	Leaves broadest above the centre, tapering to a narrow basal point; length is 3-6 times the width.	Brickell (2003)	
Kidney-shaped leaf	Roughly quarter-moon-shaped with blunt ends (on a leaf, the stalk is attached at the notched centre of the concave margin).	Brickell (2003)	
Krummholz	Creeping phanerophytes, whose stems or branches are bowed down, but whose height exceeds 50 cm vertically from the ground.	Ellenberg & Mueller-Dombois (1974)	
Lance-shaped leaf shape	Leaves broadest below the centre, tapering to a narrow tip; Length is 3-6 times the width.	Brickell (2003)	
Liana (liane)	Long and slender shoots for climbing emanate from a central axis. Shoots may be straight to variously folded in the absence of a supporting structure and the overall architecture may assume the shape of a supporting structure. The plants remains rooted in the soil.	None	
Linear leaf shape	Long and narrow leaves, with parallel margins, or almost so; length is 12 or more times the width.	Brickell (2003)	
Lobed leaf margin	A large projection of the margin, generally one that measures at least a third of the distance from the leaf's midrib to its outer edge.	Barnard <i>et al.</i> (2004)	
Malacophyllous	Soft leaves that collapse immediately when held over hot water vapour	Ellenberg & Mueller-Dombois (1974)	
Oblong leaf shape	Leaves having more or less parallel margins and with length about 2-8 times the width; the base and apex may be rounded or obtuse, not necessarily squared-off.	Barnard <i>et al.</i> (2004)	
Obovate leaf shape	Leaves with a flat form, egg-shaped in outline and broadest above the middle; length is 1.5-2 times the width.	Brickell (2003)	
Oval leaf shape	Broadly elliptic leaves, rounded at both ends, with slightly parallel sides in the middle; length is 1.5-2 times the width.	Brickell (2003)	
Ovate leaf shape	Leaves with a flat form, egg-shaped in outline and broadest below the middle; length is 1.5 times the width. The apex is more or less acute and the base rounded.	Brickell (2003); Barnard <i>et al.</i> (2004)	
Phanerophyte	Plants that grow taller than 50 cm, or whose shoots do not die back periodically to that height limit.	Ellenberg & Mueller-Dombois (1974)	
Palmatifid leaf margin	Used to describe a leaf that is deeply divided into 3-7, sometimes more, lobes. It is distinct from a palmate leaf in that the division does not extend to the basal point, so remain lobes, rather than leaflets	Brickell (2003)	
Panicle inflorescence type	A branched raceme.	Brickell (2003)	
Pinnatifid leaf margin	Applied to leaves that are pinnately divided, but not all the way down to the rachis.	Allaby (1992)	
Procumbent	Shoots spread horizontally and appressed against the substrate from a central axis, with flowers or inflorescences borne on individual shoots. Shoots do not root and are not specifically adapted from climbing.	None	



Prostrate	See procumbent	None	
Pulvinate	Cushion form	Ellenberg & Mueller-Dombois (1974)	
Raceme inflorescence type	An unbranched inflorescence consisting of an elongated stem or rachis bearing a succession of stalked flowers, the youngest at the tip.	Barnard <i>et al.</i> (2004)	
Raised basal rosette	Leaves emanating basally and spreading obliquely or laterally from a central, lateral stem, close to or on the substrate, around a central axis from which a scape often emanates.	None	
Reptant	See stoloniferous	None	
Revolute leaf margin	Leaf margins rolled downward and inward, tightly curled.	Barnard <i>et al.</i> (2004)	
Rhizomatous	A rootstock or root-like stem prostrate on or under the ground, sending rootlets downwards and branches, leaves or flowering shoots upwards. Always distinguished from a true root by the presence of buds, leaves and scales.	Retief & Hermann (1997)	
Rhizomatous shrub	Shoots emanate close to substrate level from one to several main stems, at lateral, oblique and horizontal angles with ramification of several orders. Shoots are randomly packed to form a dense aggregation. Underground root-like stems produce new shoots and roots at intervals leading to horizontal spread.	None	
Rootstock	The base of a stem from which the roots emerge. The underground overwintering stem bases of many herbaceous perennials are termed rootstocks.	Barnard <i>et al.</i> (2004)	
Rosette	Rosette plant = A plant (e.g. <i>Bellis perennis</i> , daisy) whose leaves are spread in a horizontal plane from a short, central, mostly lateral stem axis at ground level.	Allaby (1992)	
Rosulate	With leaves in a circle or rosette.	Leistner (2000)	
Rounded leaf shape	Leaves that are roughly or fully circular in outline.	Brickell (2003)	
Runner	Any horizontal spreading stem, usually fairly slender and fast-growing, capable of rooting where it touches the soil and sending up more erect shoots at intervals. Much the same as stolon.	Barnard <i>et al.</i> (2004)	
Scandent	Shoots sprawl horizontally and at substrate level from a central axis, with flowers or inflorescences borne on individual shoots. Flexible shoots do not root and may spread loosely over adjacent supporting structures or other plants without specific adaptations for climbing.	None	
Scape	A leafless pedicel or peduncle arising from ground level.	Allaby (1992); Retief & Hermann (1997)	
Scapose	Bearing one or more flowers on a scape; in the form of a scape.	Retief & Hermann (1997); Leistner (2000)	
Semi-circle shrub	Shoots emanate close to substrate level from one to several main stems, at lateral, oblique and horizontal angles with ramification of several orders. Shoots are randomly packed to form a dense aggregation. Shoots are carried aerially but often touch the substrate.	None	
Serrate leaf margin	Used to describe a finely toothed margin, usually of a leaf, with the teeth slightly curved as in a saw blade.	Brickell (2003)	
Shrub	Shoots emanate close to substrate level from one to several main stems, at various angles with ramification of several orders. Shoots are randomly packed to form a dense aggregation.	None	
Solitary flower type	A flower borne singly, not grouped in an inflorescence.	Barnard <i>et al.</i> (2004)	



Spike inflorescence type	Inflorescence in which stalkless flowers are arranged on an unbranched axis.	Brickell (2003)	
Spoon-shaped leaf	A leaf narrow at the base, gradually broadening into a blunt, rounded tip.	Brickell (2003)	
Strap-shaped leaf shape	A leaf that is narrow, with straight or curving sides; length is 6 (or more) times the width.	Brickell (2003)	
Stoloniferous	Having stolons; trailing over the surface and rooting at the nodes.	Leistner (2000)	
Sub-caespitose tuft	Shoots are loosely aggregated basally, unidirectionally and/or at oblique angles, to form a less dense tuft with growth points at the substrate level. Shoots do not emanate from a central point.	None	
Suffrutescent	Suffruticose chamaephyte = aerial shoots die back partially at the onset of unfavourable conditions and buds arise on the lower persistent stem portions.	Leistner (2000)	
Suffruticose	Woody base with herbaceous branch ends.	Ellenberg & Mueller-Dombois (1974)	
Suffrutex	A perennial plant which is slightly woody only at the base.	Retief & Hermann (1997); Leistner (2000)	
Therophyte	Annuals. Plants whose shoot and root system die after seed production and which complete their whole life cycle within one year.	Ellenberg & Mueller-Dombois (1974)	
Thyrse inflorescence type	A panicle with the secondary and ultimate axes cymose, i.e. the main axis is indeterminate and the lateral branches are determinate in their growth	Leistner (2000)	
Tree	(syn. Hydra) Shoots are always carried above substrate level by a prominent main stem that ramifies to several orders. First order ramification usually occurs from a central point at the top of the main stem.	None	
Triangular leaf shape	A triangular leaf with three sides of approximately equal length and attached to the stem at a point midway along one side.	Brickell (2003)	
Trumpet flower shape	Refers to a flower with a long, narrow tube, flaring at the throat into corolla lobes, which are usually arched backwards.	Brickell (2003)	
Tube flower shape	A flower with perianth segments fully or partially fused to form a hollow tube.	Brickell (2003)	
Tuft	Clump, cluster	Retief & Hermann (1997); Leistner (2000)	
Twiner	A climber that gains its support from other plants by its stem twining spirally around their stems. Any one species of twiner will (with few exceptions) spiral either in a clockwise or an anticlockwise direction (viewed from above).	Barnard <i>et al.</i> (2004)	
Umbel inflorescence type	Flat or round-topped inflorescence in which numerous stalked flowers are terminally borne from a single point	Brickell (2003)	
Undulate leaf margin	Wavy leaf margins, with the undulations at right angles to the plane of the leaf.	Barnard <i>et al.</i> (2004)	