

Vegetation on and adjacent to mesas in the Nama-karoo, South Africa – characteristics and comparisons

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Declaration

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

Summary

Arid lands comprise some 47.2 % of the world's land surface. Between 32 % and 35 % of these drylands are subject to some form of desertification and land degradation. South Africa is an arid country with water being a major limiting resource. The Nama-Karoo biome is an extensive tract of semi-arid vegetation comprising some 22.7 % of South Africa, characterised by low rainfall and high temperatures. Grazing is the most common form of land use in the country, and particularly in this biome. Aridity and grazing are two factors that make large areas of South Africa (including the Nama-karoo) susceptible to land degradation. The Nama-Karoo biome has been neglected in past research and is an understudied part of South Africa's vegetation.

This study is a component of a bigger umbrella project entitled "Restoration of degraded Nama-karoo rangelands: the role of conservation islands". The aim of this project was to assess the role played by isolated hills and mountains (mesas, inselbergs, etc.) in conserving the remnant biological diversity of the Nama-karoo rangelands of Namibia and South Africa. Vegetation composition, seed banks, seedling recruitment, pollination and grazing patterns and intensity on and off isolated mesas in the eastern parts of the Nama-karoo were investigated in the South African component of this project.

I report on patterns of 1) plant species diversity and 2) plant communities across the Middelburg District, Eastern Cape, South Africa. Three isolated mesas (Tafelberg, Folminkskop and Buffelskop) and their surrounding plains were selected for this study. Permanent plots were established in broad transects extending from the plains to south-eastern slopes, plateaux, north-western slopes and north-western plains of each mesa. Plots were 25 m² in size, and ten 1 m² blocks within the 25 m² plot were randomly selected and sampled. Species composition was recorded and cover values determined for all plants in every subplot.

In the eastern Nama-karoo mesas were not found to be higher in Alpha Diversity than their surrounding plains. Plains habitats were mostly equally as diverse as mesa habitats,

with some plains habitats being higher in diversity than mesa habitats. Greater differences between mesas and their surroundings were found in a parallel study in the northern parts of the Nama-karoo in Namibia, indicating that mesas are more distinct islands of diversity with an increase in aridity. In the Middelburg District, a greater presence of woody phanerophytes occurred on mesa habitats in comparison with plains habitats, a possible result of the more moist microhabitats on mesas. Cooler, moister conditions on the south-eastern slopes of the mesas led to higher Alpha Diversity there in comparison with the warmer and drier north-western slopes, a phenomenon commonly found in arid areas. In terms of Alpha Diversity, the largest mesa sampled, Tafelberg (450 m above surroundings), was not significantly more diverse than the two smaller mesas (Folminkskop and Buffelskop both being 200 m above surroundings).

Tafelberg and Buffelskop were equally high in Beta Diversity, with Folminkskop being much less diverse. Increased Beta Diversity for Tafelberg was explained by the increased size of the mesa (providing a more diverse microhabitat) relative to Folminkskop, which has the same shape and geology but is much smaller in size. High Beta Diversity values for Buffelskop were explained by the presence of degraded communities on the north-western slopes and plains, while the south-eastern slopes were some of the most diverse habitats sampled in the landscape. Mesas and plains shared few species. Proportionally fewer species were shared between the plateau and slopes of the larger Tafelberg in comparison with the smaller two mesas. Isolation of the plateau could possibly become more distinct with an increase in size of the mesa. However, Tafelberg had more species in common with the surrounding plains than did the smaller mesas. It is suggested that bigger mesas support a more diverse array of microhabitats enabling plains species to occupy selective sites on the slopes of the mesa.

Average Shannon-Wiener Alpha Diversity Indices for Middelburg were higher than that of the Nama-karoo in general. This could be explained by the higher precipitation in the eastern parts of the Nama-karoo relative to the rest. Diversity in Middelburg compared favourably with that in other arid lands of North America and Australia and was found to

be similar in patterns and determinants of diversity compared to arid lands such as those of the New World.

Regarding plant community composition, mesas were found to be distinctly different from their surrounding plains, with no shared communities between mesas and plains. The distribution of communities across the landscape was mainly attributed to a soil-moisture gradient. Mesas, compared to plains, have shallower, rockier soils coupled with very little run-off and naturally higher precipitation due to elevation. This results in a more mesic habitat. Plains, compared with mesas, have little rock cover, high percentages of bare soil and higher run-off rates than mesas, resulting in a more xeric habitat. Habitat differences such as these probably existed before the impact of domestic livestock but overgrazing has probably exacerbated the differences. The dominance structure of plant communities on the plains has probably changed in favour of toxic, spinescent or unpalatable plant species due to selective grazing by livestock. For the two dolerite-capped mesas (Tafelberg and Folminkskop) aspect and the expected cooler, moister conditions on south-eastern slopes as factors determining community composition were overridden by soil type and associated nutrient status. On Buffelskop (sandstone mesa), aspect and slope overrode soil type and associated nutrient status as determinants of community compositions.

The potential to use mesas as a source of seeds and propagules to restore degraded plains habitats is low. Approximately 28 % of species were shared between mesas and their surroundings, and not all of these species could be regarded as good colonisers. Generalist, palatable species occurring across the landscape, such as *Eragrostis obtusa*, *Felicia muricata*, *F. ovata*, *Fingerhuthia africana*, *Jamesbrittenia tysonii*, *Limeum aethiopicum*, *Pentzia incana* and *Selago albida* could have some potential for future restoration attempts.

Mesas are distinct in composition and can be regarded as islands of one vegetation type (mesas) in a sea of a different vegetation type (plains). Mesa habitats are not generally used for grazing by livestock, due to their general inaccessibility, and are not threatened

by development. Plant communities in the Middelburg area were very similar in composition to communities identified in other parts of the Nama-karoo.

Results from this study suggest that the plains are at present more degraded than the mesa habitats, but it is impossible to conclude whether or not these rangelands have stabilised given current stocking rates and climatic conditions.

The Braun-Blanquet classification system proved an effective method to describe plant communities in the semi-arid Nama-karoo. All the plots used during the duration of the study were marked by metal stakes and are therefore of a permanent nature, so that they can be resampled in future. This might possibly shed some light on questions related to resilience, stability and degradation of the karoo. Restoring rangeland in the future is an important option, however, few farmers would, in the short term, be able to afford costly restoration techniques. It is recommended that farmers inspect the condition of their veld on a regular basis, and adjust stocking rates accordingly. Veld should be rested on a regular basis, and assessment should precede the movement of stock to a camp. Most farmers plough denuded areas of veld to encourage restoration, and it is recommended that this practice be combined with reseedling, followed by rest during and shortly after germination of the seed.

Opsomming

Ariede areas beslaan tans 47 % van die aarde se land oppervlak. Tussen 32 % en 35 % van hierdie areas is onderworpe aan een of ander vorm van land degradasie. Die Nama-Karoo bioom is 'n ekstensiewe semi-ariëde area wat naastenby 47 % van Suid-Afrika beslaan. Die karoos word gekenmerk deur hoë temperature en lae reënval. Suid-Afrika is 'n ariede land en water is 'n beperkende faktor. Weiding is die algemeenste boerderypraktyk, en meer so in ariede areas soos bv. in die karoos. Die droë klimaat en hoë voorkoms van weiding as boerderypraktyk maak ekstensiewe areas (insluitende die karoos) van Suid-Afrika vatbaar vir land degradasie.

Hierdie studie is deel van 'n breër projek genaamd: "Restorasie van gedegradeerde Nama-karoo veld: Die rol van bewaringseilande". Die doel van hierdie projek was om die rol te bepaal van ge-isoleerde koppies en berge (mesas, inselberge, ens.) in die bewaring van biologiese diversiteit in die Nama-karoo van Suid-Afrika en Namibië. Plantegroeisamestelling, saadbanke, saailing oorlewing, bestuiwing en weidingsintensiteit/patrone op koppies en hulle omringende vlaktes in die oostelike dele van die Nama-karoo is ondersoek in die Suid-Afrikaanse komponent van die studie.

Ek rapporteer oor patrone van 1) plant diversiteit en 2) plantegroeigemeenskappe in die Middelburg Distrik, Oos-Kaap, Suid-Afrika. Drie ge-isoleerde koppies (Tafelberg, Folminkskop en Buffelskop) en hulle omliggende vlaktes is geselekteer vir die doel van die studie. Permanente persele is uitgelê in 'n breë lyn vanaf die suid-oostelike vlaktes na die suid-oostelike hang, oor die plato's, noord-westelike hange en noord-westelike vlaktes vir al drie koppies. Persele was 25 m² in grootte, waarvan tien 1 m² sub-persele geselekteer is binne die groter 25 m² blok. Spesies samestelling en bedekkingswaardes is bepaal vir alle plante in al die sub-persele.

Mesas was nie hoër in Alpha Diversiteit as hulle omringende vlaktes nie. Vlaktes was meestal net so hoog in diversiteit as die mesas, en somtyds selfs hoër. Groter verskille in

diversiteit is gevind in 'n parallele studie in die noordelike dele van die Nama-karoo in Namibië. Dit dui aan dat mesas moontlik meer definitiewe eilande van diversiteit is in droër gebiede. Meer houtagtige fanerofiete het voorgekom op die mesas in vergelyking met die omliggende vlaktes, 'n moontlike gevolg van 'n natter habitat op die mesas. Suid-oostelike hange was hoër in alfa-diversiteit in vergelyking met noord-westelike hange. Dit is toegeskryf aan die koeler, natter mikrohabitat van die suid-oostelike hange. Die groter mesa (Tafelberg – 450 m bo die vlakte), was nie meer divers as die twee kleiner mesas nie (Folminkskop en Buffelskop is sowat 200 m bo die vlakte).

Tafelberg en Buffelskop was ewe hoog in Beta Diversiteit, terwyl Folminkskop heelwat laer was. Hoër Beta Diversiteit vir Tafelberg kan verklaar word deur die groter oppervlak en hoogte van die mesa (voorsien 'n meer diverse mikrohabitat) in vergelyking met Folminkskop. Folminkskop het dieselfde vorm en geologiese geskiedenis as Tafelberg, maar is veel kleiner. Buffelskop was hoog in Beta Diversiteit as gevolg van 'n gedegradeerde gemeenskap op die noord-westelike hang en vlaktes, terwyl die suid-oostelike hang baie hoog was in diversiteit. Min spesies kom op beide mesas en vlaktes voor. Minder spesies is gedeel deur die plato en hange van Tafelberg in vergelyking met die plato's en hange van Folminkskop en Buffelskop. Isolasië van die plato kan moontlik hoër wees in groter mesas. Tafelberg (slegs mesa) het meer spesies in gemeen met sy omliggende vlakte as die ander twee mesas. Groter mesas soos Tafelberg kan moontlik 'n meer diverse spektrum van mikrohabitate bevat, wat sekere vlakte spesies in staat stel om te oorleef op mesa hange.

Gemiddelde alfa diversiteit vir die Middelburg Distrik was hoër as die van die res van die karoo. Dit kan verklaar word deur die hoër reënval in die oostelike dele van die karoo relatief tot die meer westelike dele. Diversiteit in Middelburg vergelyk goed met die van ander ariede lande in Noord-Amerika en Australië, terwyl patrone en faktore wat diversiteit bepaal soortgelyk was aan die van gemeenskappe in ariede lande van die Nuwe Wêreld.

Mesas en vlaktes het drasties verskil in die samestelling van hulle onderskeie plantegroiegemeenskappe, alhoewel hulle soortgelyk was in diversiteit. Geen plantegroiegemeenskappe het voorgekom op beide mesas en vlaktes nie (gedeelde plantegroiegemeenskappe). Die verspreiding van plantegroiegemeenskappe oor die landskap was toegeskryf aan 'n grond-water gradient. Mesas het, oor die algemeen, vlakker, meer rotsagtige grond en 'n hoër reënval met minder afloop as vlaktes. Vlaktes het minder rotse, 'n hoër persentasies kaal grond en vinniger afloop tempo's na reën as mesas. Hierdie faktore het tot gevolg dat mesas 'n natter habitat verteenwoordig in vergelyking met die meer ariede vlaktes. Habitatsverskille soos dié het heel moontlik klaar bestaan voor die aankoms van vee, maar oorbeweiding het die verskille in habitat tussen mesas en vlaktes groter gemaak. Selektiewe beweiding deur vee het waarskynlik tot gevolg gehad dat plante wat giftig, doringagtig of onsmaklik is, toegeneem het in plantegroiegemeenskappe, ten koste van meer smaaklike spesies.

Grondtipe en grondsamenstelling het aspek en verwagte koeler kondisies op die suid-oostelike hange onderdruk as bepalende faktore vir plantegroiegemeenskap samestelling op Tafelberg en Folminkskop (beide bedek met 'n doleriet laag). Aspek en steilte van die hange het grondtipe en grondsamenstelling onderdruk as bepalende faktore vir plantegroiegemeenskappe op Buffelskop.

Die potensiaal om mesas te gebruik as bronne van saad vir die rehabilitasie van die vlaktes was laag. Mesas en hulle omliggende vlaktes het naastebly 28 % van spesies in gemeen gehad, maar nie al hierdie spesies was goeie koloniseerders nie. Sekere smaaklike plante wat op beide mesas en vlaktes voorgekom het, kan potensiaal hê vir toekomstige restorasie doeleindes, bv. *Eragrostis obtusa*, *Felicia muricata*, *F. ovata*, *Fingerhuthia Africana*, *Jamesbrittenia tysonii*, *Limeum aethiopicum*, *Pentzia incana* en *Selago albida*.

Mesas is uniek in samestelling en kan beskou word as een plantegroeitipe in 'n see van 'n ander tipe (vlaktes). Mesas word nie oor die algemeen bewei nie (as gevolg van hulle steil hange en bergagtigheid) en word gevolglik nie bedreig deur huidige ontwikkeling

nie. Plantegroei-gemeenskappe in Middelburg is soortgelyk aan die van ander dele van die Nama-Karoo bioom.

Resultate van die studie dui aan dat die vlaktes huidiglik meer gedegradeer is as mesas, maar dit is onbekend of die veld gestabiliseer het of steeds besig is om verder te degradeer in huidige weidings- en klimaatskondisies.

Die Braun-Blanquet klassifikasiemetode is effektief vir die beskrywing van plantegroei-gemeenskappe in ariede areas. Al die persele in die studie area is gemerk met metaal paaltjies en is dus permanent. Dit maak dit moontlik om in die toekoms die persele weer te ondersoek. 'n Langtermyn datastel kan moontlik lig werp op die stabiliteit en degradasie van karoo veld. Restorasie van veld is 'n moontlikheid vir die toekoms, maar min boere kan duur restorasie metodes bekostig in die kort termyn. Boere moet hulle lande gereeld ondersoek en drakrag aanpas by die kondisie van die veld. Baie boere ploeg kaal kolle in die veld op 'n gereelde basis, en daar word voorgestel dat die praktyk gekombineer word met die saai van geskikte saad, gevolg deur 'n rusperiode tydens en na ontkieming daarvan.

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1. General introduction and literature review

South Africa is an arid land with water a major limiting resource (Hoffman & Ashwell 2001). Grazing is the most common form of land use in the country, especially in the more arid regions (Hoffman & Ashwell 2001). A combination of these two factors make large parts of South Africa susceptible to land degradation. Land degradation has been a topic of discussion for many years among South Africa's conservationists (Dean *et al.* 1995a; Hoffman *et al.* 1999) and has become a much-debated topic over the last 10 years (Hoffman & Cowling 1990b; Bond *et al.* 1994; Bousman & Scott 1994).

The primary aim of this thesis was to investigate major patterns of diversity across the landscape and to identify plant communities in relation to landscape features in the eastern parts of the Nama-karoo biome (see section 1.1, Size and Borders), an arid vegetation type in South Africa. This chapter guides the reader through the history, reasons and potential reversibility of land degradation in South Africa. It also gives the reader an understanding of the effect of landforms on the distribution of plants in arid zones, and explains how landforms can play a role in the frequency and pattern of grazing. Lastly the chapter discusses relevant research objectives and key questions regarding this study.

1.1 Size and Borders

The Karoo-Namib Region of southern Africa, as defined by Werger (1978), extends from the coastal mountain ranges parallel to the Indian Ocean in South Africa to the southern parts of Angola. In the south it covers an area wider than 1 000 km from the Atlantic coast to about 26° E, while it becomes much narrower northwards until it tapers out in Angola (Werger 1978). This phytochorion has since been divided into a desert biome, succulent karoo biome and Nama-karoo biome (Rutherford & Westfall 1986) (Fig. 1.1). The Nama-karoo biome is much bigger than the other two and covers an area of 607 235 km² (22.7 % of southern Africa), second only in size to the savanna biome (Rutherford 1997). This biome is bordered by the savanna, desert, succulent karoo, grassland and fynbos biomes (Rutherford & Westfall 1986).

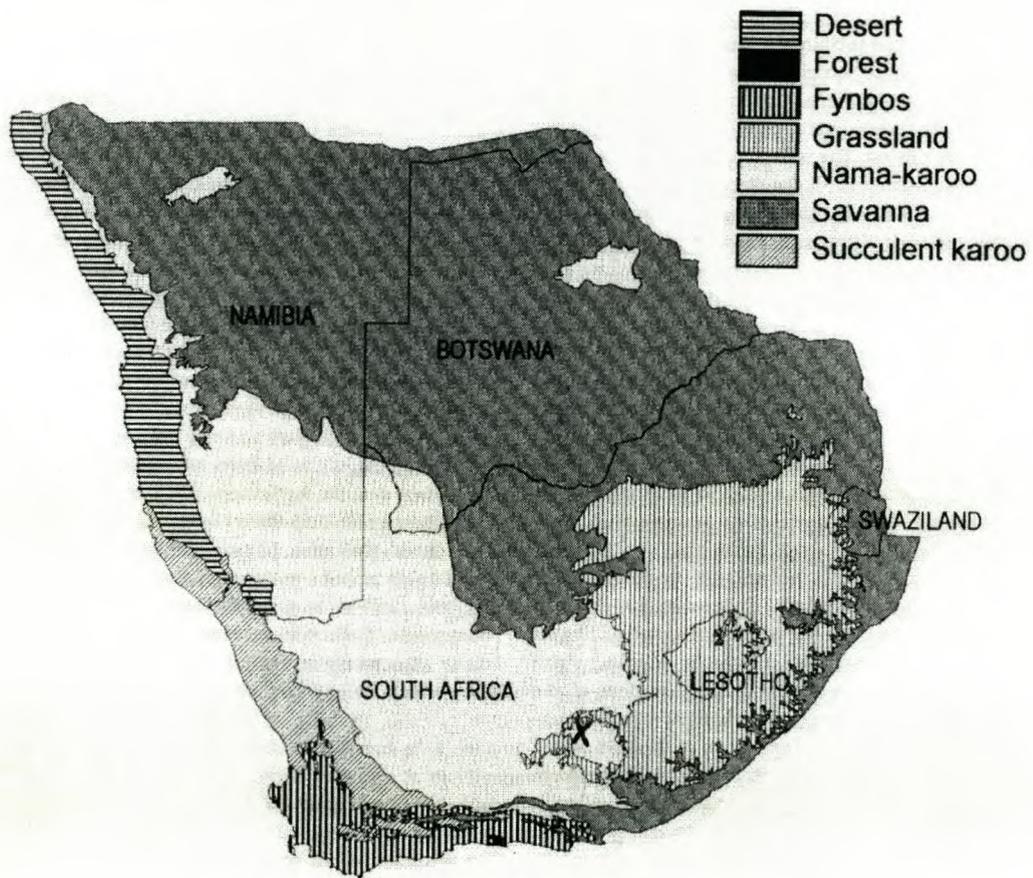


Fig. 1.1 Location of Middelburg (study region) relative to the biomes of Southern Africa. Modified from Rutherford (1997). The 'x' on the map indicates the position of Middelburg.

1.2 Landuse and management

The Nama-karoo biome is used extensively for stock production (Roux *et al.* 1981; Cowling 1986; Rutherford & Westfall 1986), with 80 % of the karoo currently belonging to private owners (mainly sheep and goat farming) (Hoffman *et al.* 1999). The main source of fodder for these animals is the natural karoo vegetation (Roux *et al.* 1981; Cowling 1986). Several authors have linked grazing by livestock in South Africa and specifically in the karoo to severe veld deterioration and vegetation change (Potts 1923; Van Reenen 1923; Kanthack 1930; Tidmarsh 1948; Acocks 1955; Roux *et al.* 1981; Roux & Vorster 1983; Roux & Theron 1986).

1.3 Problems facing arid lands

1.3.1 Some definitions

The term desertification was first used by Aubreville (Aubreville 1949 in Grainger 1990). It was originally used to refer to a process of ecological degradation that started with deforestation and ended with deserts (Aubreville 1949 in Grainger 1990). Today there are many definitions of the word, as are discussed in reviews by Grainger (1990), Thomas & Middleton (1994), and Zha & Gao (1997). Desertification was defined by the United Nations Conference on Desertification as “the diminution or destruction of the biological potential of land that can ultimately lead to desert-like conditions” (United Nations 1977). This definition was later further defined at the UN Conference on Environment and Development in 1992 as being: “land degradation in arid, semi-arid and dry sub-humid areas resulting from various factors including climate variation and human activities” (UNCED 1992).

Emotive connotations of deserts advancing over productive land are often inappropriate (Verstraete 1986) and the term dryland degradation or land degradation might be a more accurate description of reality (Hellden 1991; Le Houerou 1996) unless it is clear that degradation will lead to the creation of desert like conditions (Hellden 1991).

1.3.2 Degradation – an international perspective

Drylands represent a total of 47.2 % of the world’s surface (Le Houerou 1996). Between 32 % and 35 % of these drylands are subject to some form of desertification

(Hellden 1991, Le Houerou 1996). The main causes cited are overgrazing by livestock (Thomas & Middleton 1994; Grainger 1990; Zha & Gao; Fredrickson *et al.* 1998; Kasusya 1998; Khresat *et al.* 1998), drought (Kasusya 1998), vegetation removal (Grainger 1990; Thomas & Middleton 1994; Zha & Gao 1997; Albaladejo *et al.* 1998), improper farming practices, including overcultivation (Grainger 1990; Thomas & Middleton 1994; Khresat *et al.* 1998) and expansion of urban and rural activities at the cost of cultivatable land (Thomas & Middleton 1994; Khresat *et al.* 1998). Climate is mostly not the triggering factor but often enhances the human action (Le Houerou 1996). Desertification is caused by factors such as those mentioned, but physically takes place through loss of soil fertility and productivity, and erosion by wind and water (Le Houerou 1996; Khresat *et al.* 1998).

Several authors have in recent times questioned the extent and severity of desertification globally (Forse 1989; Hoffman & Cowling 1990b; Hellden 1991). Much of the focus of desertification has been on the edges of deserts, which expand and contract in relation to the amount of rainfall. Thirty five percent of the world is said to be at risk (Hellden 1991), but at least half of that area is hyper-arid by nature and much too dry for any kind of agriculture in any case (Warren & Agnew 1987). Hyperarid zones are not liable to undergo further desertification, but even if they are excluded some 16 % of the total land surface of the earth is still undergoing processes of desertification (Le Houerou 1996).

1.3.3 Veld deterioration and vegetation change in South Africa

Veld deterioration, desertification and vegetation change in the karoo has been a much debated and controversial issue among both farmers and conservationists in southern Africa.

1.3.3.1 Early history of veld deterioration in South Africa

Early reports of veld deterioration due to the influence of livestock in the karoo date back to as early as 1875 (Shaw 1875). Popular opinion in the early 1900's had it that large parts of the Union seemed to be drying up, and conditions then seemed to be more arid than those reported by early travellers and explorers in the 1700's and 1800's. These early travellers, such as James Backhouse in 1844, described the karoo as a grassy region with abundant and varied game, with Springboks occurring in herds

numbering thousands (Skead 1987). The Drought Investigation Commission was appointed in September 1920 to investigate the extent of and associated reasons and problems of the then proposed drying up of the Union (Anon. 1923). No proof could be found for a reduction in the amount of rainfall compared to previous decades (Anon. 1923). Vegetation deterioration was instead found to be caused by overgrazing, overstocking, herding, kraaling and an insufficient number of drinking places (Anon. 1923). Removal of the vegetation cover in turn led to erosion and a reduction of water penetrating the soil, resulting in a drying up of the Union (Anon. 1923). Overgrazing also reduced the number of palatable perennials and increased the number of annuals and plants useless for grazing (Anon. 1923). Overall productivity (people and small-stock) of the Cape Midlands is said to have decreased since 1904, the result of a decrease in carrying capacity of the veld as brought about by overstocking, overgrazing and erosion (Anon. 1923).

Thoughts on veld deterioration, desertification and vegetation change in South Africa from 1923-1948 were strongly influenced by the report of the Drought Investigation Commission. Several papers (Potts 1923; Van Reenen 1923; Kanthack 1930; Hall 1934) addressing veld deterioration, overgrazing and erosion confirm, expand on and refer to the findings of the Drought Investigation Commission. Kanthack (1930) also states that deterioration at its worst can be seen in the semi-arid regions of the country such as the karoo.

1.3.3.2 Veld deterioration in South Africa: 1948-1990

Much of the literature from 1948 onwards focuses specifically on degradation of natural veld in the karoo. The idea of a spreading of karoo vegetation at the expense of grassveld was first expressed by Tidmarsh (1948), and later repeated by Acocks (1953)(also see Acocks 1988). The karoo was said to be spreading at the expense of sweet grassveld in a northerly and easterly direction (Tidmarsh 1948; Acocks 1953), at an annual rate of 1.5 miles (2.4 km) a year in the easterly direction (Tidmarsh 1948). Continuous selective grazing was said to cause a change in the species composition of veld as the more palatable species were being over utilized by domestic stock, so that an invasion was sometimes also referred to as an increase in the cover of some species and not necessarily to one vegetation type invading another (Acocks 1953). Continuous selective grazing, together with incompatible and abusive

farming practices such as overgrazing, burning, etc. (Tidmarsh 1948), were thought to bring about a reduction in plant cover, followed by an increased loss of water by run-off, erosion, desiccation and depletion (Tidmarsh 1948; Acocks 1953). Erosion in turn reduced the depth and quality of the soil and made recovery of the vegetation slow. Increased run-off also led to erosion and silting up of rivers. Grasses were said to be almost eaten out in the karoo and unpalatable shrubs to be on the increase, both the result of selective grazing (Acocks 1953). This replacement of semi-arid sweet grassveld by karoo shrubs was not seen as part of a successional sequence but as a straightforward invasion (Acocks 1955). Once grassveld was replaced by karoo shrubs, the shrubs were said to keep the soil in a condition that prevented grasses returning (Acocks 1955). Karoo pioneers were even reported to have penetrated to as far as east of the Drakenberg (Acocks 1953).

Acocks (1953) also reported on the invasion of the arid karoo into the upper central karoo, and the succulent karoo into the arid karoo and western mountain karoo. Areas to the west were reported to no longer have a permanent, unbroken vegetation cover, and only rarely a temporary cover (Acocks 1953). The false upper karoo supposedly represented the most spectacular of all vegetation changes in South Africa, and "the conversion of 51 800 square km of grassveld into eroded karoo can only be regarded as a national disaster" (Acocks 1953).

Roux & Vorster (1983) proposed five overlapping phases of degradation to have taken place in the karoo. Primary degradation is characterised by the rapid destruction of the original pristine vegetation, followed by primary denudation, re-vegetation, secondary degradation and the desertified phase. Most of the central and eastern karoo were said to be in the stage of secondary degradation, characterised by a relatively dense cover of less desirable and unpalatable mixed shrubs, interspersed by a relictual scattering of palatable and desirable species. Major changes in karoo vegetation include the replacement of a grass dominated vegetation by a shrub dominated vegetation, loss of perennial grass cover, an increase in cover of undesirable and woody species and an increase in pioneer species (Roux & Theron 1986). The primary cause of these changes in vegetation was attributed to the impact of the extensive small stock industry (Roux & Vorster 1983; Roux & Opperman

1986; Roux & Theron 1986) through the agent of selective grazing (Roux & Theron 1986).

1.3.3.3 Veld deterioration in South Africa: recent developments

Thoughts on desertification since 1953 have substantially been influenced by the ideas expressed by De Klerk (1947), Tidmarsh (1948) and specifically Acocks (1953). Much of the published work on veld deterioration and desertification after 1953 is either based on the assumption of an expanding karoo at the expense of other vegetation types or on further variations of the hypothesis. Research focusing specifically on the karoo has greatly increased over the last \pm 20 years, covering a wide range of topics, and some of this work has challenged the traditional ideas proposed by earlier authors.

It is clear that degradation has occurred in some areas of the karoo. There are a variety of reasons including the false impression that some farmers have that their ranches are in a better condition than they actually are. Also, tempting markets can motivate a farmer to stock at higher densities than normally recommended, subsidies by the state can keep stock on land that would otherwise not have been utilised in times of drought (although this state subsidy scheme fell away in \pm 1995), and inflated land prices that encourage farmers to farm on sub economic units in marginal areas (Milton & Dean 1995).

A decrease in ranch numbers and an increase in the average ranch size (Milton & Dean 1995) are evidence that productivity on rangelands in southern Africa has declined after 1950. This change in average ranch sizes was greater for the arid grasslands and shrublands of the Eastern, Northern and Western Cape Provinces (formerly the Cape Province), and the Free State Province (formerly the Oranje Free State), in comparison with the more mesic savanna vegetation of the Gauteng, Limpopo, North-West and Mpumalanga Provinces (formerly the Transvaal Province) and the KwaZulu/ Natal Province (formerly the Natal Province) (Milton & Dean 1995). Livestock numbers in the karoo have also shown a more significant decrease in numbers over the last 100 years compared with savanna (Milton & Dean 1995).

Despite evidence of some degradation in the karoo, the extent of and reasons for desertification or dryland degradation in southern Africa and specifically in the karoo has become a topic of controversy over the last 20 years. Hoffman & Cowling (1990b) warn that most of the publications on vegetation change have appeared during or shortly after extended droughts, such as those of The Drought Investigation Committee (Anon. 1923), Kanthack (1930), Hall (1934), De Klerk (1947), Tidmarsh (1948), Klintworth (1949), the Report of the Desert Encroachment Committee (Anon. 1951) and Acocks (1953). Evidence from travellers' accounts, photographic evidence and re-surveys of previous vegetation studies do not always support the generally accepted idea of a grassy eastern karoo before the onset of European settlers and on the contrary sometimes show an increase in perennial grass cover (Hoffman & Cowling 1990b). The picture of a grassy karoo before the introduction of European livestock and the steady expansion of the karoo into the productive grasslands to the north and east as portrayed by earlier authors (Tidmarsh 1948; Acocks 1953; Roux & Vorster 1983), is more complex than once thought to be (Hoffman & Cowling 1990b). Such an increase in grass cover could possibly be attributed to an increase in the amount of summer rainfall (Hoffman & Cowling 1990b). Studies done in the eastern karoo and southern Free State confirmed that grass/shrub ratio's respond to the ratio between summer/winter rain (Hoffman *et al.* 1990).

Bousman & Scott (1994) using pollen in hyrax dung middens found grasses to have been more abundant before arrival of European settlers in the Eastern Cape Province, but the shift from grasslands to karoo shrub dominance seems to have started well before the stock of the settlers could have altered the vegetation through overgrazing. Shifts from grass dominance to shrub dominance and back has been occurring since the late Pleistocene, although overgrazing probably contributed to the latest trend (Bousman & Scott 1994). Difficulties arise when the individual responses of vegetation to overgrazing and climate are investigated, although both probably contributed to the historic vegetation changes (Bousman & Scott 1994).

Soil organic matter was used to determine past vegetation pattern with respect to the historical distribution of C₄ grasslands and C₃ shrublands (Bond *et al.* 1994). Past vegetation patterns indicate a stable shrubland zone in the south and west, a broad transition zone with grasses and shrubs in the central karoo and a grassland zone north

and east of the Orange River. The grass zone has been invaded by shrubs in the more recent past (Bond *et al.* 1994). Grasses have probably declined under grazing pressure, but grasslands do not seem to have covered most of the karoo in historical times as is commonly believed. Land use and not climate seems to be responsible for the changes (Bond *et al.* 1994).

Bosch (1988) found that severe overgrazing in the long run, together with a relatively more arid environment due to the ineffectiveness of rainfall (low cover & exposure of the soil to erosive agents) leads to karoo shrub encroachment in the semi-arid grasslands of southern Africa. This represents an easterly encroachment of the karoo biome into the grassland biome.

Evidence for the invasion of “Noorsveld” (a 1-2 m high shrubland dominated by *Euphorbia coerulescens*, dotted with trees (Acocks 1953)) by karroid shrublands is also given by Hoffman & Cowling (1990a). Both these invasions were predicted by Acocks (1953). No significant evidence was however found that the karoo was invading river valleys at the expense of subtropical thicket, also predicted by Acocks (Hoffman & Cowling 1990a). Karoo shrubland is more resilient to heavy continuous grazing than subtropical thicket, since no significant changes seem to have occurred in karoo shrubland in response to heavy continuous grazing (Hoffman & Cowling 1990a).

Some rangelands in the eastern karoo show an increase in annual and perennial grasses, and an increase in perennial shrubs and stability in numbers of succulent dwarf shrubs in comparison with levels in 1950. These improvements in range condition are attributed to successful management by the grazier, and not to changes in rainfall seasonality (Palmer *et al.* 1990).

These often conflicting views can be summarised as mostly supporting three models (Dean *et al.* 1995b). De Klerk (1947), Tidmarsh (1948) and particularly Acocks (1953) supported the view of karoo expansion along a broad front at the expense of other vegetation types such as grasslands (Dean *et al.* 1995b). Another model suggests that expansion of the karoo has not occurred along a broad front but rather as the result of degraded patches in the landscape that can overlap, giving the whole

process a patchy appearance (Dean *et al.* 1995b). The third model recognises that there may well have been an expansion of the karoo into adjacent grasslands, but also recognises the dynamic nature of rangelands in that grasses could again become dominant given certain conditions (Dean *et al.* 1995b).

1.4 Reversibility, recovery and restoration

Vegetation degradation seems to commonly occur as a stepwise process with every step being more degraded than the previous one. Several names have been used to describe these various states of degradation, such as steps (Milton *et al.* 1994), domains of attraction (Bosch 1988), thresholds of drought resilience (Fuls & Bosch 1991) and different states (Milton & Hoffman 1994). Once these semi-arid and arid rangelands have reached a certain state of degradation it is unlikely that they will recover through the withdrawal of livestock alone (Fuls & Bosch 1991; Milton & Hoffman 1994). Severely overgrazed rangelands might only recover through active intervention such as soil reclamation and re-seeding, while less severely degraded vegetation might be able to improve by resting after key rain events and seed set coupled with rotational grazing at recommended stocking rates (Milton & Hoffman 1994).

Several problems are associated with the recovery of degraded rangelands. Semi-arid grasslands were found to be very sensitive to grazing after drought, and heavily grazed vegetation took longer to recover after drought than vegetation that was only lightly grazed (Danckwerts & Stuart-Hill 1988). Milton *et al.* (1995) also found recovery of karoo vegetation after a drought to be extremely slow, taking many years to reach the same carrying capacity it had before the drought. *Tripteris sinuatum* (DC) (a palatable shrub species, formerly *Osteospermum sinuatum* (DC) T. Norl.) seed production and recruitment in karoo shrublands was severely reduced in the presence of grazing (Milton 1992). Overgrazing was found to reduce the perennial vegetation cover in semi-arid grasslands, and vegetation on overgrazed patches often consisted mostly of annuals and pioneer grasses (Fuls 1992). Degraded patches also had severe crusting, reduced rainfall penetration and increased erosion. Such severely overgrazed patches often have difficulty in recovering due to lack of favourable microhabitats in which seed production, germination and seedling survivorship can be successful (Fuls 1992) or because soil loss and altered soil conditions prevent the

recruitment of perennial plants (Milton & Hoffman 1994). Inadequate seed production by defoliated plants and competition from established unpalatable plants can further reduce passive recovery of overgrazed rangeland (Milton & Hoffman 1994).

Restoration also becomes more costly in terms of loss of secondary productivity and energy spent at every step of the degradation process (Milton *et al.* 1994). Degraded rangelands do not earn a lot of money, so it is unlikely that the farmer would be able to afford to rest the farm for a year or more (Milton *et al.* 1994). Wealthy farmers are often the ones that can afford to invest in rehabilitation. Rangelands must be maintained at a “step one” level (Milton *et al.* 1994) (growth of forage plants could be restored by altering the grazing season/stocking intensity/animal type; no changes in secondary productivity, fauna, and soil) by livestock reduction in dry years (Milton *et al.* 1994).

1.5 Landforms and Mesas

1.5.1 Environmental gradients

Landforms can play an important role in the distribution of plants and animals by controlling environmental gradients of moisture and temperature (Swanson *et al.* 1988). Environmental factors are known to determine plant species richness and community composition, with different species occupying different positions along such an environmental gradient (Aronson & Shmida 1992).

The most important environmental variable controlling species richness and community composition in arid and semi-arid ecosystems is moisture availability (Hillel & Tadmor 1962; El-Ghareeb & Shabana 1990; Parker 1991; Bertiller *et al.* 1995; Beyer *et al.* 1998). Moisture availability is often not linked to precipitation *per se*, but rather to soil characteristics that have an indirect effect on the availability of water such as percentages of silt, clay, sand and gravel (El-Ghareeb & Shabana 1990; Parker 1991; Bertiller *et al.* 1995), profile depth (Bertiller *et al.* 1995), slope angle, variation in geological substrate (Parker 1991) and aspect (Parker 1991; Bertiller *et al.* 1995). Rocky slopes may, for instance, have an increased availability of water in comparison with plains and riverbeds because of rocks retarding runoff, preventing the formation of a soil crust, slowing down the rate of evaporation and increasing the

depth of moisture penetration (Hillel & Tadmor 1962). Landscapes can play an important role in the variation of water content in the soil, with uplands normally being wetter (Coronato & Bertiller 1996).

1.5.2 Other landform effects

Other landform effects include the effect of parent materials, the flow of organisms and propagules, and the frequency and pattern of agents such as fire, wind and grazing (Swanson *et al.* 1988). Landforms might indirectly control movement of animals and create patches of higher and lower grazing intensity due to features such as steep slopes/cliffs, lack of water on top, etc. Composition of vegetation might be altered through selective grazing by domestic herbivores in patches with higher grazing pressure, while patches with lower grazing pressure or no grazing might represent the original plant/animal life as it was before domestic herbivores were introduced. Vegetation composition on landforms can therefore potentially be different from that of the surroundings, with some landforms or parts of them representing a more relictual vegetation composition than the surrounding altered landscape. Interactions between various landform effects coupled with site history can be so complex that it might be impossible to tease out individual landform effects (Swanson *et al.* 1988).

1.5.3 Landform effects in the Nama-karoo

Flat topped mesas, hillocks and sharp ridges of doleritic origin are a general and important feature of Nama-karoo landscapes. These dolerite intrusions are of the same age as the lavas of the Drakensberg Group and occur scattered through beds of the Ecca and Beaufort Groups (Visser 1986). Dolerite is more resistant to weathering than the rest of the landscape and gives rise to a very uneven topography, showing as elevated landforms (Visser 1986).

Rubin & Palmer (1996) found floristic patterns in the central Nama-karoo to correlate with coarse environmental variables such as elevation, rainfall, substrate and land type. Most important in terms of contributing to biotic diversity was a moisture gradient extending from the high rainfall escarpment down to the relatively low rainfall flats. The distribution of different communities in the eastern parts of the Nama-karoo was also broadly correlated with a similar topographical/moisture gradient, where dwarf shrublands were gradually replaced by taller shrublands and

eventually by grasslands as the amount of precipitation increased (Palmer 1991). Rocky dykes and sills are associated with higher soil moisture, supporting mesic grasses and woody shrubs (Palmer & Hoffman 1997). Slope and aspect related differences are also reflected in the species composition and structure. Cooler southern slopes support taller shrubs than the warmer northern slopes, which in turn support shorter plants with dwarf shrubs dominating lower elevations and C₃ grasses dominating higher elevations (Palmer & Hoffman 1997).

1.6 Rationale for thesis

Mesas are a general feature of the karoo landscape. By default, the vegetation composition on these mesas is likely to differ from the surrounding flatlands in terms of species composition, density and cover. These differences can primarily be attributed to differences in habitat (soil and climate gradients associated with geology and altitude), but differences in grazing history and intensity might also play an important role.

Mesas generally have more rocks and less bare soil than surrounding flatlands. Increased rockiness, coupled with shallower soils and a high percentage cover of rocks in the soil profile, increase the available moisture on these mesas, in comparison with the flatlands. Slope and aspect combine to create cooler, wetter SE slopes in comparison with warmer, drier NW slopes. Mesas also have different temperature and rainfall fluctuations than flatlands. In essence, mesas can not only be regarded as potential islands in a sea of degraded flats, but also as patches of one habitat type surrounded by a relative homogenous matrix of another, completely different habitat type.

Some of these mesas have steep sides or are fenced off and are therefore not as accessible to livestock as are the surrounding plains. Plants that are continually grazed are at a potential disadvantage compared to less palatable plants due, for example, to an inability to produce and set seeds. Seed banks surrounding a mesa in the Middelburg District, eastern Cape, consisted primarily of ephemeral species, while seed banks on the less impacted mesa consisted of palatable and persistent grass and shrub species (Jones 2000). Vegetation composition in the long term might in this way be altered and unpalatable or spinescent plants will increase at the expense of

more palatable species. Most of the Nama-karoo has been used for extensive small-stock farming since approximately 200 years ago. Vegetation on these mesas might potentially be in a less degraded state than that of the surrounding plains, providing us with clues as to what the vegetation composition of the karoo used to be like 200-250 years ago.

In this study, vegetation on and adjacent to mesas was studied in the eastern parts of the Nama-karoo, Middelburg District (see Chapter 2, Study Area). Transects were sampled over the landscape starting on the south eastern flats of a mesa, and extending over the slopes and plateau of the mesa to the north western flats (see Chapter 3, Material and Methods). Three mesas and surrounding flats were studied in total. Sampling was plot-based at set distance intervals, with all plots being sampled for plant species diversity and cover values for all plants (see Chapter 3, Material and Methods).

1.7 Research objectives

- A) To investigate whether mesas in the karoo serve as islands of enriched biodiversity and a source of propagules to the surrounding degraded plains.
- B) To classify the vegetation using previous studies and vegetation analysis techniques.
- C) To investigate the differences between vegetation on the mesas to that on the surrounding flats in terms of species diversity, cover and composition.
- D) To compare the results of this study with other studies done both locally and internationally in terms of diversity, cover, dominant species and families.
- E) To add to the knowledge about the vegetation of the karoo as an understudied part of southern Africa (Hilton-Taylor & Moll 1986; Palmer & Hoffman 1997).

1.8 Key questions

Diversity (Chapter 4)

- 1) What is the composition of the vegetation in terms of total species numbers, dominant families and genera?
- 2) Are the mesas higher in floristic/habitat diversity than the surrounding landscape and are they therefore of special management/conservation value?
- 3) How do the three mesas differ from one another in terms of floristic diversity?

- 4) How similar/different are the plateaux, slopes and plains from each other for each of the mesas in terms of species shared?
- 5) How does plant diversity in Middelburg compare with diversity in other vegetation types?

Classification and composition (Chapter 5)

- 1) What plant communities can be identified across the landscape?
- 2) How do environmental variables such as aspect, slope, substrate, rock, cover, soil texture, nutrient availability, soil depth, moisture availability and altitude influence the composition and distribution of plant species across the landscape?
- 3) What plants occur on the mesas that do not occur on the flats and *vice versa*?
- 4) What is the potential of mesas for restoration?
- 5) Are mesas worthy of special conservation status?
- 6) How do plant communities in Middelburg compare to communities in the rest of the Nama-karoo biome?

The study area is described in detail in Chapter 2. Materials and Methods are expanded upon in Chapter 3. The questions raised above are addressed in Chapters 4 & 5. Final concluding remarks and management recommendations are provided in Chapter 6.

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2. Study area

2.1 Location of study area

The study was conducted in the Middelburg District, Eastern Cape Province (Fig. 1.1). The Middelburg District is situated in the eastern parts of the Nama-karoo biome (General Introduction – Chapter 1), with the border of the grassland biome less than 100 km to the east of Middelburg. This specific region has been the focus of much of the controversy on desertification and land degradation in South Africa (Hoffman & Cowling 1990). Some authors have proposed that the ratio between shrubs and grasses vary in response to fluctuations in summer rainfall (Hoffman *et al.* 1990), and that the widely accepted Acocksian view (Acocks 1953) of a grassy eastern karoo before the onset of European settlers might not necessarily be true (Hoffman & Cowling 1990; Bond *et al.* 1994; Bousman & Scott 1994).

2.2 Land use – historical and modern

Middelburg has a rich history in land use with some of the farms dating back to the early 1800's (Southey 1990). The farm Tafelberg Hall (now sub-divided into the farms Tafelberg Hall, Thorn Springs and The Mimosas) is thought to be one of the first fenced farms in South Africa (Southey 1990). The perimeter fence, which still remains in places, dates back to \pm 1880, and is a national monument. Productivity in this region has declined over the last 100 years based on a decrease in ranch numbers, coupled to an increase in the average ranch size (Milton & Dean 1995), even more so than in other vegetation types. Many farmers are not able to make a living on small farms that in the past were large enough to farm on, and today most farmers in the Middelburg District require farms in the vicinity of 3 000 ha (P MacEwan & T van der Walt, pers. comm.).

Modern land use in most of the district consists of commercial sheep farms, typical of most of the karoo (Roux *et al.* 1981; Cowling 1986; Rutherford & Westfall 1986). Cattle farming (Nguni cattle and others) in the district is on the increase, particularly in the neighbouring district of Graaff-Reinet.

2.3 Topography

This study extended over six commercial stock farms (Table 2.1). Topographically the area consists of many different landforms typical of the karoo, such as isolated mesas, low ridges, mountain ranges and extensive flatlands (Fig. 2.2). Three isolated mesas (Tafelberg, Folminkskop and Buffelskop) together with their surrounding plains were selected for the study. Two of these (Tafelberg and Folminkskop) had a resistant flat-topped dolerite cap, while the third mesa consisted mainly of sandstones and mudstones (Buffelskop).

Table 2.1 Approximate sizes and grid references of the farms where sampling occurred.

	Grid references (farmhouse)	Size (hectares)
Tafelberg Hall	31°29.2' E 25°12.0' S	2 400
Thorn Springs	31°38.8' E 25°11.3' S	2 600
The Mimosas	31°37.0' E 25°10.5' S	4 000
Greyville	31°33.6' E 25°9.1' S	3 700
Buffelskop	31°31.9' E 25°6.1' S	1 200
Buffelspoort	31°32.9' E 25°7.1' S	2 500

2.4 Effect of abiotic environment on vegetation composition and distribution

Vegetation composition and distribution is often influenced by the distribution, size and shape of different landforms (General Introduction – Chapter 1). Mesas such as those in the Middelburg District often differ from the surrounding flatlands in terms of environmental variables (Fig. 2.1). Mesas are moister, have shallower soils, have different parent materials, have distinct slopes and aspects, have different grazing histories and current land use and have a different soil nutrient status *etc.*, than the surrounding flatlands. Vegetation composition and distribution across the Middelburg landscape is potentially determined by the many gradients of moisture, temperature and nutrients that are associated with these different landforms in the district.

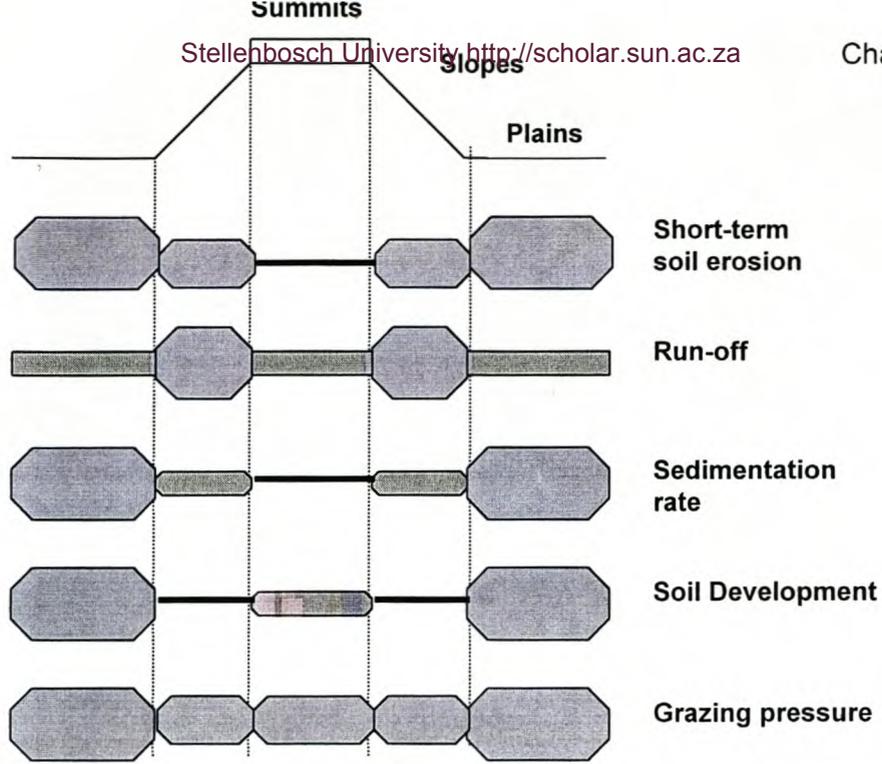


Fig. 2.1 Comparative environmental parameters for plateaux, slopes and plains habitats (modified from Burke *et al.* 2002).



Fig. 2.2 Topography of the study area showing the distribution of isolated mesas and other landforms across the landscape. The photograph was taken from the north-western plateau of Tafelberg Mesa. Spitskop is the complex in the foreground, with Folminkskop to the left and slightly more distant from the centre of the photograph. Buffelskop is on the left back immediately beyond Folminkskop.

2.5 Abiotic environment

2.5.1 Soils

Soils on the flats in the study area are described as weakly structured overlying hard rock (Ellis & Lambrechts 1986). An analysis of soil collected from the study area indicated that all essential elements (Potassium, Phosphorus, Calcium, Magnesium) and trace elements are present at levels suitable for plant growth (Jones 2000). Soil depth on the plains was normally deeper than 0.80 m (personal observation), but was variable depending on the specific location (e.g. eroded hardpans, riverbeds, sandy areas, rock outcrops, etc.). Soil depth on the mesas rarely exceeded 0.40 m (personal observation). The A profile in the region is predominantly sandy with the B profile being higher in clay content (Ellis & Lambrechts 1986). Mud-, silt-, claystones and dolerite occur abundantly across the landscape.

2.5.2 Precipitation

Mean annual rainfall across the Nama-karoo varies from 60-400 mm (Palmer & Hoffman 1997), diminishing from east to west (Cowling 1986; Venter *et al.* 1986; Palmer & Hoffman 1997). The greater part of the karoo however rarely receives more than 250 mm per year (Cowling 1986). Most of the karoo receives mainly summer rain except for the south-western and western parts, which receives autumn rain (Venter *et al.* 1986; Palmer & Hoffman 1997). These parts are transitional to the winter rainfall succulent karoo (Palmer & Hoffman 1997). Rainfall reliability, expressed as the percentage frequency of years of rainfall greater than or equal to 85 % of the average, decreases rapidly from more than 70 % in the south-east and south-west to less than 50 % in the north (Venter *et al.* 1986). Severe droughts are of frequent occurrence and rainfall fluctuates above and below average in approximate 15 – 20 years rainfall cycles in the summer rainfall area (Tyson 1986; Venter *et al.* 1986).

Middelburg receives an average of 341 ± 115 mm per year (Rainfall data for Tafelberg Hall, data supplied by William Asher, pers. comm.). Most of this falls in the summer months of December, January and February (40 %), with June, July and August (8 %) being the driest on average (Fig. 2.3, Fig. 2.4). Rainfall for the study area during the duration of the study was normal to above-normal (Average rainfall

for 1996-1999 was 389 mm per year compared to the long term average of 341 mm per year). Most of the rain in the Middelburg District is in the form of tropical low pressure systems moving in from further north and from local thundershowers, both of these events occurring primarily in Summer.

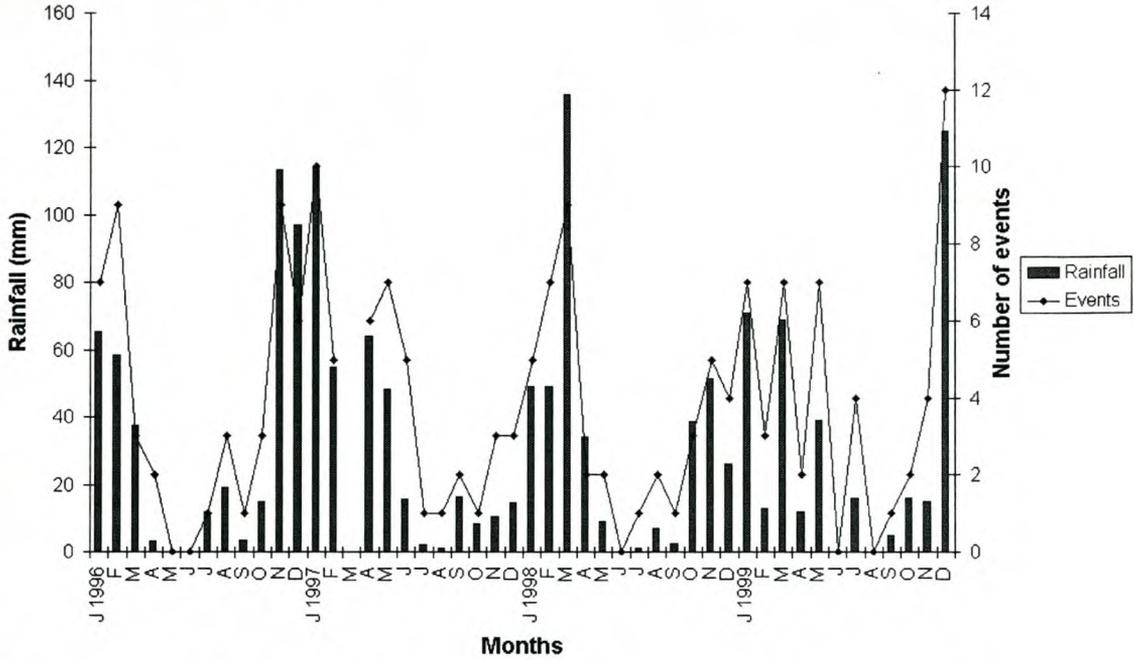


Fig. 2.3 Rainfall for Tafelberg Hall from 1996-1999. Events are the number of times rain fell in the given month. Data supplied by William Asher, pers. comm.

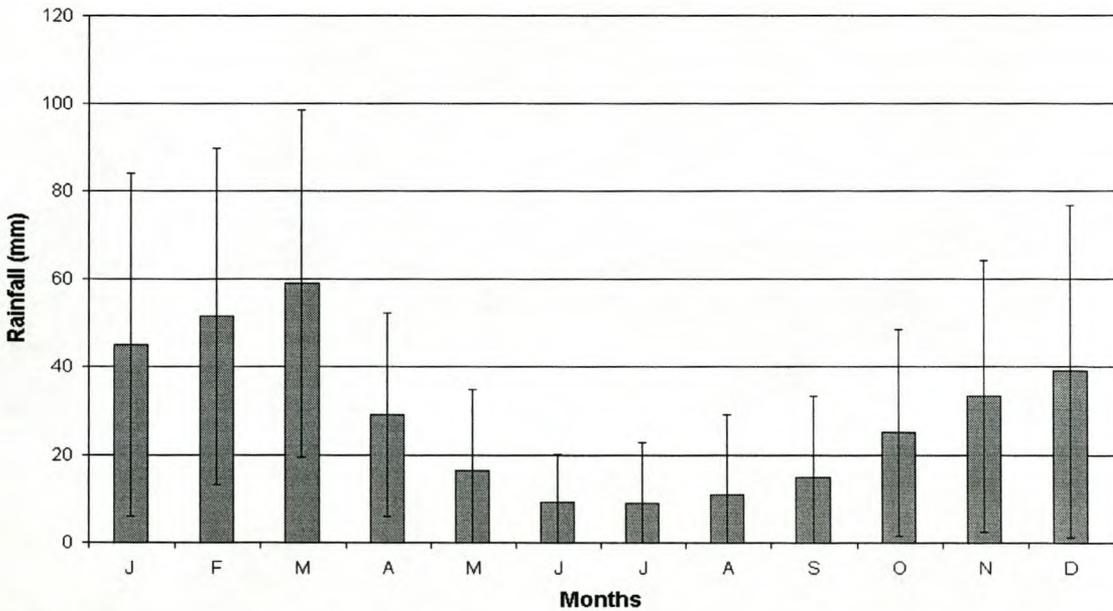


Fig. 2.4 Average monthly rainfall for Tafelberg Hall from 1898-1996. Data supplied by William Asher, pers. comm.

The effect of elevation resulting in an increase in precipitation was very apparent during this study, with high lying areas receiving more rain than the lower lying areas. Tafelberg, Folminkskop and Buffelskop, for instance, are often covered in low clouds, and it sometimes rains on the mesas while the surrounding plains are dry (Personal observations). High rock cover on the mesas also increases the relative local effect of precipitation due to runoff concentrating the water to between rock areas.

2.5.3 Temperatures

Large fluctuations in air temperatures in the karoo exist both daily and seasonally (Venter *et al.* 1986, Desmet & Cowling 1999). A difference of 25 °C between day/night temperatures is for instance not unusual (Venter *et al.* 1986). Temperature range increases with an increase in elevation (Palmer & Hoffman 1997) with greatest annual and daily temperature variation occurring in the upper karoo (Cowling 1986). Mean maximum temperatures are high in January (> 30 °C) and low in July (< 0 °C) (Palmer & Hoffman 1997; Desmet & Cowling 1999). Mean annual temperature broadly follows the contours with the coolest areas extending from Sutherland (grid reference 3320 BC) in an east-north-easterly direction towards Middelburg (Venter *et al.* 1986). Lowest minimum temperatures are often found towards the centre of the subcontinent, showing both the effects of continentality and elevation (Werger 1986).

Average annual temperatures for Middelburg range from ± 22.5 °C in summer to ± 7.5 °C in winter (Fig. 2.5). Mean minimum temperatures often reach below 0 °C in winter, with the coldest months being from May to August. Maximum temperatures are often in the high thirties (38 °C), with December to February being the hottest months (Fig. 2.5) (Directorate Climatology, S.A. Weather Bureau).

High lying areas such as Tafelberg, Folminkskop and Buffelskop are noticeably cooler than the surrounding flats at any given time of the day, with the southern slopes being coolest.

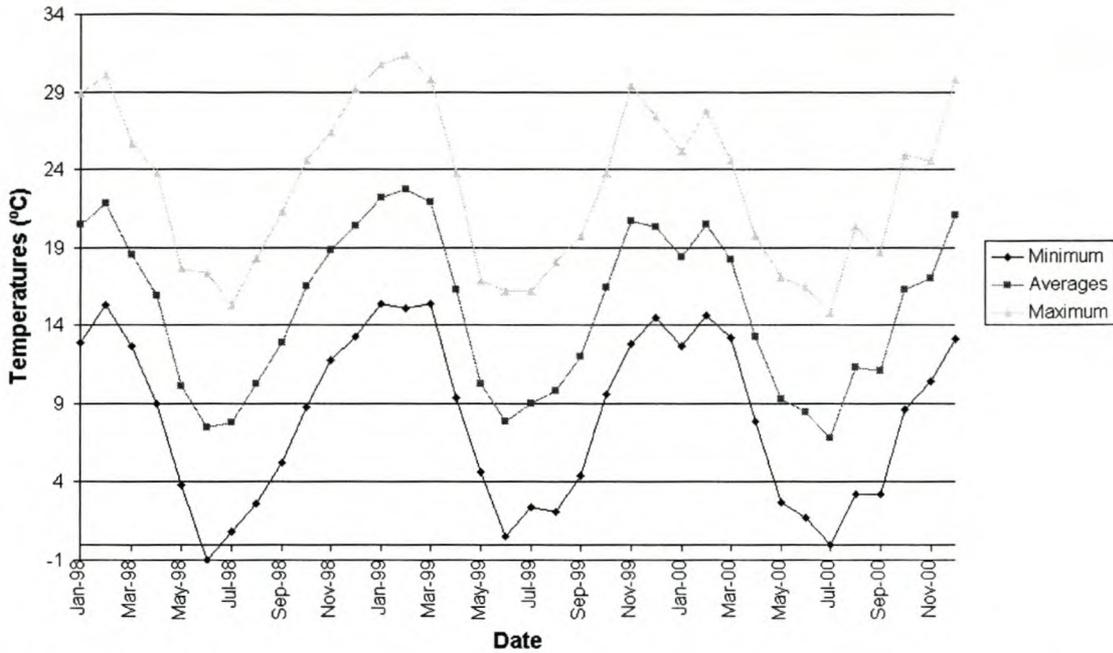


Fig. 2.5 Average, minimum and maximum temperatures for the Middelburg District from January 1998 – December 2000 (Directorate Climatology, S.A. Weather Bureau).

2.5.4 Frost and Snow

The incidence of frost is highest in the high altitude areas such as Sutherland (180 days per year)(Venter *et al.* 1986) and the upper karoo, while the areas in the south and west have a low incidence of frost (Cowling 1986). Frost can however occur throughout the whole biome (Palmer & Hoffman 1997) and can have important ecological implications (Venter *et al.* 1986). Middelburg has an average of 43 days a year with temperatures of 0 °C and below. The first frost occurs in late April to early May and the last from mid to end of September (Directorate Climatology, S.A. Weather Bureau).

Snow occurs often on the high altitude areas of the escarpment (Cowling 1986) and has occasionally been seen on the mesas in the Middelburg District (personal observation).

2.5.5. Wind

Wind is a common feature of karoo landscapes and it is therefore not surprising that nearly 50 % of plant species in the karoo are mainly wind dispersed (Hoffman &

Cowling 1987). In the eastern interior these dry winds are predominantly from the south-east in winter and the north-west in summer, and in the western interior from the north and south-west respectively (Werger 1986).

Dominating winds in Middelburg are from the south-east (December to June) and north-west/south-east (July to November) (Table 2.2). Average windspeed is mostly in the range of 1.6 – 3.5 m/s (33 % of all wind), but is often as high as > 8 m/s (7 % of all wind) (Directorate Climatology, S.A. Weather Bureau).

Table 2.2 Average wind direction and wind speed (m/s) in January and July for the Middelburg District. Data supplied by Directorate Climatology, S.A. Weather Bureau.

	January	July
N	8 m/s	12
NNE	2	2
NE	2	1
ENE	2	1
E	4	12
ESE	19	14
SE	15	7
SSE	12	2
S	5	1
SSW	1	0
SW	1	1
WSW	2	2
W	7	7
WNW	7	10
NW	7	14
NNW	6	14

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3. Materials and Methods

3.1 Distribution of sites across the landscape

Sites were established on three isolated mesas (Tafelberg, Folminkskop and Buffelskop) and the plains surrounding them (Fig. 3.1). These sites were located on the north-western (actual direction, hereafter refer to as NW) and south-eastern (hereafter refer to as SE) slopes and plains of all three mesas, as well as on the plateaux. NW and SE slopes represent the greatest exposure to maximum and minimum temperature extremes respectively. Features on the plains, such as ridges or hillocks were avoided as they may represent plant communities specific to these features and were not necessarily representative of the vegetation typically found on either slopes, plains or mesa plateaux.

A total of seventeen sites were established on Tafelberg, of which three were on the plateau, three on each of the NW and SE slopes, and four on each of the NW and SE plains (directions taken from the center of the plateau). Sites on the plateau were selected in such a way that one was located on the NW part of the plateau, one on the SE part of the plateau, and the third one in the central part of the plateau. The sites on the NW and SE parts of the plateau were not equal distances from the slopes, so as to minimize the possible effects of edge effects. Sites on the slopes were selected in such a way that one was located on the lower slopes, one on the middle slopes, and one on the top slopes. Sites on the plains were ± 300 m apart, starting as close as possible to the bottom of the slopes.

Folminkskop (1400 m) and Buffelskop (1400 m) are 200 m lower than Tafelberg (1600 m). Fifteen sites were located on Folminkskop, spread over all slopes and aspects, while Buffelskop had a total of 14 sites. Three sites were established on the plateau of Folminkskop, but on Buffelskop only two sites were established due to its uneven shape (not a flat plateau). On both Folminkskop and Buffelskop only two sites were established on each of the NW and SE slopes due to shorter slopes than Tafelberg. These sites were selected in such a way that one site was on the lower

slope and the other on the upper slope. Sites on the plains of Folminkskop and Buffelskop were selected the same way as those of Tafelberg (± 300 m apart, starting as close as possible to the bottom of the slope). Sites on all mesas were selected randomly. Table 3.1 provides details on habitat and position of each site.

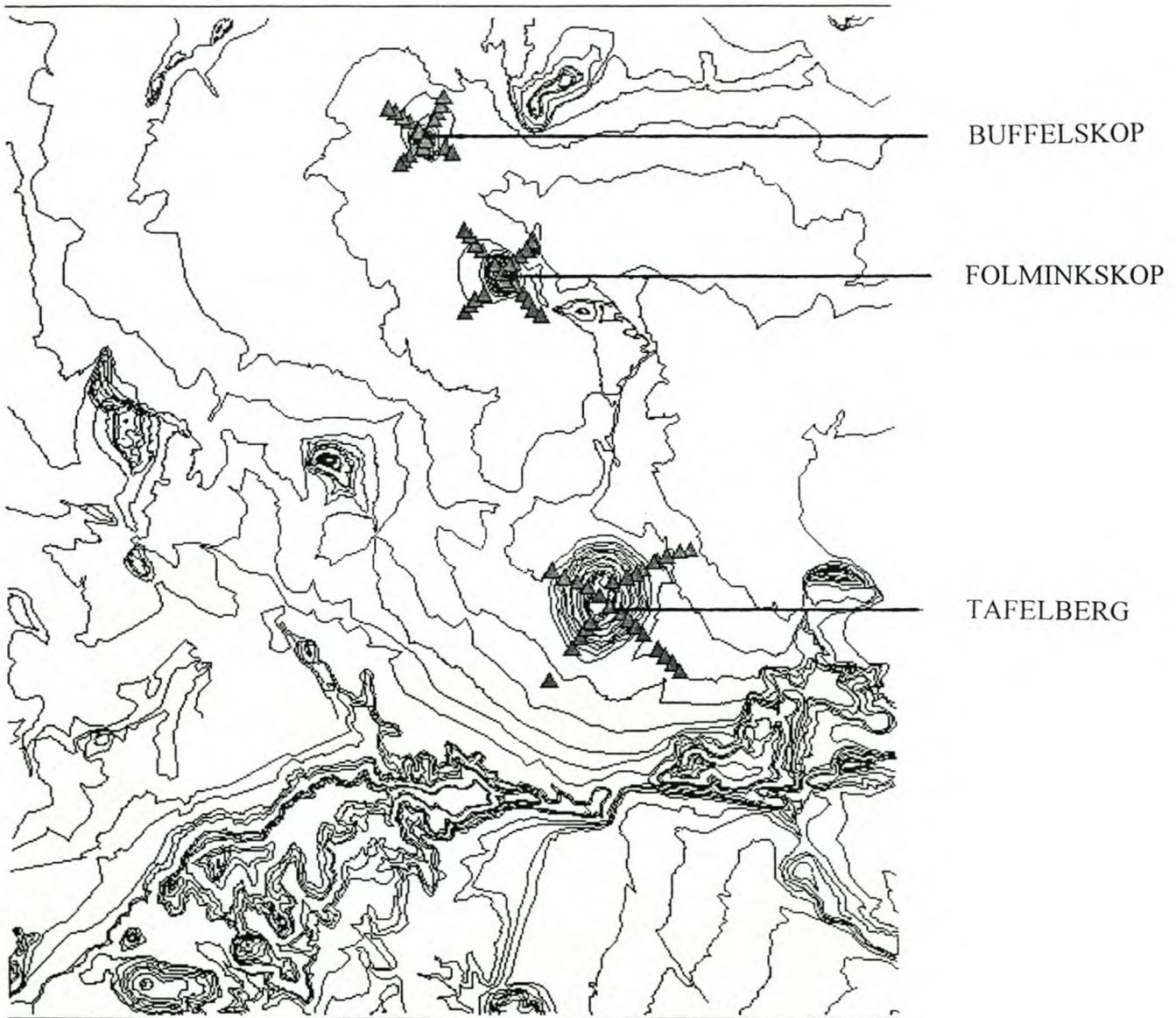


Fig. 3.1 Distribution of sites across the Middelburg landscape. ▲ indicates position of sample sites. Although sites were sampled on NE and SW slopes and plains, data were not included in this thesis.

Mesa	Site	Site code	Habitat	Latitude	Longitude	Altitude	
Tafelberg	NW Plain 4 (furthest from mesa)	NW PL 4	Plain	25.0000000000	-31.7000000000	1250 m	
	NW Plain 3	NW PL 3	Plain	25.0000000000	-31.7000000000	1250	
	NW Plain 2	NW PL 2	Plain	25.0000000000	-31.7000000000	1250	
	NW Plain 1	NW PL 1	Plain	25.0000000000	-31.7000000000	1200	
	NW Slope lower	NW SL	Slope	25.1563703620	-31.6402075960	1300	
	NW Slope middle	NW SM	Slope	25.1601835610	-31.6414851750	1400	
	NW Slope upper	NW SU	Slope	25.1630915100	-31.6425797600	1600	
	Plateau NW	PL NW	Plateau	25.1650631700	-31.6437511700	1650	
	Plateau Center	PL CEN	Plateau	25.1666855000	-31.6472595000	1650	
	Plateau SE	PLAT SE	Plateau	25.1686856700	-31.6472010000	1650	
	SE Slope upper	SE SL U	Slope	25.2517165033	-31.6486201700	1400	
	SE Slope middle	SE SL M	Slope	25.1742445000	-31.6497985000	-	
	SE Slope lower	SE SL L	Slope	25.1764241700	-31.6504428300	1300	
	SE Plain 1	SE PL 1	Plain	25.1830723920	-31.6587265600	1200	
	SE Plain 2	SE PL 2	Plain	25.1851540260	-31.6601938980	1250	
	SE Plain 3	SE PL 3	Plain	25.1873935900	-31.6619104610	1200	
	SE Plain 4	SE PL 4	Plain	25.1892825910	-31.6638608280	1200	
	Folminkskop	NW Plain 4 (furthest from mesa)	NW PL 4	Plain	25.1285158050	-31.5532963310	1250
		NW Plain 3	NW PL 3	Plain	25.1301215150	-31.5548285840	1250
		NW Plain 2	NW PL 2	Plain	25.3136655970	-31.5567451770	1250
NW Plain 1		NW PL 1	Plain	25.1337957980	-31.5583375620	1300	
NW Slope lower		NW SL	Slope	25.1361800000	-31.5609200000	1350	
NW Slope upper		NW SU	Slope	25.1374557930	-31.5617653370	1400	
Plateau NW		PL NW	Plateau	25.1382315860	-31.5632727500	1450	
Plateau Center		PL CEN	Plateau	25.1394408550	-31.5638001870	1450	
Plateau SE		PLAT SE	Plateau	25.1401689080	-31.5656244640	1400	
SE Slope upper		SE SL U	Slope	25.1410543720	-31.5664741260	1350	
SE Slope lower		SE SL L	Slope	25.1431617580	-31.5669440470	1300	
SE Plain 1		SE PL 1	Plain	25.1453805880	-31.5690656670	1250	
SE Plain 2		SE PL 2	Plain	25.1467206400	-31.5708858270	1250	
SE Plain 3		SE PL 3	Plain	25.1481592800	-31.5729943410	1250	
SE Plain 4		SE PL 4	Plain	25.1503027500	-31.5744368640	1250	
Buffelskop		NW Plain 4 (furthest from mesa)	NW PL 4	Plain	25.1075118360	-31.5227579590	1200
	NW Plain 3	NW PL 3	Plain	25.1093674220	-31.5237059880	1200	
	NW Plain 2	NW PL 2	Plain	25.1114961060	-31.5248124210	1250	
	NW Plain 1	NW PL 1	Plain	25.1135133560	-31.5261093360	1250	
	NW Slope lower	NW SL	Slope	25.1159054470	-31.5278113740	1300	
	NW Slope upper	NW SU	Slope	25.1162074940	-31.5283380980	1350	
	Plateau NW	PL NW	Plateau	25.0000000000	-31.5000000000	1350	
	Plateau SE	PLAT SE	Plateau	25.1177425330	-31.5306911190	1400	
	SE Slope upper	SE SL U	Slope	25.0000000000	-31.5000000000	1250	
	SE Slope lower	SE SL L	Slope	25.0000000000	-31.5000000000	1250	
	SE Plain 1	SE PL 1	Plain	25.1232870940	-31.5324833590	1200	
	SE Plain 2	SE PL 2	Plain	25.1252440300	-31.5337373600	1200	

Table 3.1 Detailed information for all sites sampled in the study area. Latitude and longitude data are presented in decimal degrees.

3.2 Site design

Every site consisted of six, 5x5 m plots, situated adjacent to each other. This study is a component of a broader project entitled “Restoration of degraded Nama-karoo rangelands: the role of conservation islands”. Three of these plots were used for the vegetation component of the project (this thesis), and the other three for a seed bank component of the same over-arching project (Jones 2000). This was done to ensure that every site would be statistically viable as a unit on its own (minimum replication of three required). When standing with ones’ back to the mesa cliff, the first plot on the left was used as a vegetation plot, the next as a seed bank plot, etc. (Fig. 3.2).

Sites codes on the plains referred to the position of the sites in relation to the relative distance from the mesas. Buffelskop NW plain 1, 2, 3, 4 (e.g. Field code: NWPL1, 2, 3, 4 B; read as NW plains 1, 2, 3, 4 Buffelskop) would, for instance, have referred to the four sites on the plain on the NW side of the mesa Buffelskop, with 1 being closest to the base of the mesa and 4 being furthest away from the base. For plains, slopes and plateau sites, A, B or C referred to three of the six 5x5 m plots mentioned above, with A being the one furthest to the left when standing with your back to the cliff of the relative mesa. Site codes for the slopes referred to the relative height of the site above the surroundings, e.g. Tafelberg SE slope lower (Field code: SESL T; read as SE slopes lower Tafelberg) would have referred to the lower slope on the SE aspect of Tafelberg mesa. In the same way PLNWB T (read as plateau NW B Tafelberg) would have referred to the NW parts of Tafelberg’s plateau, B.

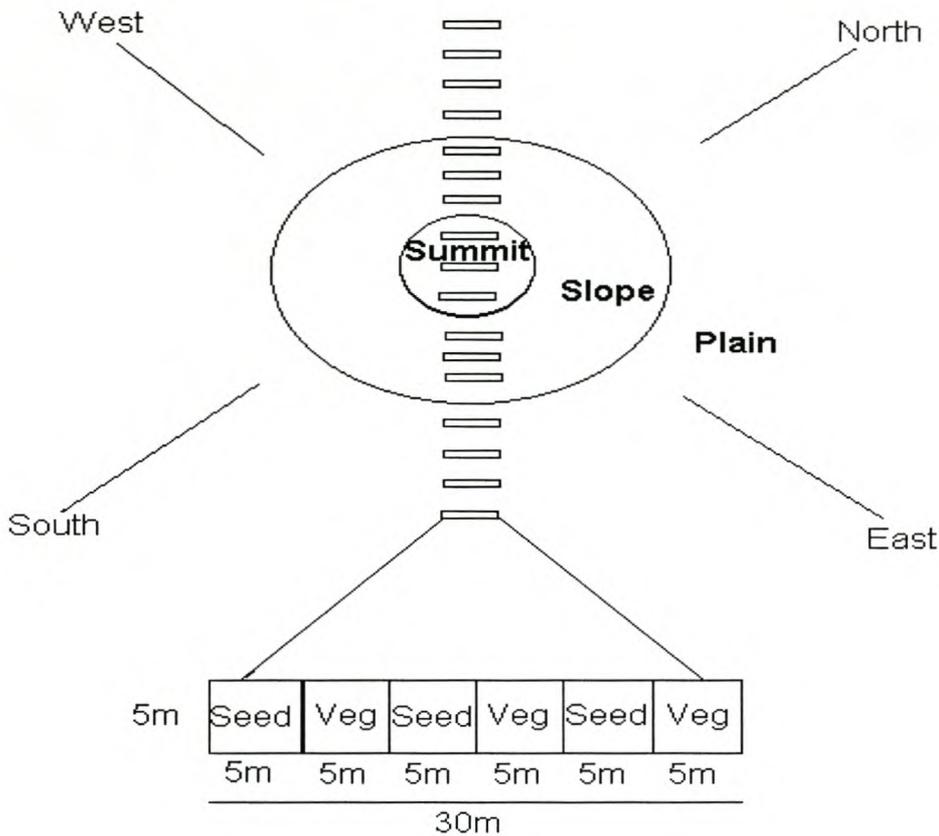


Fig. 3.2 Distribution of sites across each of the three mesas and plot layout.

3.3 Plot size

Species area curves were conducted at the beginning of the project to determine the minimal sampling area (Kent & Coker 1992), with two replicate curves on the plateau of Tafelberg, and another two on the SE plain of Tafelberg mesa. Minimum areas were found to be 2-3 m² for the plateau of Tafelberg, and 1-2 m² for the SE plain of Tafelberg (Fig. 3.3 and 3.4). Minimum area was taken as the point on the curve where the slope most rapidly approached the horizontal (Barbour *et al.* 1987). The nearby Grootfontein Agricultural College (Middelburg, Eastern Cape Province) also uses a plot size of 12-14 m² for their vegetation studies. In order to ensure that the majority of species would be captured during the sampling, a plot size of 25 m² (5x5 m) was used throughout the project.

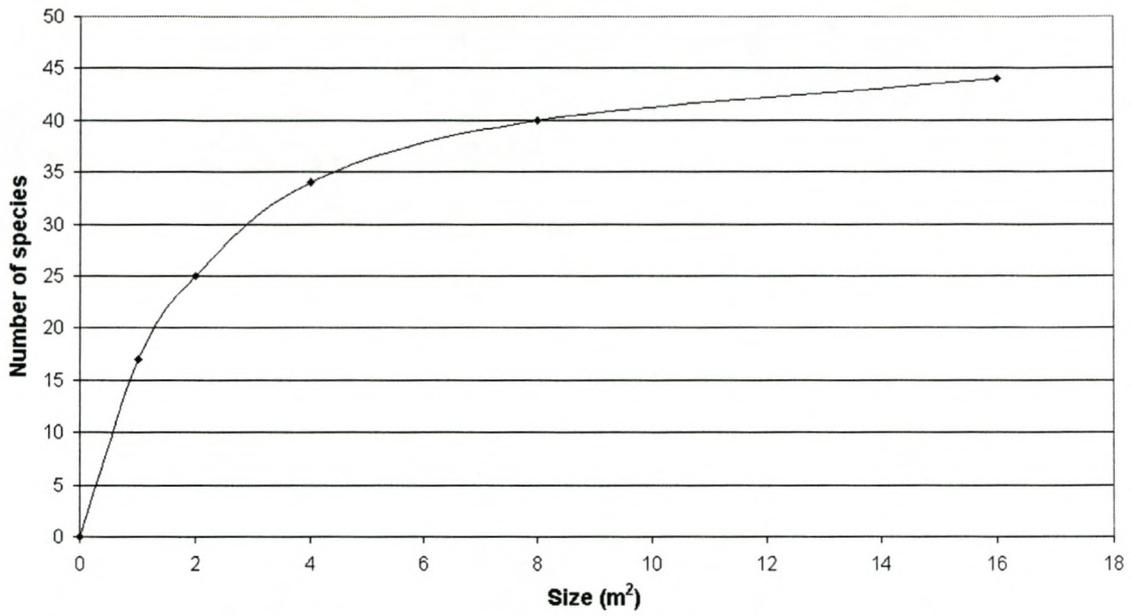


Fig. 3.3 Average cumulative species area curve for Tafelberg summit (n = 2)

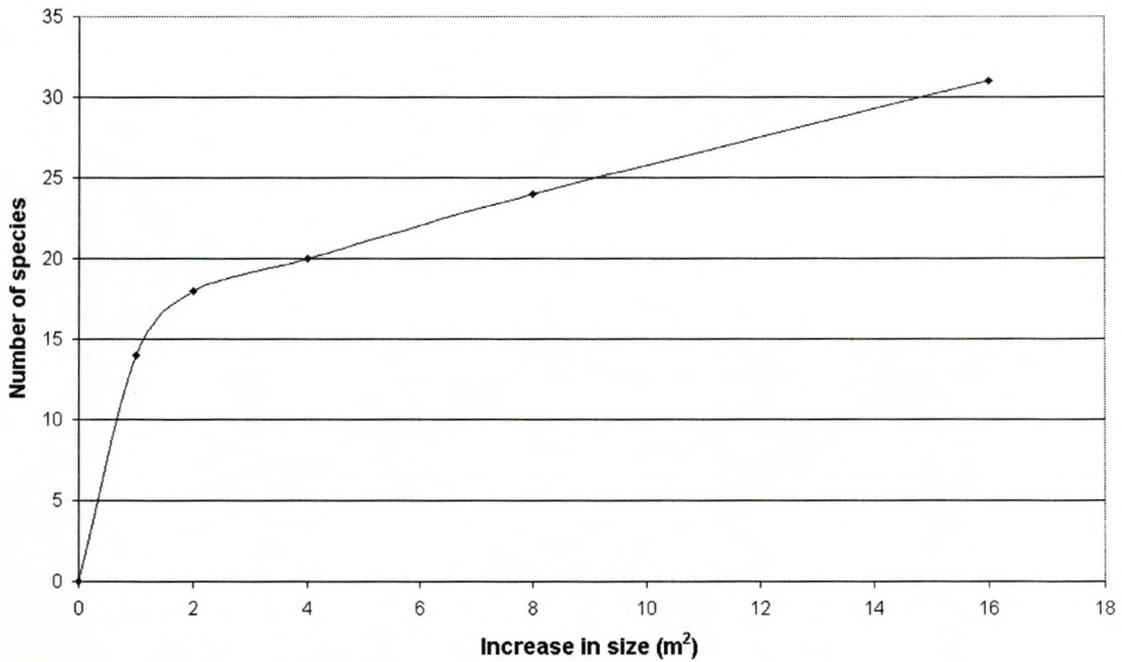


Fig. 3.4 Average cumulative species area curve for Tafelberg SE flats (n = 2)

For the purpose of the vegetation study, every plot was sub-sampled. Ten subplots of 1 m² were selected randomly from each 5x5 m plot. The purpose of this sampling procedure was to speed up the sampling process while at the same time still sampling an adequate area of the plot. All sites were permanently marked using six iron rods to enable future visitation and a GPS reading was taken.

3.4 Vegetation measurements

3.4.1 Type of data

Plots were sampled for density and cover of perennial plant species (those species surviving longer than a year). Density is defined here as the number of individuals per sample size while cover is defined as the percentage cover of plant material covering the ground when viewed from above. Annuals, bulbs, ferns, mosses and seedlings were included in the vegetation analysis despite their temporal nature, since most of the plots were sampled at roughly the same time of the year. Where possible no plant specimens were taken from inside the plots so as not to disturb the plots in any way for future sampling.

3.4.1.1 Density

Cover values were used in data analysis in this thesis, although density of all plants was recorded as well. Grasses mostly consisted of a number of clonal individuals clumped together and in such instances the number of clumps were given as a density count. Grasses that formed a continuous or nearly continuous layer were only assessed using cover values. Some plants were multi-stemmed and would typically appear as numerous individuals although they were clonal, i.e. they were joined together below the surface of the soil. In cases like this (e.g. *Lycium cinereum*), density was given as the number of rough clumps and is again not always, though mostly, a true reflection of density of stems. Plants such as *Pentzia incana* form stolons that develop roots at the tips and in time give rise to independent individuals. Density in such cases was given as the number of plants with apparent root systems. Sometimes species such as *Bulbostylus* and some grasses occurred as individuals at extremely high densities of up to 200 + individuals per 1 m² subplot. In these cases only a cover value was given and no density count was made.

3.4.1.2 Cover

Cover was recorded as the maximum projected canopy cover of each perennial species. Some plants did not have a large circumference but were very tall (1-2.5 m). In these cases a higher value for estimated cover was given than would normally have been the case so that the spatial size of the plant was factored into the estimate. Bare soil/debris was defined as the total area of visible bare soil/debris as seen from above when standing next to the subplot. Total percentage cover for a subplot often exceeded 100 %. This was the case when large shrubs or small trees extended over and covered rocks, grasses and other plants. Total percentage cover for a subplot may then in extreme cases have been as high as 170 %. Plants rooted outside a plot but extending aurally into the subplot were given actual estimated density and cover values but were noted as "excluded". A plant was thus able to have included and excluded cover values in one subplot. This distinction was made for in case a separate analysis on just one of the values was needed in future. Included and excluded values were combined in the analysis of the data.

3.5 Soil sampling and analysis

Open- and closed-canopy soil samples were taken from the plateaux, slopes and surrounding plains of Tafelberg, Folminkskop and Buffelskop. Samples were taken at approximately 2.5 m intervals, roughly 1 m outside the perimeter of each plot (Jones 2000). These samples were air-dried after which it was sent to the Soil Analysis laboratories at Elsenburg (Department of Agriculture). The soils were analyzed for chemical and physical attributes (Jones 2000).

3.6 Data Analysis

Data analysis for Chapter 4 (Diversity) and Chapter 5 (Classification) are discussed in detail in the Material and Methods sections of the relevant chapters.

The National Botanical Institute (Pretoria) identified plants to species level wherever possible. Voucher specimens are held at the University of Stellenbosch. Collection numbers of unidentified (up to species level) specimens are available on request from

Dr. K.J. Esler, Department of Botany, University of Stellenbosch. Nomenclature of plant taxa follows the checklist of the National Vegetation Database (Mucina *et al.* 2000) imbedded within the local TvWin 1.98c database, and which features the national flora checklist of PRECIS system of the National Botanical Institute dated January 2000. Some recent nomenclature changes were implemented as well (genera *Maytenus* and *Gymnosporia*, *Homeria* and *Moraea*, *Walafrida* and *Selago*).

3.7 References

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4. Diversity

Abstract

Knowledge about plant species diversity is important for identifying areas vulnerable to species loss and for predicting the impact of such losses on the community. Alpha, Beta and Gamma Diversity on and off isolated mesas was investigated across Nama-karoo communities in the eastern Cape, South Africa. Species composition and cover was measured in plots along a transect extending from the SE plains and slopes, across the plateaux, onto the NW slopes and plains of three mesas (Tafelberg, Folminkskop and Buffelskop). Mesas were not found to be higher in Alpha Diversity in comparison to their surroundings. Greater differences in diversity were found between mesas and their surroundings in a parallel study in Namibia, indicating that mesas could be more distinct islands of diversity with an increase in aridity. Moister microhabitats (including features such as drainage lines) found on mesas resulted in an increase in woody phanerophytes on mesas relative to the plains. Mesa size was not a determinant of diversity as bigger and smaller mesas were similar in average Alpha Diversity values. The biggest mesa, Tafelberg (450 m above surroundings), was higher in Beta Diversity than a smaller mesa of similar size and geology (Folminkskop). High Beta Diversity values for one of the smaller mesas, Buffelskop (200 m above surroundings) could be explained by the presence of degraded communities in the NW slopes and plains, coupled with areas high in diversity on the SE slopes. Mesas and plains shared few species. Proportionally fewer species were shared between the plateau and slopes of the bigger Tafelberg in comparison with species shared between the slopes and plateaux of the two smaller mesas (200 m above surroundings). Isolation of the plateau could become more distinct with an increase in mesa size. However, Tafelberg shared more species with the surrounding plains than did the two smaller mesas. Bigger mesas support a more diverse array of microhabitats than do smaller mesas, enabling plant species to occupy selective sites on the slope of the mesa. Diversity in Middelburg was higher than the average for the Nama-karoo, a possible result of the higher rainfall in the eastern parts of the Nama-karoo. Diversity compared favourably with that in other arid lands of North America and Australia.

4.1 Introduction

In this chapter, patterns of Alpha and Beta Diversity and their determinants across the Middelburg landscape were investigated. Diversity in the Middelburg landscape was also compared to that of other vegetation types in southern Africa and internationally.

Species diversity in relation to processes such as evolution and stability is one of the central issues in ecology. Diversity is also of importance in conservation because of the threat posed by industrialization and urbanization (Naveh & Whittaker 1979). Knowledge about species diversity patterns is important for identifying areas vulnerable to species loss and for predicting the impact of such losses on the community (Cowling *et al.* 1989).

Species richness in southern Africa is amongst the highest in the world, and even when the rich Cape flora is excluded, the southern African flora is still higher in diversity than that of tropical areas such as Brazil and Asia, and even Australia that also has tropical and temperate areas (Gibbs Russell 1987). The high diversity of southern Africa's arid lands is often overshadowed by the high diversity of the Cape Floristic Region (Cowling & Hilton-Taylor 1999).

4.1.1 Definitions and measurement

Species diversity can be described as richness in species (Whittaker 1972). Species numbers alone are, however, not always accurate because not all species in a community have the same number of individuals. Species evenness or equitability is the distribution of individuals among the species (Whittaker 1972, Barbour 1987), with evenness being at its maximum when all species have the same number of individuals (Barbour 1987). Both richness and evenness are important properties of all samples (Whittaker 1975). Species dominance and the area sampled are also critical concepts in the comparison of diversity between communities (Whittaker 1975). Numbers of species in a given community tend to increase with an increase in the area sampled (Whittaker 1975).

Diversity can be subdivided into various components. Total diversity or Gamma Diversity is a function of local diversity (Alpha Diversity) and of the turnover of

species between habitats (Beta Diversity) (Whittaker 1972). This can also be expressed by the equation: $\text{Gamma Diversity} = \text{Alpha Diversity} \times \text{Beta Diversity}$.

Alpha Diversity is diversity within a homogenous habitat, and is often termed “within habitat” diversity, “point” diversity, or “local diversity”. Various tests to compare Alpha Diversity exist. In this study I have selected total species number (s), Simpson Diversity Index (D) (Simpson 1949) and Shannon-Wiener Diversity Index (H') (Pielou 1975) to describe Alpha Diversity for the Middelburg region. Both Simpson and Shannon-Wiener Diversity Indices are widely used to describe and interpret plant diversity across the world. “S” refers simply to the maximum number of species that occur in a given habitat. The Simpson Diversity Index is more affected by the most abundant species, whereas the Shannon-Wiener Diversity Index is a better indicator of the importance of the intermediate species and the full importance value sequence (Whittaker 1972; Whittaker 1975).

Beta Diversity can be described as between-habitat diversity and incorporates the concept of species turnover across a habitat gradient. It reflects on how similar or different a range of habitats is in terms of species shared between them. Some of the simplest ways to measure Beta Diversity is that of Whittaker (1960), Wilson & Shmida (1984) and Cody (1975) (see 4.2 for more details).

Historical processes control Gamma Diversity through the speciation of ecological equivalents in similar habitats along environmental gradients (Cody 1986). The slopes of species area curves would be steeper in regions with higher Gamma Diversity than in regions with lower Gamma Diversity (Shmida 1985). Beta and Gamma Diversities can be difficult to separate because most geographical gradients have some degree of environmental change and therefore habitat change (Cody 1986).

4.1.2 Determinants of diversity

The effect of environmental conditions on the diversity of plants is a complex issue, with many different responses. Equilibrium models explain coexistence of species in terms of niche differentiation (Tilman 1982; Cody 1986), whereas non-equilibrium models ascribe diversity to a variety of processes that prevent one species dominating

the community (Grime 1973). Non-equilibrium models of species diversity propose that diversity would be highest with a moderate amount of disturbance (grazing, mowing, burning, trampling, etc.) (Grime 1973). Low diversity in highly stressed conditions can be attributed to less species that are adapted to cope with the conditions, and low diversity in low stress environments can be attributed to the dominance of the community by one or two species (Grime 1973).

4.1.2.1 Soil moisture

Variations in soil moisture availability may be one of most important causes of spatial heterogeneity in plant communities (Evenari *et al.* 1971). Soil moisture availability is one of the primary limiting resources in an arid system (Cowling *et al.* 1994). Diversity is not always correlated with an increase in moisture availability. An increase in diversity with a decrease in rainfall is common and may sometimes be attributed to an increase in the range of resources (coupled with an increase in structural diversity) and therefore an increase in diversity (Whittaker & Niering 1975; Naveh & Whittaker 1979). In some areas maximum diversity is found in areas of intermediate moisture availability (Whittaker & Niering 1975) and in other areas diversity might increase with an increase in elevation and moisture. Whittaker & Niering (1975) found that diversity in the Santa Catalina Mountains in Arizona, USA, increased with a decrease in elevation and an increase in drought.

4.1.2.2 Environmental stress

An increase in environmental stresses such as overgrazing (Palmer & Cowling 1994) or pollution generally decreases diversity, but light to moderate grazing seems to increase diversity (Whittaker 1975). Grazing might increase diversity in a community by preventing species from becoming dominant in the community (Whittaker 1975). Extreme conditions might limit the amount of species that are able to survive in those conditions, thus reducing diversity in such areas. In habitats where there are open spaces or disturbance, diversity might be greater because of the tradeoffs between species that are good competitors but poor colonists, and species that are poor colonists but poor competitors. This may allow species that compete for the same resource to co-exist (Tilman & Pacala 1993). The influence of drought on diversity seems to be less marked than that of temperature (Whittaker 1972; Whittaker 1975).

Grazing can play an important role in determining diversity in plant communities. There seems to be an optimum grazing pressure for maximum species diversity (Naveh & Whittaker 1979). Grazing above the optimum grazing pressure reduces diversity by allowing certain aggressive and unpalatable species to survive and dominate the community, while grazing below the optimum allows woody plants or taller grasses to outcompete the other plants (Naveh & Whittaker 1979). Some communities that have been grazed for thousands of years seem to have evolved to support species that are resistant to grazing. These communities may actually show an increase in diversity with an increase in grazing pressure as opposed to communities that have not evolved with grazing (Naveh & Whittaker 1979). Higher diversity in these communities occurs in response to the combined influence of stress by fire, grazing and drought, as well as the heterogeneity of mountainous habitats. Rocky soils offer a higher diversity in microsites, and constant grazing pressure favours smaller plants that can divide the microsites more finely (Naveh & Whittaker 1979).

Previous studies have shown that maximum species diversity occurs at some intermediate level of disturbance (Cowling *et al.* 1989).

4.1.2.3 Instability

Instability (e.g. unpredictable rainfall and temperatures) generally seems to act as an inhibitor of diversity, through limiting the increase in the range, complexity and density of species in a given habitat (Whittaker 1972). At the same time instability can increase the diversity of responses to cope with the unstable conditions (Whittaker 1972; Whittaker 1975).

4.1.2.4 Dominance

Diversity of a plant community may be strongly influenced by the dominance structure of plants in the community. The effect of dominance on diversity is often inverse and seems to depend on the nature of the dominant species through the control they have on light and soil conditions (Whittaker 1972; Whittaker 1975).

4.1.2.5 Rocky habitats

It is generally accepted that rocky habitats are more diverse than adjacent plains habitats because of greater soil moisture heterogeneity and in turn a longer structural niche axis (Montana 1990). Surface properties of rocks and soils in the Negev have been shown to influence the distribution of soil moisture (Yair *et al.* 1980). Patterns of species diversity and distribution were in turn correlated with the geological surface structure (Olsvig-Whittaker *et al.* 1983). Rocky hillsides in the desert generate runoff, and soil patches in-between absorb water. Distribution and volume of rocks have a direct influence on the distribution of soil moisture, creating a higher degree of heterogeneity (Olsvig-Whittaker *et al.* 1983).

Vegetation of rocky outcrops in the Free State Province (formerly the Orange Free State Province) had low species diversity but contained a variety of life forms (Malan *et al.* 1998). Vegetation of these outcrops was in a degraded state due to overgrazing by livestock combined with a few years of below average rainfall (Malan *et al.* 1998). Stuart-Hill *et al.* (1984) recorded a relatively strong presence of woody species on rocky outcrops in African semi-arid savannas. More favourable moisture conditions occurred on rocky outcrops due to greater runoff and greater volume of soil occupied by rocks which in turn lead to relatively more moisture available for the soil (Stuart-Hill *et al.* 1984; Fuls *et al.* 1993). South-facing slopes in the southern Free State Province were also found to have greater species diversity than north-facing slopes (Malan *et al.* 1998). This was said to be caused by the more direct sunlight and resulting warmer microclimate on the northern slopes (Malan *et al.* 1998).

Montana (1990) found a landform gradient along which vegetation types were ordered. Greatest species richness was found at relatively low levels of soil moisture, and not at the extreme of the water availability gradient (Montana 1990). The study area had a great diversity in land forms (Montana 1990), which is a common feature of warm deserts (Ehleringer 1985). The increase in diversity was correlated with an increase in rockiness (habitat structure) (Montana 1990).

4.1.2.6 Growth form diversity

The length of the structural niche axis is determined by the range of environmental conditions suitable for plant growth, so that in the end climate determines the number of growth forms that can exist in a community (Cowling *et al.* 1994). Community growth form diversity in such a system would determine species diversity in the community (Cowling *et al.* 1994). Cowling *et al.* (1994) found a strong relationship between growth form diversity and species richness for the Nama-karoo. They also found a positive relationship between climatic heterogeneity and growth form diversity (Cowling *et al.* 1994). Slope habitats had a weaker correlation between climatic heterogeneity and growth form diversity because of an improved effectiveness of rainfall events (better runoff and storage conditions) (Cowling *et al.* 1994). However, rocky habitats were not found to have significantly higher species or growth form diversity at the community level in comparison with adjacent flats (Cowling *et al.* 1994). More species were sampled overall from the rocky habitats than from the adjacent plains habitats, probably reflecting a longer structural niche axis and higher Beta Diversity on the rocky sites (Cowling *et al.* 1994).

Diversity may sometimes be higher in temporally variable conditions in comparison with those that are stable. Co-existing species may experience different average environments when growing in a fluctuating environment enabling more species to persist in such a habitat than there are resources. Annual and understorey herbs might be able to persist in such habitats by exploiting these temporal fluctuations (Tilman & Pacala 1993).

4.1.3 Diversity in Arid Zones

South Africa's arid lands are unusually rich in species (Cowling & Hilton-Taylor 1999). Total number of species for the whole Karoo-Namib Region is said to be in the excess of 7 000 species (Hilton-Taylor & Le Roux 1989).

4.1.3.1 Nama-karoo versus succulent karoo

The succulent karoo is much more diverse than the Nama-karoo (Cowling & Hilton-Taylor 1999), with a total of about 4 849 species in the succulent karoo (Hilton-Taylor 1996). Cowling *et al.* (1994) found succulent karoo communities to be on average 1.6

times richer than Nama-karoo communities. Diversification of certain families in the succulent karoo has been greater than in the Nama-karoo (Cowling & Hilton-Taylor 1999).

4.1.3.2 Composition of communities in the succulent and Nama-karoo

It is less well known exactly how many species are in the Nama-karoo, but Gibbs-Russell (1987) gives a value of about 2 147 species for a core area of 30 % of the Nama-karoo. Nama-karoo and succulent karoo communities differ in the composition of their floras (Cowling & Hilton-Taylor 1999). The succulent karoo is characterised by dominance of Aizoaceae (including Mesembryanthemaceae), Iridaceae and Geraniaceae (Cowling & Hilton-Taylor 1999), while Nama-karoo communities are typically characterized by dominance of Asteraceae, Poaceae and Fabaceae (Shmida 1985). Werger (1978) describes the Nama-karoo as an open dwarf steppe dominated by Asteraceae, Poaceae, Aizoaceae, Mesembryanthemaceae and Liliaceae. Diversity of Chenopodiaceae in the succulent and Nama-karoo are reportedly abnormally low for arid lands (Cowling & Hilton-Taylor 1999).

4.1.3.3 Distinctiveness of the Nama-karoo

All the biomes in southern Africa are floristically distinct except the Nama-karoo biome (Gibbs Russell 1987). It is the only biome that does not have differential families that will distinguish it from the other biomes. The Nama-karoo biome showed highest similarities with the savanna, grassland and desert biomes, and lowest similarity with the fynbos biome (Gibbs Russell 1987). These close relationships between the Nama-karoo biome and the others are the result of the many species shared between these biomes (Gibbs Russell 1987). Very few genera have centres of diversity in the Nama-karoo alone (Gibbs Russell 1987). Species numbers for the Nama-karoo are low in comparison with the other biomes, especially if the large area that it covers is taken into account (Gibbs Russell 1987, Cowling *et al.* 1989). The Nama-karoo is not closely related to the succulent karoo and is more closely related to the savanna biome than the succulent karoo (Gibbs Russell 1987).

4.1.3.4 Growth-form diversity

The Nama-karoo is well known to have a high diversity of growth forms. Dykes and sills in the Nama-karoo landscape are associated with conditions of higher moisture, hosting mesic grasses and woody plants with strong grassland and savanna biome affinities respectively (Palmer & Hoffman 1997). Nama-karoo communities are reported by others to be relatively poor in species richness and growth forms (Cowling *et al.* 1989). Habitats with more heterogeneous soil moisture conditions in the southern succulent karoo/Nama-karoo ecotonal area were found to have a higher local diversity and growth form diversity than habitats on the adjacent flats (Milton 1990).

4.1.3.5 Slope and aspect

Slope and aspect related differences are reflected in species composition and structure (Palmer & Hoffman 1997). Palmer & Hoffman (1997) found taller shrubs to be more abundant on the cooler, wetter, southern slopes and shorter plants to be more abundant on warmer, drier northern slopes. Cover on the northern slopes was sparser, with dwarf shrubs dominating at low elevation and C₃ grasses at higher elevations (Palmer & Hoffman 1997).

4.1.3.6 Alpha Diversity for Nama-karoo sites

Alpha Diversity for the Nama-karoo biome was found to be the lowest in South Africa (1.8; Phytochorological Diversity – a variation on the Shannon-Wiener Diversity Index), in comparison with, for instance, Renosterveld (33) (Cowling *et al.* 1989). Nama-karoo and forest biomes were the most species poor of all the biomes. Communities in the Nama-karoo constitute a matrix of long-lived shrubs, which are then interspersed by shorter-lived species such as grasses. Overgrazing may lead to a reduction or elimination of certain species or growth forms, thereby further reducing species richness (Hoffman 1988).

4.1.3.7 Beta Diversity in Nama-karoo sites

Few empirical studies have been done on Beta Diversity (plant patterns) (Cowling *et al.* 1989). No Beta or Gamma Diversity values were reported by Cowling *et al.*

(1989) for the Nama-karoo, but they expect it to be poor. Cowling & Hilton-Taylor (1999) also found Beta Diversity in the Nama-karoo to be low.

4.1.3.8 Comparative diversity for Nama-karoo

On an international scale, the Nama-karoo has a rich flora for an arid region and is said to be richer than the Sonoran Desert that is twice its size (Cowling *et al.* 1989). Species diversity in Nama-karoo communities was found to have a mean of 47 (Phytochorological Diversity – a variation on the Shannon-Wiener Diversity Index) on a 1 000 m² scale (Cowling & Hilton-Taylor 1999), slightly higher than that recorded for the Sonoran Desert, which is some of the richest vegetation in terms of species and growth form diversity in North America (Whittaker & Niering 1975). Communities in the Nama-karoo were found to be similar in patterns and determinants of diversity than those from other arid land such as the New World (Cowling & Hilton-Taylor 1999). Alpha Diversity of SA vegetation types was not found to differ much from similar vegetation types elsewhere in the world (Cowling *et al.* 1989). Nama-karoo scrubland communities were found to be slightly less diverse than semi-arid communities in North America (Cowling *et al.* 1989).

4.2 Methods

A detailed description of the sampling methods used and plot layout is provided in Chapter 3. Diversity indices were calculated using the computer program SPECIES DIVERSITY AND RICHNESS, PISCES Conservation Ltd (Henderson & Seaby 2001). Simpson (1949), Shannon-Wiener (Pielou 1975) Indices and total *s* (total species number) were used to determine Alpha Diversity, while Whittaker (1960), Wilson & Shmida (1984) and Cody (1975) Diversity Indices were used for Beta Diversity.

Simpson:
$$D = \sum p_i^2$$

Shannon-Wiener:
$$H' = -\sum p_i \ln p_i$$

Where *s* is the total number of species in the sample, and *p_i* is “the proportion of all individuals in the sample that belong to species *i*.”

Whittaker: $\beta_w = S/\alpha - 1$

Cody: $\beta_c = \frac{g(H) + l(H)}{2}$

Wilson & Shmida: $\beta_T = [g(H) + l(H)]/2\alpha$

Where S = total number of species in the system, α = the average sample diversity where each sample is a standard size and diversity is measured as species richness, g(H) is the number of species gained along the transect and l(H) is the number of species lost over the same transect. Whittaker, Wilson & Shmida and Cody Diversity Indices all make use of absence/presence data and take no account of the abundance or dominance of individual species (Magurran 1992). Magurran (1992) provides a detailed review of diversity indices.

4.3 Results

4.3.1 What is the composition of the vegetation in terms of total species numbers, dominant families and genera?

Total species diversity amounted to some 353 species, including annuals, perennials and bulbs (Appendix 4.7.1, section 4.7). Plants were sampled from inside and outside permanent plots, and across the whole landscape over an area of approximately 100 km². These species were subdivided into 61 families and 199 genera. The average species/genus ratio was 1.77, the average species/family ratio was 5.79, and the average genus/family ratio was 3.26 (Appendix 4.7.1, section 4.7).

The most diverse families in terms of number of species were Asteraceae (78 species), Poaceae (36), Crassulaceae (18), Fabaceae (14), Chenopodiaceae (13), Mesembryanthemaceae (13) Hyacinthaceae (10) and Aizoaceae (9). The least diverse families in terms of species diversity (all represented by 1 species) were Adiantaceae, Apiaceae, Araliaceae, Aspleniaceae, Aytoniaceae, Boraginaceae, Celastraceae,

Commelinaceae, Dipsacaceae, Eriospermaceae, Loganiaceae, Menispermaceae, Myrsinaceae, Oleaceae and Ranunculaceae (Appendix 4.7.1, section 4.7).

The largest number of genera were found in the following families: Asteraceae (42 genera), Poaceae (26), Mesembryanthemaceae (11), Fabaceae (8), Aizoaceae (7), Hyacinthaceae (5), Crassulaceae (4), Cyperaceae (4), Iridaceae (4), Lamiaceae (4) and Scrophulariaceae (4). The lowest (all represented by 1 species) include among others Sterculiaceae, Asparagaceae, Anacardiaceae, Ebenaceae, Oxalidaceae and Polygalaceae (Appendix 4.7.1, section 4.7).

The most diverse genera in terms of number of species/genus ratio was *Crassula* (14 species), *Hermannia* (9), *Pteronia* (8), *Asparagus* (7), *Eragrostis* (7), *Amaranthus* (6), *Helichrysum* (6), *Pelargonium* (6), *Pentzia* (6), *Salsola* (5) and *Wahlenbergia* (5). The least diverse was, among many (all represented by 1 species), *Myrsine*, *Ceterach*, *Tripteris*, *Ursinia*, *Cadaba*, *Maytenus*, *Kalanchoe* and *Cedrostis* (Appendix 4.7.1, section 4.7).

4.3.2 Are the mesas higher in diversity than the surrounding landscape and are they therefore of special management/conservation value?

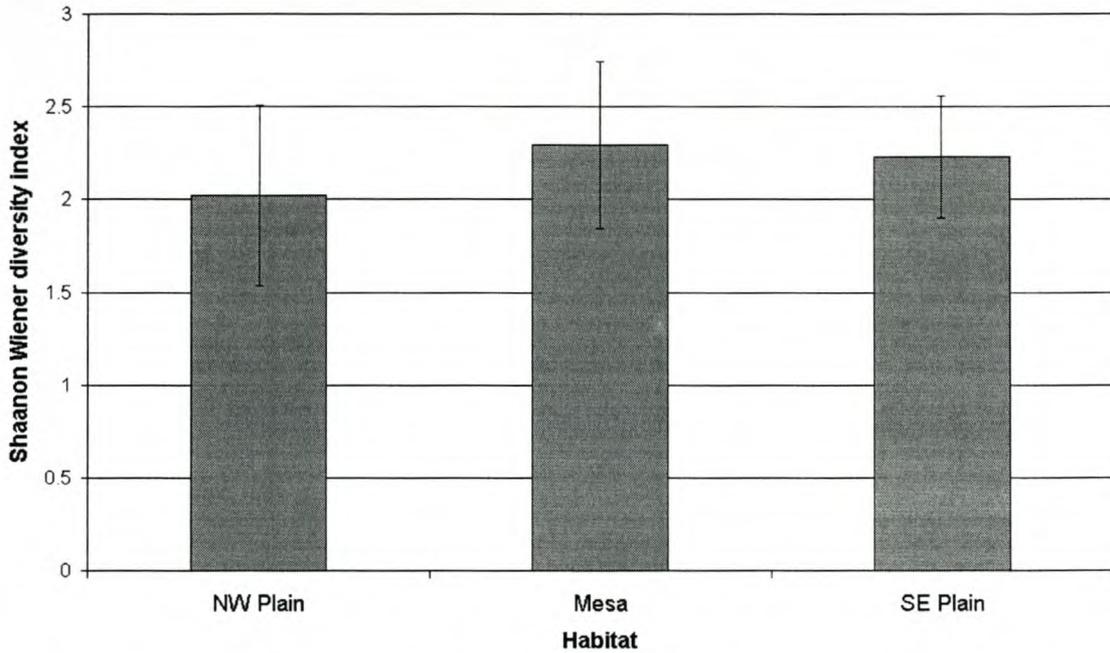


Fig. 4.1 Shannon-Wiener diversity averages for Tafelberg, Folminkskop and Buffelskop. Slopes and plateau values were combined to form one value for mesas. Data presented as averages \pm SE (Standard Error, hereafter only referred to as SE).

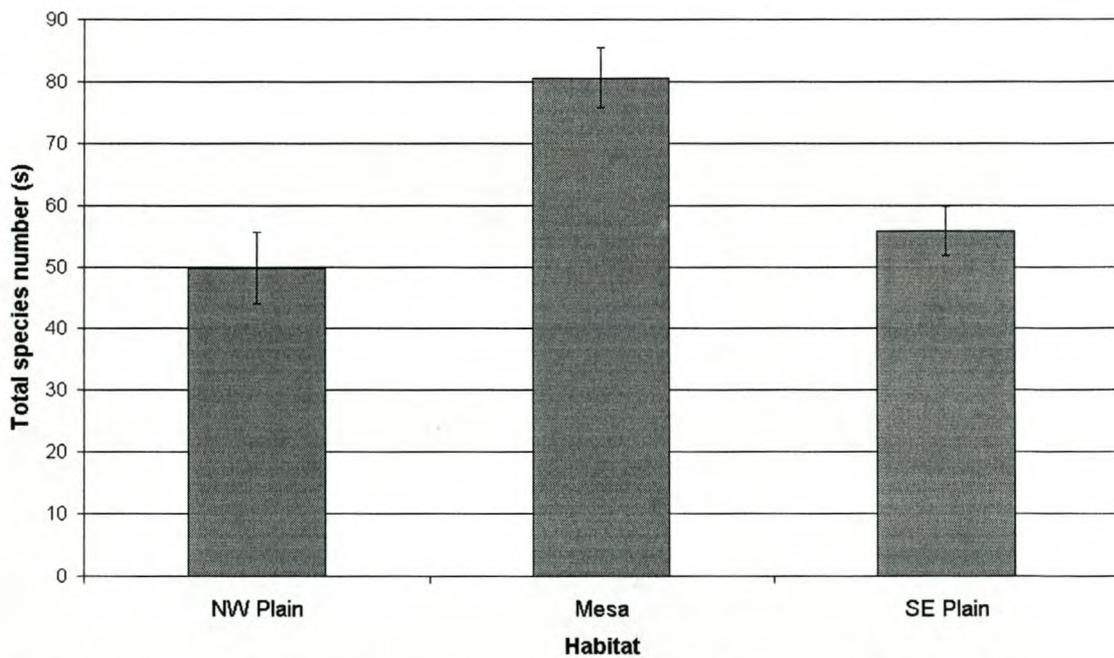


Fig. 4.2 Total species numbers (s) averages for Tafelberg, Folminkskop and Buffelskop. Slopes and plateau values were combined to form one value for mesas. Data presented as averages \pm SE.

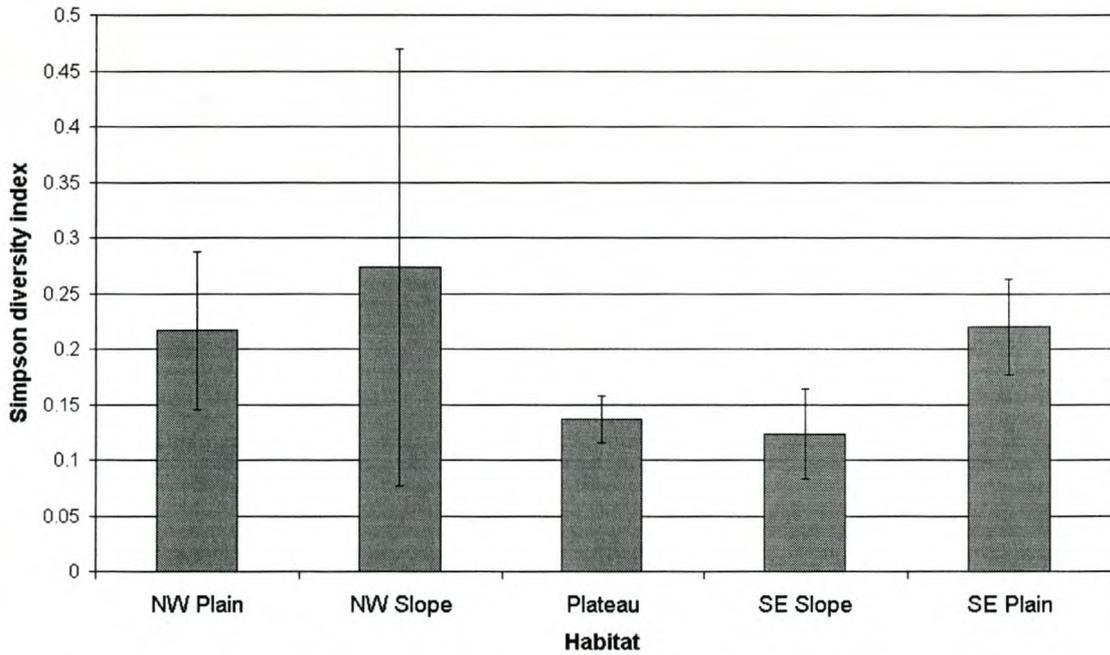


Fig. 4.3 Simpson diversity averages for Tafelberg, Folminkskop and Buffelskop. Data presented as averages \pm SE.

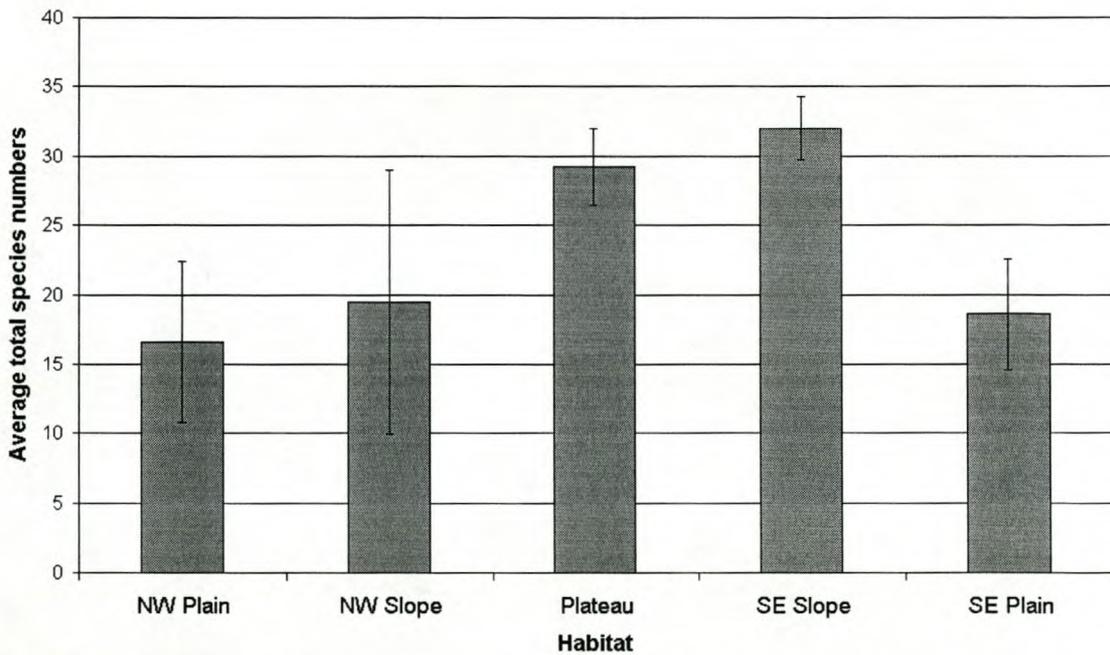


Fig. 4.4 Average total species numbers (s) for Tafelberg, Folminkskop and Buffelskop. Data presented as averages \pm SE.

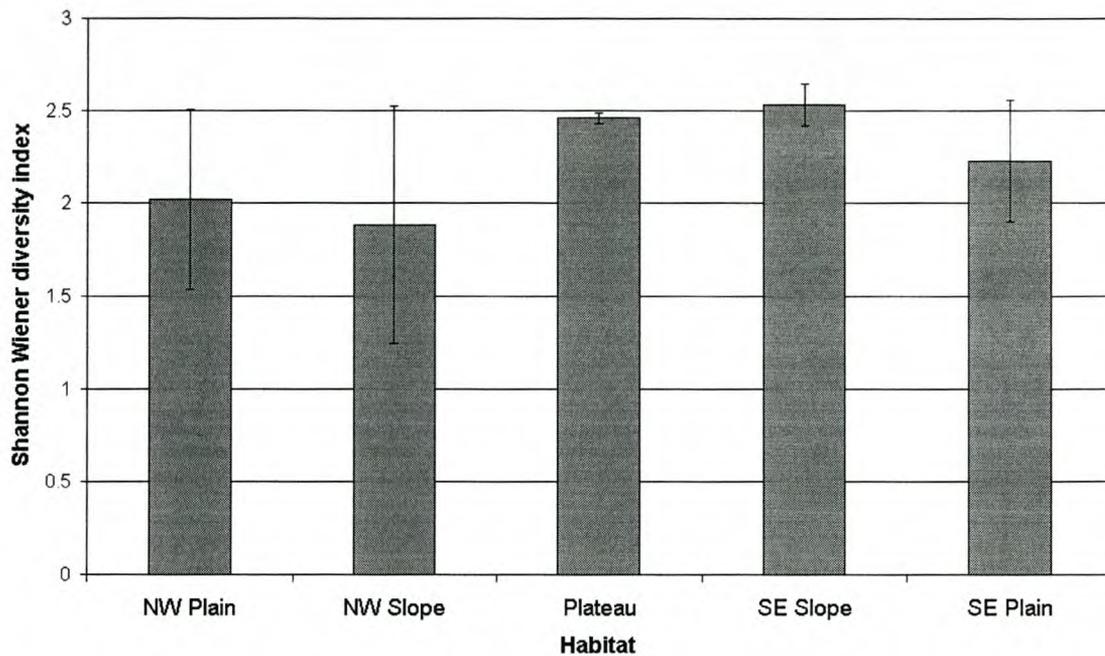


Fig. 4.5 Shannon-Wiener diversity averages for Tafelberg, Folminkskop and Buffelskop. Data presented as averages \pm SE.

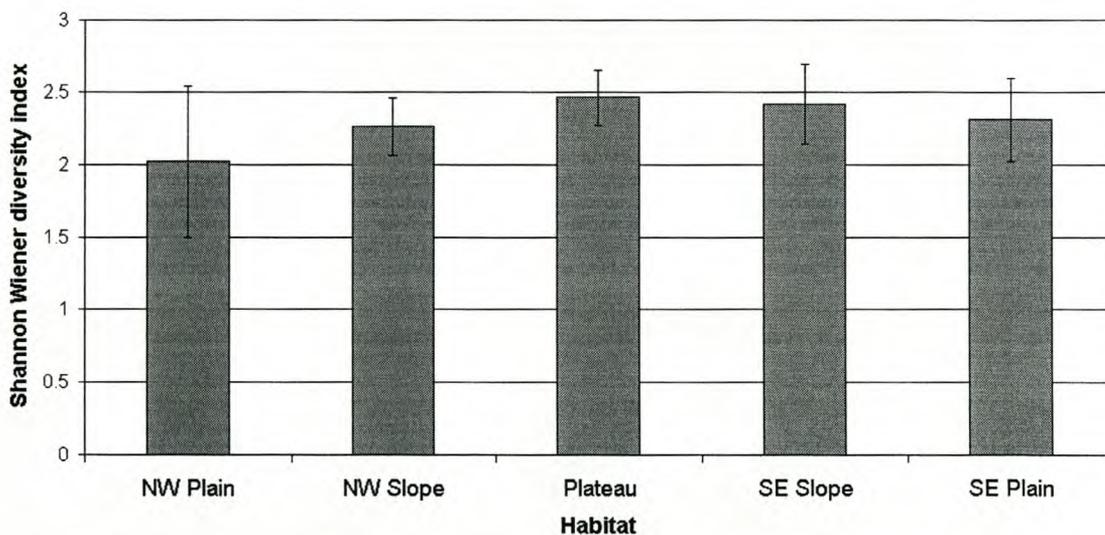


Fig. 4.6 Shannon-Wiener diversity averages for Folminkskop. Individual plots values have been combined into one average value per habitat. Data presented as averages \pm SE.

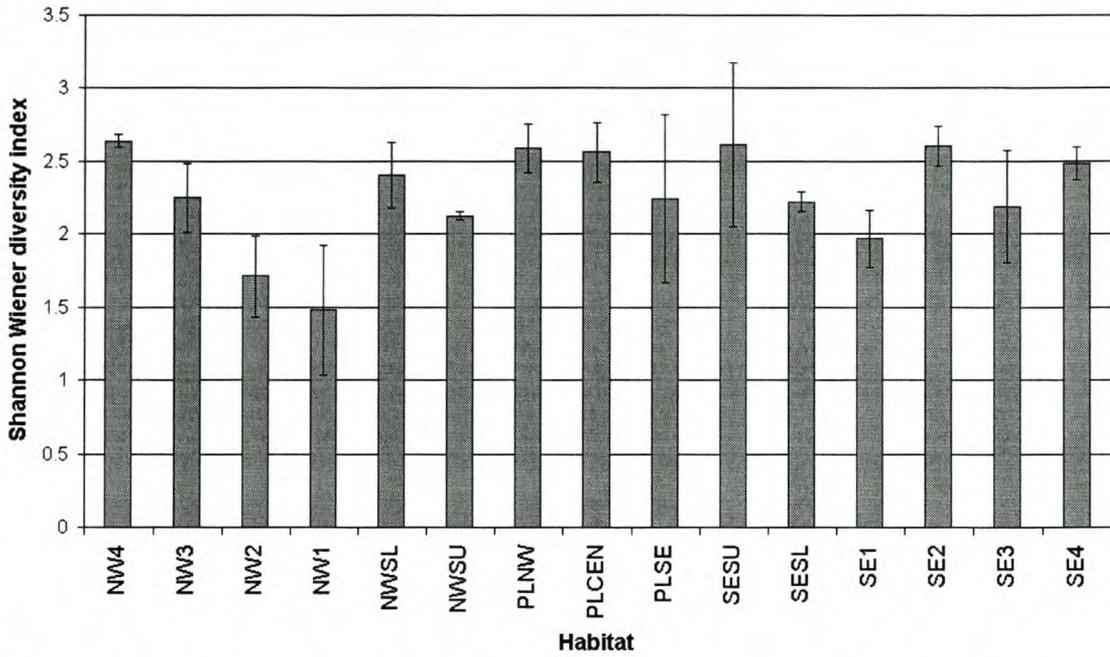


Fig. 4.7 Shannon-Wiener diversity averages for Folminkskop. Values for individual plots in the major habitats are presented. Data presented as averages \pm SE.

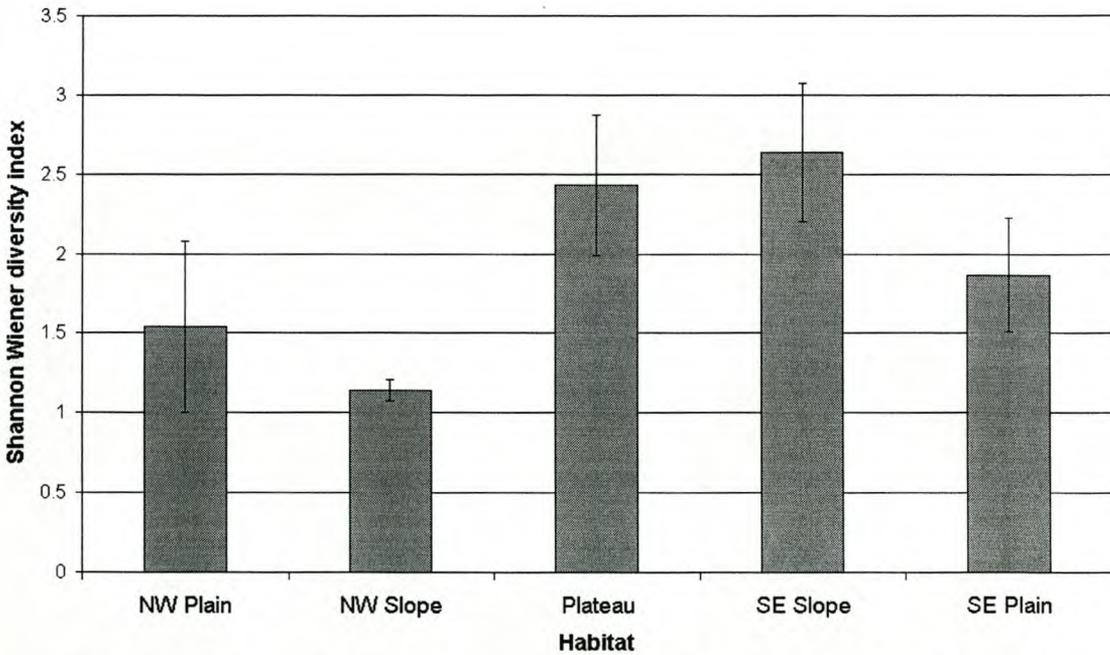


Fig. 4.8 Shannon-Wiener diversity averages for Buffelskop. Individual plots values have been combined into one average value per habitat. Data presented as averages \pm SE.

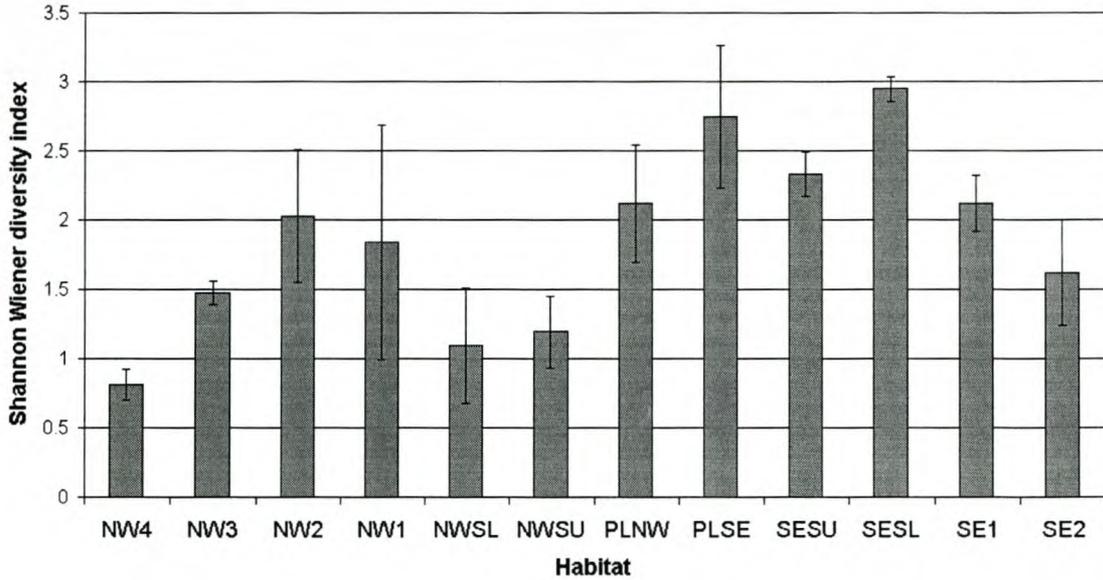


Fig. 4.9 Shannon-Wiener diversity averages for Buffelskop. Values for individual plots in the major habitats are presented. Data presented as averages \pm SE.

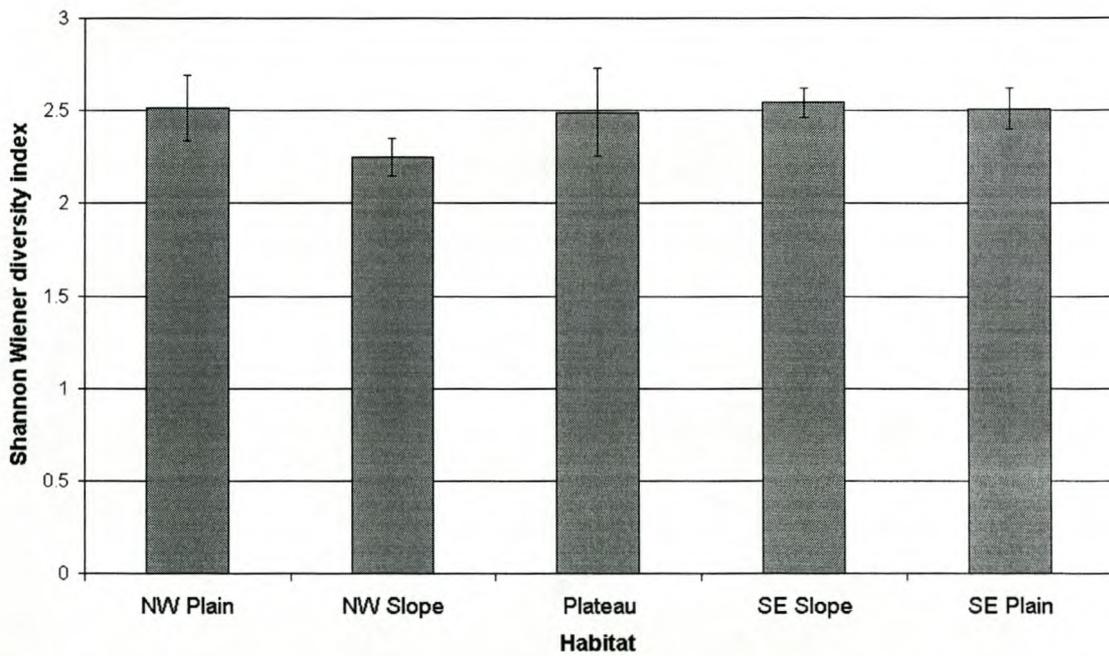


Fig. 4.10 Shannon-Wiener diversity averages for Tafelberg. Individual plots values have been combined into one average value per habitat. Data presented as averages \pm SE.

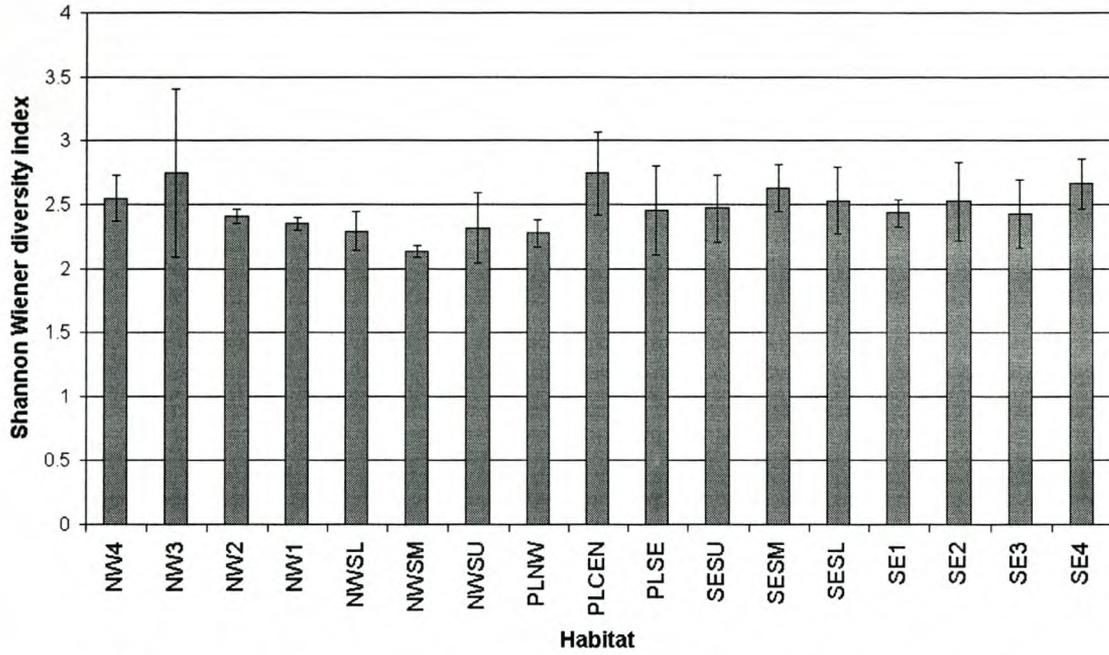


Fig. 4.11 Shannon-Wiener diversity averages for Tafelberg. Values for individual plots in the major habitats are preserved. Data presented as averages \pm SE.

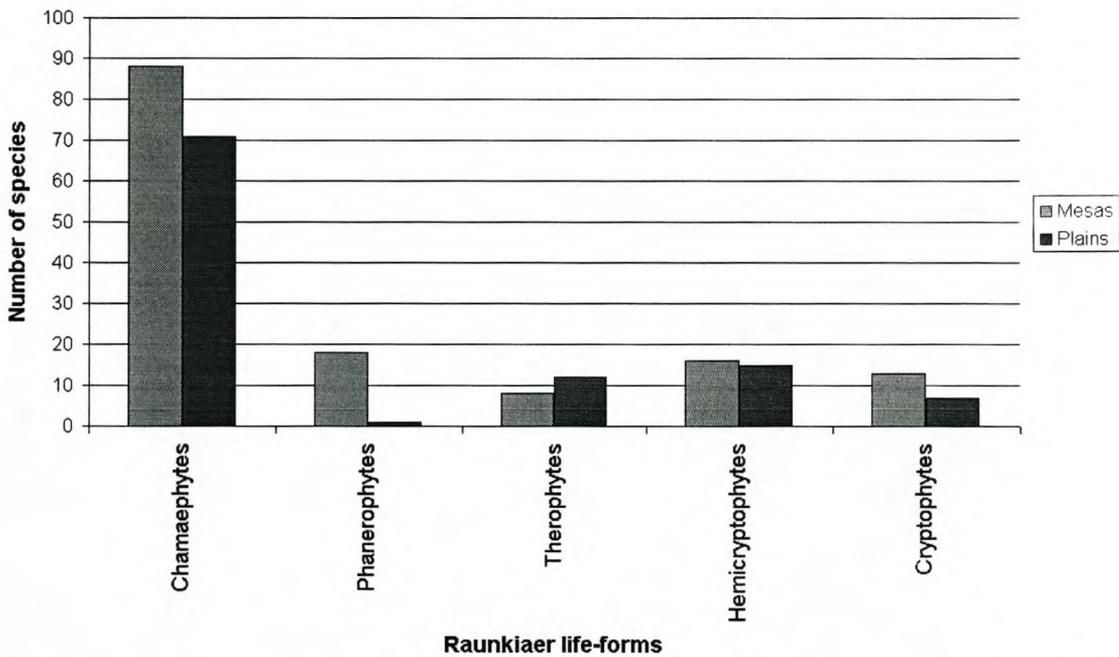


Fig. 4.12 Relative proportions of Raunkiaer life-forms on the mesas versus plains habitats.

On average, mesa habitats were higher in diversity compared to the surrounding plains habitats (Fig. 4.1; Fig. 4.2). SE slopes were higher in diversity than NW slopes (Fig. 4.3; Fig. 4.4; Fig. 4.5), with the most diverse habitats being the plateaux and SE slopes. These differences were, however, not significant, with plains communities being almost equally as diverse as mesa communities. High variability in the data became obvious when the data were examined in more detail. Folminkskop had slightly higher Shannon-Wiener Diversity Indices compared to the surrounding plains, although these differences were not significant due to large error bars (Fig. 4.6). Significant differences existed between individual sites sampled (Fig. 4.7), but these differences were lost when averages were used (Fig. 4.6). Similar significant differences were also apparent for Buffelskop (Fig. 4.8 & Fig. 4.9) and Tafelberg (Fig. 4.10 & Fig. 4.11), although Tafelberg's data were less variable. Both mesa and plains habitats were equally diverse in growth forms (Fig. 4.12). Mesa habitats had a higher proportion phanerophytes in comparison to plains habitats (Fig. 4.12).

4.3.3 How do the three mesas differ from one another in terms of diversity?

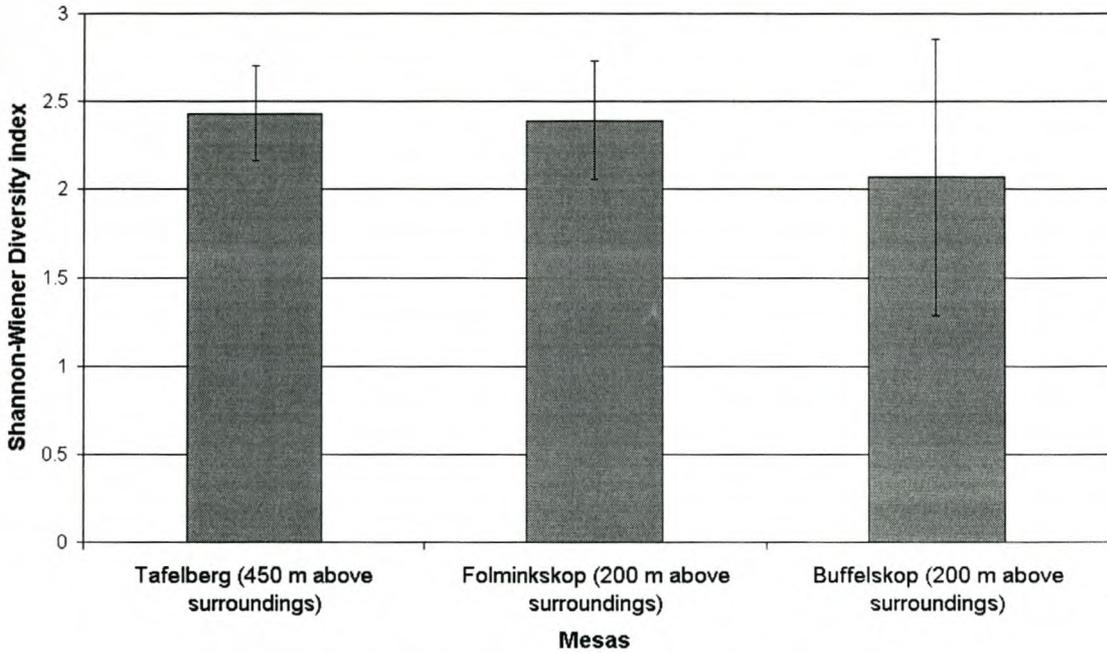


Fig. 4.13 Average Shannon-Wiener diversity per mesa (plains excluded). Data presented as averages \pm SE.

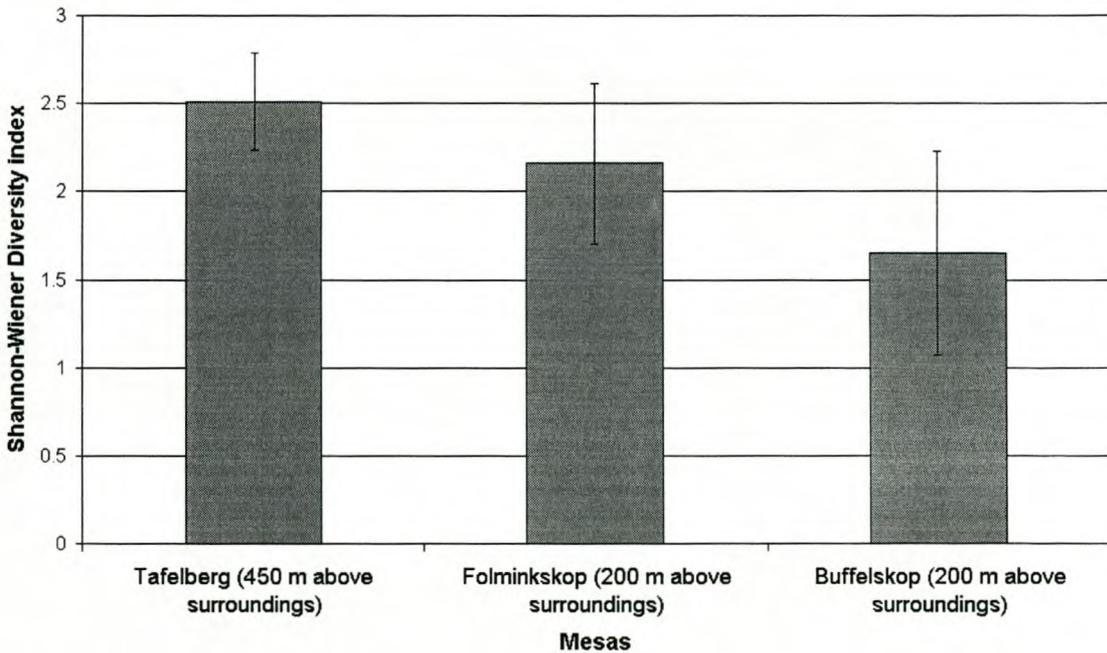


Fig. 4.14 Average Shannon-Wiener diversity per mesa (plains alone, mesa excluded). Data presented as averages \pm SE.

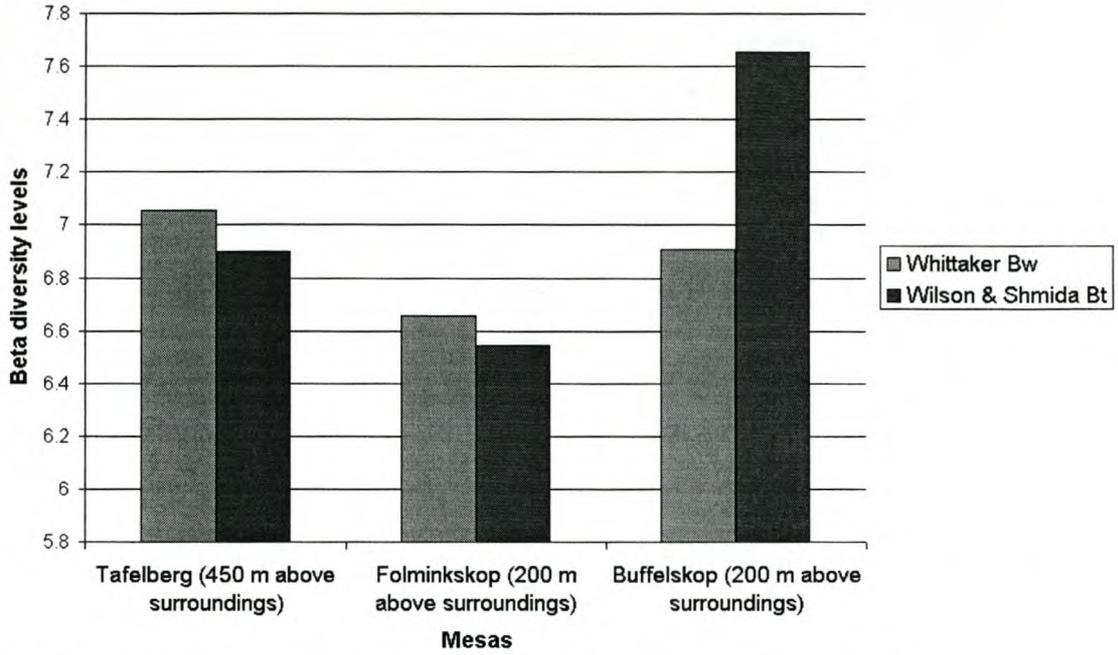


Fig. 4.15 Whittaker and Wilson & Shmida Beta Diversity values for Tafelberg, Folminkskop and Buffelskop (all sites).

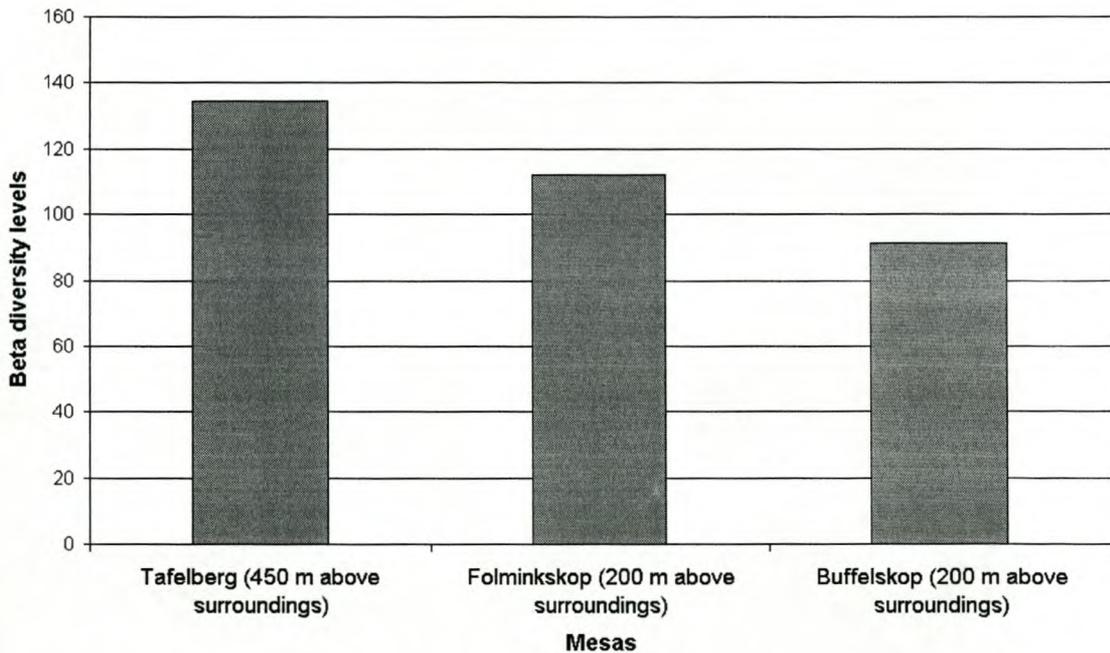


Fig. 4.16 Cody Beta Diversity values for Tafelberg, Folminkskop and Buffelskop (all sites).

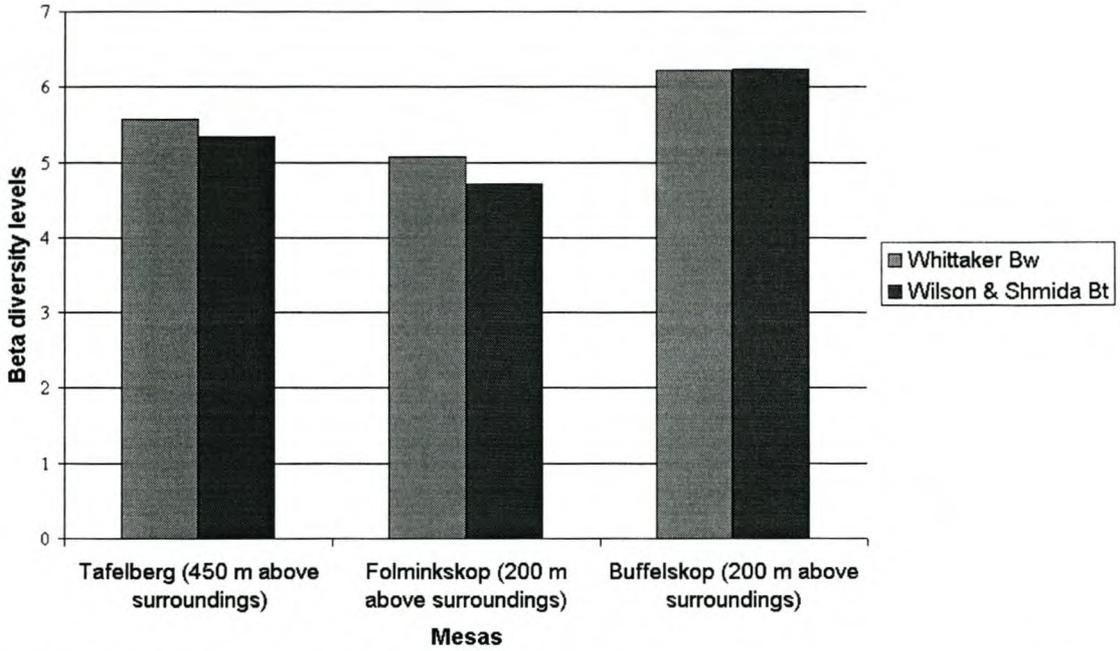


Fig. 4.17 Whittaker and Wilson & Shmida Beta Diversity values for the transect NW plains to plateau (Tafelberg, Folminkskop and Buffelskop).

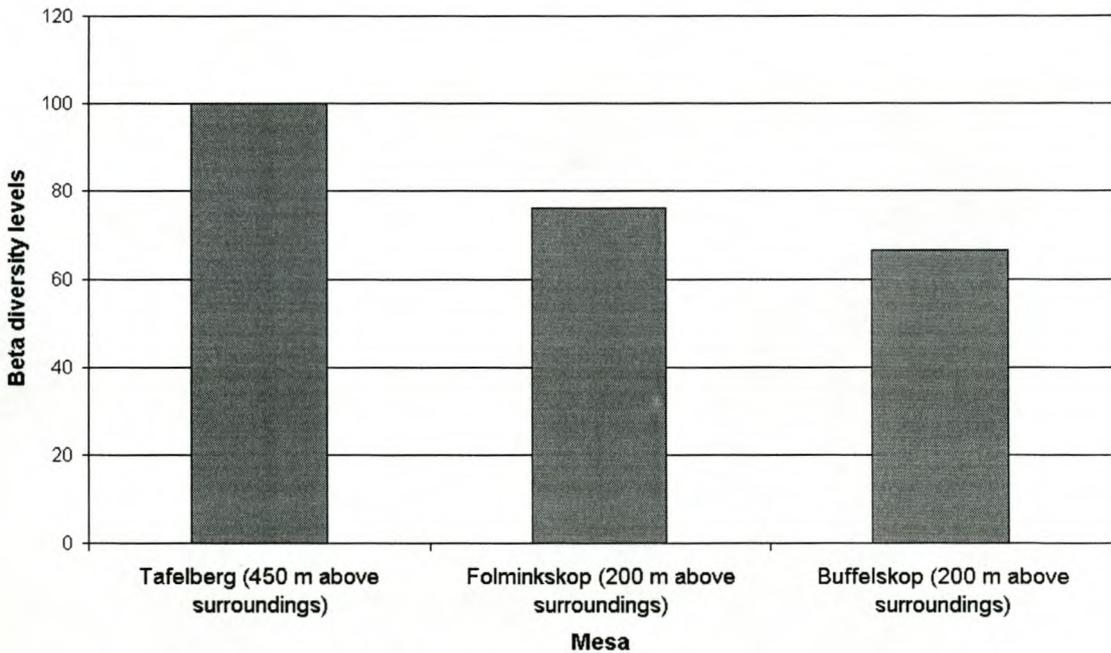


Fig. 4.18 Cody Beta Diversity values for the transect NW plains to plateau (Tafelberg, Folminkskop and Buffelskop).

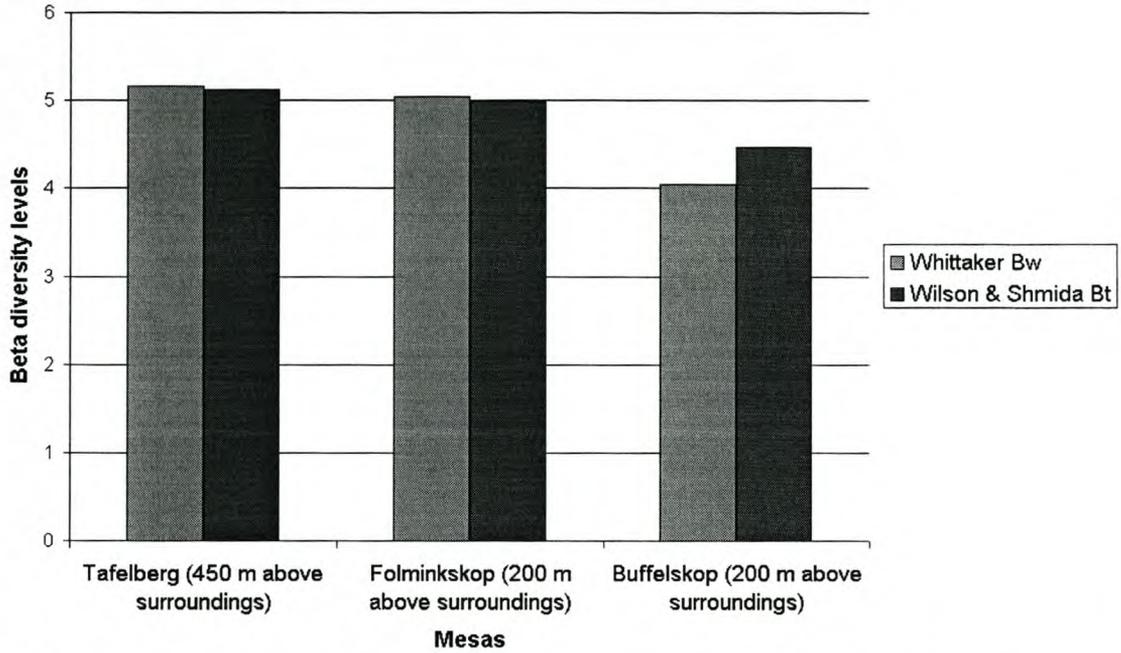


Fig. 1.19 Whittaker and Wilson & Shmida Beta Diversity values for the transect SE plains to plateau (Tafelberg, Folminkskop and Buffelskop).

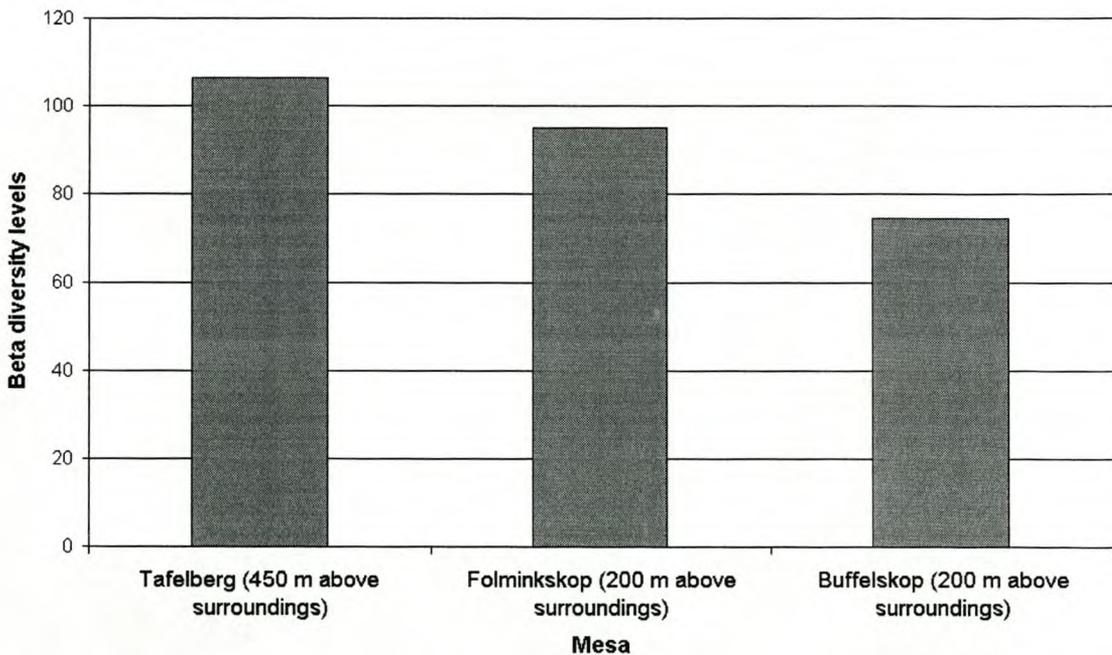


Fig. 4.20 Cody Beta Diversity values for the transect SE plains to plateau (Tafelberg, Folminkskop and Buffelskop).

Average Shannon-Wiener diversity was highest for Tafelberg, followed by Folminkskop. Buffelskop had the lowest values (Fig. 4.13). The plains surrounding Tafelberg were more diverse than the plains surrounding the other mesas, with Buffelskop's plains being the lowest in diversity (Fig. 4.14). These differences were, however, not significant.

Total Beta Diversity was highest for Tafelberg (Whittaker Diversity Index) and Buffelskop (Wilson & Shmida Diversity Index) and lowest for Folminkskop (Fig. 4.15). Tafelberg had the highest Cody Diversity Index, with Folminkskop second highest and Buffelskop lowest (Fig. 4.16).

Beta Diversity for the transect NW plains to plateau was highest for Buffelskop, with Folminkskop having the lowest values and Tafelberg in an intermediate position (Fig. 4.17). Cody Diversity Indices for the same transect had Tafelberg as being most diverse, followed by Folminkskop and lastly Buffelskop (Fig. 4.18).

Beta Diversity for the transect SE plains to plateau was highest for Tafelberg, with Buffelskop having the lowest values and Folminkskop in an intermediate position (Fig. 4.19). Cody Diversity Indices for the same transect had Tafelberg as being most diverse, followed by Folminkskop and lastly Buffelskop (Fig. 4.20).

4.3.4 How similar/different are the plateaux, slopes and plains from each other for each of the mesas?

	Tafelberg		Folminkskop		Buffelskop	
Total sp. number	157	-	131	-	94	-
	Shared sp.	%	Shared sp.	%	Shared sp.	%
Plains & Slopes	31	19.8	21	16.0	11	11.7
Plains & plateau	22	14.0	19	14.5	13	13.8
Plateau & slopes	27	17.2	36	27.5	24	25.5
Mesa & plains	38	24.2	26	19.9	17	18.1

Table 4.1 Shared species between the different habitats of the three mesas. Comparisons were within mesas and not between mesas.

Tafelberg shared far less species between its plateau and slopes than Folminkskop and Buffelskop (Fig. 4.1). However, in total, Tafelberg shared more species with its surroundings than the smaller Folminkskop and Buffelskop. Plains and slopes of Tafelberg had most species in common, followed by that of Folminkskop. Buffelskop had least species in common between its plains and slopes (Fig. 4.1).

4.4 Discussion

4.4.1 What is the composition of the vegetation like in terms of total species numbers, dominant families and genera?

Composition of vegetation in the Middelburg District was typical of Nama-karoo communities, dominated by Asteraceae, Poaceae, Fabaceae and Aizoaceae (Shmida 1985; Werger 1978). Chenopodiaceae is of low importance in the Nama-karoo and succulent karoo (Cowling & Hilton-Taylor 1999), but was of relatively high importance in the Middelburg District (see Appendix 4.7.1). This could have been as a result of the many disturbed areas such as old lands or recently ploughed areas, which are favoured by this family.

4.4.2 Are the mesas higher in diversity than the surrounding landscape and are they therefore of special management/conservation value?

Mesas were expected to be significantly more diverse than the surrounding landscape due to increased habitat diversity, less intense grazing pressure, increased rockiness, less extreme conditions and an increase in precipitation due to their elevated nature (see 4.1.2).

However, mesas were not significantly more diverse, although there did seem to be a general trend of slightly increased diversity in comparison to the surrounding landscape. Plains habitats such as those surrounding Tafelberg were often equally as diverse as mesa habitats and were in some cases even more diverse than mesa habitats.

Diversity in the southern Free State Province was lower on mesas than on the plains (Malan *et al.* 1998), comparing well with similar results where Cowling *et al.* (1989) found diversity on mesas in the karoo not to be higher than that of the adjacent plains.

More species were however sampled from upland habitats than from plains habitats, indicating that uplands (such as mesas or hills) might have a larger species pool than flatlands although they have similar Alpha Diversity (Cowling *et al.* 1989). More plant species were collected (including all areas outside the plots as well) in total from mesa habitats in the Middelburg District than from plains habitats, indicating that this might be the case for Middelburg as well. A bigger species pool but similar Alpha Diversity values indicated a more diverse microhabitat on the mesas in comparison with the surrounding flatlands.

Mesas in the northern parts of the Nama-karoo in Namibia (Burke *et al.* 2002) were significantly more diverse than the surrounding landscape. Middelburg is situated in the eastern parts of the Nama-karoo and receives relatively high rainfall in comparison with more arid parts of the Nama-karoo such as those in Namibia. Mesas in Middelburg could be considered to be relatively mesic islands in a matrix of xeric plains, but the differences in aridity between mesas and their surroundings were far greater in the more arid parts of the Nama-karoo than in Middelburg. Greater differences in aridity between mesas and their surroundings in Namibia, possibly contributed to the mesas being more distinct islands of diversity compared to the less diverse plains (Burke *et al.* 2002). However, it is possible that differences in substrate between Middelburg and Namibia might also have contributed to the differences in diversity found between the two areas, but this was not tested for by Burke *et al.* (2002).

The slightly higher diversity on mesas can be attributed to a more favourable microhabitat. Rocky habitats such as the mesas often have higher habitat heterogeneity (Montana 1990), higher soil moisture heterogeneity and more suitable microsites. These in turn are positively correlated with higher species diversity (Olsvig-Whittaker 1983). Non-equilibrium theory states that diversity would be at a maximum at an intermediate level of disturbance (Grime 1973). Plains habitats were much more disturbed than mesas in terms of grazing, trampling and erosion. Fewer plants on the plains were able to cope with the adverse conditions occurring there. Disturbance levels on the slopes might have been at an intermediate level of disturbance through grazing by natural herbivores, thus increasing diversity by not allowing any species to become dominant and out compete all others. The

microclimate of the plains was subject to more variable and sometimes extreme fluctuations in moisture and temperature conditions, or extreme conditions of drought and heat in comparison with the mesas. Instability is known to decrease diversity (Whittaker 1972; Whittaker 1975).

Simpson Diversity Indices for the plains were slightly higher than that of the mesas, indicating a higher dominance structure of certain species on the plains. Certain annual grasses and undesirable (unpalatable, spinescent and toxic) shrubs were present in unnaturally high concentrations in the vegetation (Chapter 5), possibly the result of a history of continuous grazing pressure favouring undesirable plants. Dominance of certain species on the plains could also have led to a decrease in diversity, since dominance often has an inverse effect on diversity through the control of moisture and light by dominant species (Whittaker 1972; Whittaker 1975).

Mesas and plains in the Middelburg District had a wide array of growth forms. Plains communities were characterised by chamaephytes, hemicryptophytes and cryptophytes, with phanerophytes often restricted to conditions of higher soil moisture such as drainage lines or riverbeds. Mesa communities were characterised by an abundance of different sizes of phanerophytes, but also by the abundance of chamaephytes, hemicryptophytes and cryptophytes. The occurrence of phanerophytes on the mesas was much higher than on the plains, a possible result of the moister microhabitat on mesas (Roberts 1965). A strong presence of woody species was also recorded on rocky outcrops in the grassland biome (Stuart-Hill *et al.* 1984), due to a more favourable moisture regime associated with high percentages of surface rocks and rocks in the soil profile.

Unpalatable, spinescent and toxic plants were more common on the plains than on the mesas (personal observation). Mesa habitats were often characterised by the high frequency of palatable grasses such as *Themeda triandra* and *Digitaria eriantha*, while the numbers of unpalatable species like *Chrysocoma ciliata* and *Ruschia intricata* were very low. Undesirable plants (unpalatable, spinescent and toxic) could potentially have developed higher cover values on the plains due to their ability to set more seed in comparison with palatable species that were continuously grazed (Milton 1992; Milton 1995).

Plateau and SE slope habitats were slightly more diverse on average than the other slope and plains habitats. SE slopes are known to be cooler habitats due to aspect (Malan *et al.* 1998), while plateau habitats would also have received elevated precipitation due to altitudinal differences. Increased diversity is often linked with an increase in precipitation (Naveh & Whittaker 1979). In arid zones such as Middelburg optimum precipitation for maximum diversity might have been maximum precipitation such as that of a mesa plateau due to the arid nature of the environment. SE slopes were more diverse than NW slopes. NW slopes represent the warmest aspect in the Southern Hemisphere, while SE slopes represent the coolest, moistest aspect. Malan *et al.* (1998) also found southern slopes to be more diverse than northern slopes in the southern Free State Province, and ascribed this to the difference between the warmer northern slopes and the cooler moister southern slopes. Increased diversity was linked to increased moisture availability (Naveh & Whittaker 1979) on the SE aspect.

Patterns of Alpha Diversity across the Middelburg landscape were strongly linked to pockets of diversity in localised patches in the landscape. Abnormalities in Alpha Diversity values could be attributed to moisture heterogeneity, as influenced by factors such as slope, rockiness, soil depth and soil texture, as well as the influence of disturbance and overgrazing (Chapter 5). Pockets of diversity, as influenced by these factors, made the data highly variable. Sites exceptionally low or high in species diversity might have been overlooked if only averages were used instead of individual site values.

Vegetation in the Middelburg District consisted of two completely different habitat types supporting communities that were very different from each other but equally diverse. This was also reflected in the classification of communities (Chapter 6) with the main division in the Twinspan table being between mesas communities and plains communities.

4.4.3 How do the three mesas differ from one another in terms of diversity?

Tafelberg (450 m above surroundings) had slightly higher average Alpha Diversity than Folminkskop (200 m above surroundings) and Buffelskop (200 m above

surroundings), with Buffelskop being least diverse. These trends were however not significant. Tafelberg was much higher (250 m higher) than the other 2 mesas. Slightly higher average Alpha Diversity values were probably due to more diverse microhabitats with an increase in mesa area. Higher mesas also received, on average, more precipitation, possible contributing to the slightly higher diversity found on Tafelberg. Folminkskop and Buffelskop were of equal size, but Buffelskop was slightly less diverse. Slope angles on Buffelskop were sometimes so steep and unstable that some slopes were almost denuded of vegetation, and consequently very low in diversity. Buffelskop was also more accessible to livestock and consequently was grazed more intensely than the other two mesas, possible contributing to a decreased diversity (Chapter 5).

Both Tafelberg and Folminkskop were dolerite capped, but Buffelskop primarily consisted out of sandstone. Relieves of Buffelskop often plotted out differently than those of Tafelberg and Folminkskop in the ordination diagrams in Chapter 5, indicating distinct differences in substrate compared to the substrates of Tafelberg and Folminkskop (see Chapter 5). The lower average Alpha Diversity values for Buffelskop (despite being the same size as Folminkskop), in comparison with Alpha Diversity values for Tafelberg and Folminkskop, could possibly also be attributed to differences between more doleritic soils of Tafelberg and Folminkskop compared to the sandstone dominated soils of Buffelskop.

The plains surrounding Tafelberg had higher average Alpha Diversity values than the plains of Folminkskop and Buffelskop, with Buffelskop's plains being the lowest in diversity. This possibly reflected the presence of areas of decreased diversity in the latter such as temporal wetlands, coupled with differences in grazing history and management between the different farms and camps. Few species were shared between mesas and their surroundings, making it unlikely that the increased diversity for the plains of Tafelberg was linked to the slightly increased diversity for the mesa relative to the other two mesas. The NW plains of Folminkskop was highly degraded in some patches, with a high cover of plants indicative of disturbance such as *Blepharis capensis*. The NW plains of Buffelskop extended into a temporal wetland area characterised by few plants and low diversity. Pockets of decreased diversity

such as these were most probably responsible for the lower averages for the plains of Folminkskop and Buffelskop relative to that of Tafelberg.

Tafelberg and Buffelskop were almost equally high in total Beta Diversity (depending on the index used), with Folminkskop in an intermediate position. High Beta Diversity values for Tafelberg could possibly be due to the effect of a more diverse microhabitat on the mesa, as caused by the increased size of the mesa in comparison with the two smaller mesas (Tafelberg was 450 m above surroundings, Folminkskop and Buffelskop both 200 m above surroundings). Folminkskop was similar to Tafelberg in shape and geology, and the lower total Beta Diversity value for Folminkskop relative to Tafelberg could be explained by the smaller mesa size in the former. Total Beta Diversity values for Buffelskop were unusually high (as diverse as Tafelberg) given that Buffelskop was the same size as Folminkskop. This could be explained by looking at the individual Beta Diversity transects. Values of Beta Diversity transects from the NW plains to the plateau for Buffelskop were higher than that of the other two mesas, with Folminkskop being the lowest. Transects done from the SE plains to the plateau showed that Tafelberg had the highest Beta Diversity value followed by Folminkskop; and lastly Buffelskop. The NW plains of Buffelskop extended into a seasonal pan area low in Alpha Diversity, while the NW slope was very steep and almost denuded of vegetation. At the same time the SE slopes were very high in Alpha Diversity. Thus the high variation in Alpha Diversity influenced the Beta Diversity values on these transects.

Species replacement rates on sandstone were found to be higher than that on dolerite for comparable environmental conditions (Palmer & Cowling 1994). This was caused by the presence of a degraded community caused by recent over-utilisation by domestic herbivores (Palmer & Cowling 1994). Species replacement rates on sandstone in the Middelburg District were also higher than that of dolerite for comparative environmental conditions and landforms. Degraded communities caused by over-utilisation, coupled with degraded slope communities due to excessively steep slopes were responsible for the relative higher species replacement rates for sandstone mesas in the Middelburg District.

In contrast to Cody Diversity Indices, Whittaker and Wilson & Shmida Diversity Indices incorporate a standardisation by average sample richness. Cody Diversity Indices do not have such a standardization and place more importance on species gain and loss along a transect. Differences between the different Beta Diversity indices in the dataset are ascribed to the differences in emphasis between Cody Diversity Indices and, on the other hand, Whittaker and Wilson & Shmida Diversity Indices (Magurran 1992).

Beta Diversity for some areas were abnormally high due to the presence of pockets of increased and decreased diversity in the landscape. Species replacement rates were higher on sandstone than on dolerite, caused by the presence of a degraded community on the sandstone mesa.

4.4.4 How similar/different are the plateaux, slopes and plains from each other for each of the mesas?

Mesas and plains shared few species. The relative proportion (%) of species shared between the plateau and slopes of a big mesa like Tafelberg (450 m above surroundings) were less than that shared between the plateaux and slopes of the smaller mesas (200 m above surroundings). This suggested that isolation of the plateau became more distinct with an increase in size of the mesa, with bigger mesas supporting more unique vegetation on their plateaux than smaller mesas.

Tafelberg mesa (plains excluded) had proportionally more species in common with the surrounding plains than did the smaller mesas with their surroundings. This seemed a contrasting result because bigger mesas would be expected to share less with the plains due their increased elevation and size, while smaller mesas would be expected to share more species between the mesa and the plains due to their relatively lower elevation. However, bigger mesas supported a more diverse array of microhabitats that enabled plains species to occupy certain sites on the slopes of the mesa, while smaller mesas had lower habitat heterogeneity and did not have sites that enable plains species to persist on the slopes of the mesa.

The relatively few species shared between mesas ($\pm 20\%$) indicated that mesas had a low potential to be used as a possible source of plants to rehabilitate plains habitats.

Species common to both habitats such as *Felicia ovata*, *Felicia muricata*, *Jamesbrittenia tysonii*, *Pentzia incana*, *Selago albida*, *Limeum aethiopicum*, *Fingerhuthia africana* and *Eragrostis obtusa* could have some future potential rehabilitation uses. These species are all highly palatable and do not seem to require specific habitat conditions for growth as they occur in all habitats in the landscape.

Plains habitats have been subject to grazing for a considerable period of time (>200 years) (Hoffman *et al.* 1999) and were in a more degraded condition than mesa habitats which were more protected from grazing due to their inaccessible nature. Mesa habitats are generally not readily utilised except by grazers (sheep put into a slope camp would be restricted to the watering point at the bottom of the slope for most of the day). Mesas are currently not under threat through human development.

Mesas were primarily different from plains by default due to the complete differences in habitat. However, some species that naturally occurred on both mesa and plains habitats before the impact of selective grazing by domestic herbivores might now be restricted to mesa habitats. Mesas represent a relictal habitat and potential safe haven for species under intense grazing pressure on the surrounding plains.

4.4.5 How does plant diversity in Middelburg compare with diversity in similar vegetation types?

Average Shannon-Wiener Alpha Diversity Indices for Middelburg (2.32) were much higher than those recorded for the Nama-karoo by Cowling *et al.* (1989), who suggested that a Phytochorological Diversity (a variation on the Shannon-Wiener Diversity Index) of 1.8 was an acceptable average for the karoo. The lowest Alpha Diversity found for Middelburg was 0.69 while values ranged up to a maximum of 3.2. The eastern parts of the Nama-karoo would be expected to have a higher diversity in comparison to average values for the karoo. Precipitation in the eastern karoo is much higher than in the rest of the karoo, with higher moisture availability being correlated to higher diversity. Values provided for the Nama-karoo might also exclude mesas and focus on plains habitats, but this was not clearly stated by Cowling *et al.* (1989).

Nama-karoo communities are much less diverse than succulent karoo communities (Cowling *et al.* 1989) which are known for their high diversity (Cowling & Hilton-Taylor 1999). The Nama-karoo is the least distinctive of all the biomes with about 10% of the species being shared with the other biomes. It has the strongest relationships with the succulent karoo and desert biomes (Cowling *et al.* 1989). Compared to the other biomes in southern Africa the Nama-karoo has a low diversity, especially if its large area is taken into account (Cowling *et al.* 1989). The highest Alpha Diversity values for Middelburg (3.2; Phytochorological Diversity – a variation on the Shannon-Wiener Diversity Index) are very low in comparison with other species rich vegetation types in South Africa such as Renosterveld (33) (Cowling *et al.* 1989).

However, Nama-karoo communities have a rich flora for a semi-arid region (Cowling *et al.* 1989), and the Middelburg District would compare favourably with other arid lands of North America and Australia. Communities in the Nama-karoo were found to be similar in patterns and determinants of diversity than those from other arid lands such as the New World (Cowling & Hilton-Taylor 1999).

4.5 Final conclusions

Mesas were not found to be higher in Alpha Diversity than their surroundings. Mesa size was not a determinant of diversity, since bigger and smaller mesas were similar in Alpha Diversity values. Mesas could be more distinct islands of diversity with an increase in aridity. SE slopes supported more diverse communities than NW slopes due to the cooler, moister microhabitats typical of SE slopes in the Southern Hemisphere. Few species was shared between mesas and their surroundings. The bigger mesa, Tafelberg, shared more species with the surrounding plains in comparison to the two smaller mesas, possibly due to a more diverse microhabitat on the slopes. Pockets of increased and decreased diversity occur across the Middelburg landscape as determined by factors such as soil depth, slope, rockiness and grazing intensity. Diversity in Middelburg compare favourable with that in other arid lands of North America and Australia.

4.6 References

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4.7 List of appendixes

Appendix 4.7.1 - Species list of the Middelburg District, arranged according to family and genus. Counts of number of species encountered per genus, number of species per family and number of genera per family are provided. Species included in this list have been sampled across the entire study area, including the plots.

ASTERACEAE (continue)	<i>Othonna picrostoides</i> Harv.			
	<i>Pegolettia baccaridifolia</i> Less.	2		
	<i>Pegolettia retrofracta</i> (Thunb.) Kies			
	<i>Pentzia globosa</i> Less.	6		
	<i>Pentzia incana</i> (Thunb.) Kuntze			
	<i>Pentzia lanata</i> Hutch.			
	<i>Pentzia punctata</i> Harv.			
	<i>Pentzia quinquefida</i> (Thunb.) Less.			
	<i>Pentzia sphaerocephala</i> DC			
	<i>Phymaspermum parvifolium</i> (DC.) Benth. & Hook. ex Jacks.	1		
	<i>Pseudognaphalium luteo-album</i> (L.) Hilliard & B.L. Burt	3		
	<i>Pseudognaphalium oligandrum</i> (DC.) Hilliard & B.L. Burt			
	<i>Pseudognaphalium undulatum</i> (L.) Hilliard & B.L. Burt			
	<i>Pteronia erythrochaeta</i> DC.	8		
	<i>Pteronia glauca</i> Thunb.			
	<i>Pteronia glomerata</i> L.f.			
	<i>Pteronia micronata</i> DC.			
	<i>Pteronia punctata</i> E. Phillips			
	<i>Pteronia sordida</i> N.E.Br.			
	<i>Pteronia stachelinoides</i> DC.			
	<i>Pteronia tricephala</i> DC.			
	<i>Rosenia humilis</i> (Less.) Bremmer	1		
	<i>Schkuhria pinnata</i> (Lam.) Cabrera	1		
	<i>Senecio cotyledonis</i> DC.	3		
	<i>Senecio linifolius</i> L.			
	<i>Senecio radicans</i> (L.f.) Sch.Bip.			
	<i>Sonchus dregeanus</i> DC.	1		
<i>Tagetes minuta</i> L.	1			
<i>Tarhonanthus camphoratus</i> L.	1			
<i>Tripteris aghillana</i> DC. var. <i>aghillana</i>	1			
<i>Ursinia nana</i> DC subsp. <i>nana</i>	1			
<i>Vernonia capensis</i> (Houtt.) Druce	2			
<i>Vernonia</i> sp.				
<i>Xanthium spinosum</i> L.	1			
AYTONIACEAE	<i>Plagiochasma rupestris</i> (G. Forst) Steph. var. <i>Rupestris</i>	1	1	1
BORAGINACEAE	<i>Lappula capensis</i> (DC.) Gurke	1	1	1
BRASSICACEAE	<i>Heliophila suavissima</i> Burch. ex DC.	1	3	2
	<i>Lepidium africanum</i> (Burm.f.) DC. subsp. <i>africanum</i> <i>Lepidium trifurcum</i> (Sond.) Marias	2		
CACTACEAE	<i>Opuntia aurantiaca</i> Lindl.	2	2	1
	<i>Opuntia lindheimeri</i> (plaint missing)			
CAMPANULACEAE	<i>Lighthfootia nodosa</i> H.Buek	1	6	2
	<i>Wahlenbergia androsacca</i> A.OC.	5		
	<i>Wahlenbergia cerna</i> (Thunb.) A.DC.			
	<i>Wahlenbergia</i> sp. <i>Wahlenbergia tenella</i> (L.f.) Lammers var. <i>tenella</i> <i>Wahlenbergia undulata</i> (L.f.) A.D.C.			
CAPPARACEAE	<i>Cadaba aphylla</i> (Thunb.) Wild	1	3	3
	<i>Dianthus basuticus</i> Burt Davy subsp. <i>basuticus</i> var. <i>basuticus</i> cf	1		
	<i>Silene burchellii</i> Oth var. <i>burchellii</i>	1		
CELASTRACEAE	<i>Gymnospora buxifolia</i>	1	1	1
CHENOPODIACEAE	<i>Atriplex nummularia</i> Lindl. subsp. <i>nummularia</i>	4	13	3
	<i>Atriplex semibaccata</i> R.Br.			
	<i>Atriplex suberecta</i> I. Verd			
	<i>Atriplex vestita</i> (Thunb.) Aellen			
	<i>Chenopodium botryodes</i> Sm.	4		
	<i>Chenopodium carinatum</i> R.Br.			
	<i>Chenopodium glaucum</i> L.			
	<i>Chenopodium mucronatum</i> Thunb.			
	<i>Salsola calluna</i> Fenzl ex C. H. Wright	5		
	<i>Salsola kali</i> L. <i>Salsola smithii</i> Botsch. <i>Salsola tuberculata</i> (Moq.) Fenzl <i>Salsola tuberculatifomis</i> Botsch.			
COMMELINACEAE	<i>Commelina africana</i> L. var. <i>africana</i>	1	1	1
CONVOLVULACEAE	<i>Convolvulus hidentatus</i> Bernh. apud C. Krauss	3	4	2
	<i>Convolvulus hoedckerianus</i> Peter			
	<i>Convolvulus sagittatus</i> Thunb.			
	<i>Turbina</i> sp.	1		
CRASSULACEAE	<i>Adromischus schuldhamus</i> (Poelln.) Poelln.	1	18	4
	<i>Cotyledon orbiculata</i> L. var. <i>orbiculata</i>	2		
	<i>Cotyledon papillaris</i> L.f.			
	<i>Crassula capitella</i> Thunb. subsp. <i>capitella</i>	14		
	<i>Crassula capitella</i> Thunb. subsp. <i>thyrsiflora</i> (Thunb.) Toelken			
	<i>Crassula cotyledonis</i> Thunb.			
	<i>Crassula dependens</i> Bolus subsp. <i>Transvaalensis</i> (Kuntze) Toelken			
	<i>Crassula lanceolata</i> (Eckl. & Zeyh.) Endl. ex Walp. subsp. <i>Lanceolata</i>			
	<i>Crassula lanuginosa</i> Harv. var. <i>lanuginosa</i>			
	<i>Crassula montana</i> Thunb. subsp. <i>quadrangularis</i> (Schonland) Toelken			
	<i>Crassula muscosa</i> L. var. <i>muscosa</i>			
	<i>Crassula obovata</i> Haw. var. <i>obovata</i>			
	<i>Crassula orbicularis</i> L.			
	<i>Crassula perfoliata sensu</i> Thunb.			
	<i>Crassula rupestris</i> Thunb. subsp. <i>rupestris</i>			
	<i>Crassula tabularis</i> Dinter cf			
	<i>Crassula tetragona</i> L. subsp. <i>acutifolia</i> (Lam.) Toelken			
<i>Kalanchoe rotundifolia</i> (Haw.) Haw.	1			
CUCURBITACEAE	<i>Cucumis myriocarpus</i> Naudin subsp. <i>leptodermis</i> (Schweick.) C. Jeffrey & P. Halliday	2	3	2
	<i>Cucumis zeyheri</i> Sond.			
	<i>Kedrostis africana</i> (L.) Cogn.	1		

CYPERACEAE	<i>Ibulostylis humilis</i> (Kunth) C.B. Clarke	1	5	4
	<i>Cyperus usitatus</i> Burch. var. <i>usitatus</i>	1		
	<i>Mariscus rehmannianus</i> C.B. Clarke	1		
	<i>Schoenoplectus decipiens</i> (Nees) J. Raynal	2		
	<i>Schoenoxiphium sparticum</i> (Wahlb.) C.B. Clarke			
DIPSACACEAE	<i>Scabiosa columbaria</i> L.	1	1	1
EBENACEAE	<i>Diospyros austro-africana</i> De Winter var. <i>microphylla</i> (Burch.) De Winter	3	3	1
	<i>Diospyros lycioides</i> Desf. subsp. <i>lycioides</i>			
	<i>Diospyros scabrida</i> (Harv. Ex Hiern) De Winter var. <i>cordata</i> (E.Mey. ex. A.DC.) De Winter			
ERIOSPERMACEAE	<i>Eriospermum</i> sp.	1	1	1
EUCLEA	<i>Euclea crispa</i> (Thunb.) Guerke	1	1	1
EUPHORBIACEAE	<i>Euphorbia brachiata</i> E. Mey. ex Boiss.	3	4	2
	<i>Euphorbia inaequilatera</i> Sond. var. <i>inaequilatera</i>			
	<i>Euphorbia mauritanica</i> L. var. <i>mauritanica</i>			
	<i>Phyllanthus incurvus</i> Thunb.	1		
FABACEAE	<i>Acacia karoo</i> Hayne	1	15	9
	<i>Indigostrum parviflorum</i> (B. Heyne ex Wight & Arn.) Schrire subsp. <i>parviflorum</i> var. <i>parviflorum</i>	1		
	<i>Indigofera acutisepala</i> Conrath ex. Baker f. (aricoma)	3		
	<i>Indigofera exigua</i> Eckl. & Zeyh.			
	<i>Indigofera sessilifolia</i> DC.			
	<i>Lessertia brachystachya</i> DC.	3		
	<i>Lessertia carnosae</i> Eckl. & Zeyh.			
	<i>Lessertia pauciflora</i> Harv. var. <i>pauciflora</i>			
	<i>Lotononis crumana</i> Burch. ex Benth.	1		
	<i>Medicago laciniosa</i> (L.) Mill.	1		
	<i>Melolobium burchelli</i> N.E.Br.	1		
	<i>Polhillia connata</i> (Harv.) C.H. Stirt.	1		
	<i>Sutherlandia frutescens</i> (L.) R.Br.	2		
	<i>Sutherlandia microphylla</i> Burch. Ex DC.			
GERANIACEAE	<i>Monsonia brevirostrata</i> R.Knuth	1	7	2
	<i>Pelargonium abrotanifolium</i> (L.f.) Jacq.	6		
	<i>Pelargonium aridum</i> R.A. Dyer			
	<i>Pelargonium dichondrifolium</i> DC.			
	<i>Pelargonium multicaule</i> Jacq. subsp. <i>multicaule</i>			
	<i>Pelargonium ramosissimum</i> (Cav.) Willd.			
HYACINTHACEAE	<i>Albuca bifoliata</i> R.A. Dyer	4	10	5
	<i>Albuca juncifolia</i> Baker			
	<i>Albuca setosa</i> Jacq. FP			
	<i>Albuca</i> sp.			
	<i>Dipcadi</i> sp.	1		
	<i>Ornithogallum</i> sp.	3		
	<i>Ornithogallum</i> sp.			
	<i>Ornithogallum delarouche</i> subsp. <i>aridum</i>			
	<i>Rhadamanthus</i> sp.	1		
<i>Urginea</i> sp.	1			
ILLECEBRACEAE	<i>Herniaria erckertii</i> Herm. subsp. <i>erckertii</i> var. <i>erckertii</i>	2	2	1
	<i>Herniaria erckertii</i> Herm. subsp. <i>pulvinata</i> Chaudri			
IRIDACEAE	<i>Gladiolus permealibis</i> D.Delaroche subsp. <i>edulis</i> (Burch. ex Ker Gawl.) Oberm.	1	4	3
	<i>Gynandriris simulans</i> (Baker) R.C. Foster	1		
	<i>Moraea pallida</i>	2		
	<i>Moraea polystachya</i> (Thunb.) Ker Gawl.			
LAMIACEAE	<i>Leonotis acynifolia</i> (Burm.f.) Iwarsson	1	6	4
	<i>Salvia namaensis</i> Schinz	2		
	<i>Salvia verbenaca</i> L.			
	<i>Stachys cymbalaria</i> Briq.	2		
	<i>Stachys linearis</i> Burch. ex Benth.			
	<i>Teucrium africanum</i> Thunb.	1		
LOGANIACEAE	<i>Buddleja glomerata</i> Wendl. f.	1	1	1
MALVACEAE	<i>Abutilon sonnerati</i> (Cav.) Sweet	1	4	3
	<i>Anisodonteia bryoniifolia</i> (L.) Bates	1		
	<i>Hibiscus pusillus</i> Thunb.	2		
	<i>Hibiscus trionum</i> L.			
MENISPERMACEAE	<i>Cissampelos capensis</i> L.f.	1	1	1
MESEMBRYANTHE	<i>Aridaria noctiflora</i> (L.) Schwantes subsp. <i>straminea</i> (Harv.) Gerbaulet	1	13	10
	<i>Drosanthemum duplexiae</i> L.Bolus	1		
	<i>Mesembryanthemum karrooense</i> L. Bolus	1		
	<i>Mestoklema elatum</i> N.E. Br. ex Glen	2		
	<i>Mestoklema tuberosum</i> (L.) N.E.Br. ex Glen var. <i>tuberosum</i> cf			
	<i>Phyllobolus splendens</i> (L.) Gerbaulet subsp. <i>splendens</i>	1		
	<i>Psilocaulon coriarium</i> (Burch.) N.E.Br.	2		
	<i>Psilocaulon junceum</i> (Haw.) Schwantes			
	<i>Rabiea albinota</i> (Haw.) N.E. Br. var. <i>albinota</i>	1		
	<i>Ruschia britteniae</i> L.Bolus	2		
	<i>Ruschia intricata</i>			
	<i>Stomatium middelburgense</i> L.Bolus cf	1		
	<i>Trichodiadema rogersiae</i> L. Bolus	1		
	MYRSINACEAE	<i>Myrsine africana</i> L.		
OLEACEAE	<i>Olea europaea</i> L. subsp. <i>africana</i> (Mill.) P.S.Green	1	1	1
OXALIDACEAE	<i>Oxalis depressa</i> Eckl. & Zeyh.	3	3	1
	<i>Oxalis heterophylla</i> DC.			
	<i>Oxalis smithiana</i> Eckl. & Zeyh.			
PAPAVERACEAE	<i>Argemone mexicana</i> L. forma <i>mexicana</i>	2	2	1
	<i>Argemone ochroleuca</i> Sweet subsp. <i>ochroleuca</i>			

POACEAE	<i>Aristida adscensionis</i> L.	2	36	25
	<i>Aristida diffusa</i> Trin. subsp. <i>diffusa</i>			
	<i>Cenchrus ciliaris</i> L.	1		
	<i>Chloris virgata</i> Sw.	1		
	<i>Cymbopogon plurinodis</i> (Stapf) Stapf ex Burt Davy	1		
	<i>Cynodon incompletes</i> Nees	1		
	<i>Dactyloctenium giganteum</i> Fisher & Schweick.	1		
	<i>Digitaria eriantha</i> Steud.	1		
	<i>Ehrharta calycina</i> Sm var. <i>calycina</i>	1		
	<i>Enneapogon desvauxii</i> P.Beauv.	2		
	<i>Enneapogon scorparius</i> Lehm.			
	<i>Eragrostis bergiana</i> (Kunth) Trin.	7		
	<i>Eragrostis bicolor</i> Nees			
	<i>Eragrostis chloromelas</i> Steud.			
	<i>Eragrostis curvula</i> (Schrad.) Nees			
	<i>Eragrostis lehmanniana</i> Nees var. <i>lehmanniana</i>			
	<i>Eragrostis obtusa</i> Munro ex Ficalho & Hiem			
	<i>Eragrostis tef</i> (Zucc.) Trotter			
	<i>Eriachys paspaloides</i> (Vahl) Lanza & Mattei	1		
	<i>Fingerhuthia africana</i> Lehm.	1		
	<i>Heteropogon contortus</i> (L.) Roem. & Schult.	1		
	<i>Hyparrhenia hirta</i> (L.) Stapf	1		
	<i>Melica racemosa</i> Thunb.	1		
	<i>Oropetium capense</i> Stapf.	1		
	<i>Panicum maximum</i> Jacq.	2		
	<i>Panicum schinzii</i> Hack.			
	<i>Phragmites mauritanus</i> Kunth	1		
	<i>Setaria verticillata</i> (L.) P.Beauv.	1		
	<i>Sorghum bicolor</i> (L.) Moench subsp. <i>drummondii</i> (Steud.) de Wet	1		
	<i>Sporobolus fimbriatus</i> (Trin.) Nees	1		
	<i>Stipagrostis obtusa</i> (Delile) Nees	1		
	<i>Themeda triandra</i> Forssk.	1		
	<i>Tragus berteronianus</i> Schult.	2		
	<i>Tragus koelerioides</i> Asch.			
	<i>Urochloa brachyura</i> (Hack.) Stapf	2		
	<i>Urochloa panicoides</i> P.Beauv.			
POLYGALACEAE	<i>Polygala asbestina</i> Burch.	2	2	1
	<i>Polygala ephedroides</i> Burch.			
POLYGONACEAE	<i>Polygonum aviculare</i> L.	1	2	2
	<i>Rumex lanceolatus</i> Thunb.	1		
PORTULACACEAE	<i>Anacampseros albidiflora</i> Poelln.	1	4	3
	<i>Portulaca hereroensis</i> Schinz	2		
	<i>Portulaca oleracea</i> L.			
	<i>Talinum caffrum</i> (Thunb.) Eckl. & Zeyh.	1		
RANUNCULACEAE	<i>Clematis brachiata</i> Thunb.	1	1	1
ROSACEAE	<i>Cliffortia dispar</i> weim.	1	1	1
RUBIACEAE	<i>Anthospermum monticola</i> Puff	1	2	2
	<i>Galium capense</i> Thunb. subsp. <i>garijense</i> (Sond.) Puff	1		
SANTALACEAE	<i>Colpoon compressum</i> P.J. Bergius	1	5	2
	<i>Thesium hystrix</i> A.W.Hill	4		
	<i>Thesium lineatum</i> L. f.			
	<i>Thesium</i> sp.			
	<i>Thesium spartioides</i> A.W.Hill			
SCROPHULARIACEAE	<i>Alectra orobanchoides</i> Benth.	1	7	5
	<i>Aptosimum procumbens</i> (Lehm) Steud.			
	<i>Jamesbrittenia atropurpurea</i> (Benth.) Hillard subsp. <i>atropurpurea</i>	2		
	<i>Jamesbrittenia tysonii</i> (Hiem) Hilliard			
	<i>Nemesia cynanchifolia</i> Benth.	2		
	<i>Nemesia</i> sp.			
	<i>Sutera halmifolia</i> (Benth.) Kuntze	1		
SELAGINACEAE	<i>Selago albida</i> Choisy	4	4	1
	<i>Selago geniculata</i>			
	<i>Selago paniculata</i>			
	<i>Selago saxatilis</i>			
SOLANACEAE	<i>Lycium acutifolium</i> E.Mey. ex Dunal	3	6	2
	<i>Lycium cinereum</i> Thunb. Sensu lato			
	<i>Lycium oxycarpum</i> Dunal			
	<i>Solanum namaquense</i> Dammer	3		
	<i>Solanum tomentosum</i> L.			
	<i>Solanum villosum</i> Mill.			
STERCULIACEAE	<i>Hermannia pulchella</i> L.f.	9	9	1
	<i>Hermannia cernua</i> Thunb. subsp. <i>erodioides</i> (Burch. ex DC.) De			
	<i>Hermannia cuneifolia</i> Jacq. var. <i>cuneifolia</i>			
	<i>Hermannia cuneifolia</i> Jacq. var. <i>glabrescens</i> (Harv.) I.Verd.			
	<i>Hermannia filifolia</i> L.f. var. <i>filifolia</i>			
	<i>Hermannia linearifolia</i> Harv.			
	<i>Hermannia minutiflora</i> Engl.			
	<i>Hermannia pulchella</i> L.f.			
	<i>Hermannia pulverata</i> Andrews			
THYMELAEACEAE	<i>Gnidia microphylla</i> Meisn.	2	2	1
	<i>Gnidia polycephala</i> (C.A. Mey.) Gilg			
VERBENACEAE	<i>Chascanum cuneifolium</i> (L.f.) E.Mey.	1	2	2
	<i>Lantana rugosa</i> Thunb.	1		
VISACEAE	<i>Osyris lanceolata</i> Hochst. & Steud.	1	2	2
	<i>Viscum rotundifolium</i> L.f.	1		
ZYGOPHYLLACEAE	<i>Tribulus terrestris</i> L.	1	3	2
	<i>Zygophyllum gilfillanii</i> N.E. Br	2		
	<i>Zygophyllum incrustatum</i> E. Mey. Ex Sond.			
Unknown species	Round bulb	1		
Total Families: 61	Total Species: 353	Total Genera: 199	-	-

5. Classification of the Vegetation

Abstract

Plant community composition and distribution on and off isolated mesas were investigated across the Nama-karoo in the Eastern Cape Province, South Africa. Species composition and cover was measured in plots along a transect extending from the SE plains and slopes, across the plateaux, onto the NW slopes and plains of three mesas (Tafelberg, Folminkskop and Buffelskop). Data were then analysed according to the Braun-Blanquet classification system, using the computer packages TWINSpan and CANOCO. Mesa communities were found to be distinctly different from plains communities, with no shared communities between the two habitats. The distribution of communities across the landscape was attributed to a soil-moisture gradient. Differences in habitat probably existed before the impact of domestic livestock, but overgrazing has likely probably exacerbated the differences. Toxic, spinescent and unpalatable species have increased in the vegetation, possibly at the expense of palatable species due to selective grazing by livestock on the plains. The potential to use mesas as sources of seeds and propagules for the surrounding degraded plains is low, since few species are shared between the two habitats. However, generalist, palatable species such as *Felicia muricata*, *Eragrostis obtusa*, *Pentzia incana* etc., could have some potential for future restoration. Dolerite capped mesas such as Tafelberg and Folminkskop had a general slope community shared between the two mesas. Aspect and the expected cooler, moister conditions on SE slopes, as factors determining community composition for the dolerite mesas, were overridden by soil type and associated nutrient status. In xeric sandstone mesas such as Buffelskop, soil type and associated nutrient status were overridden by aspect and slope as determinants of community composition. Mesa habitats were not grazed by livestock due to their inaccessible nature, and were not threatened by current land use practices. Plains habitats were often degraded, a consequence of 200 years of selective grazing. Plant communities in Middelburg were very similar in composition to communities in the rest of the Nama-karoo biome, with many shared genera and species.

5.1 Introduction

Vegetation patterns in arid landscapes remain relatively understudied despite the fact that these landscapes comprise 47% of all terrestrial land (UNEP 1992). One of the largest continuous tracts of arid land in the southern hemisphere is the karoo semi-desert encompassing two biomes, the succulent karoo of the Winter Rainfall Region and the Nama-karoo occurring primarily in the Summer Rainfall Region of southern Africa (Desmet & Cowling 1999). Information on the Nama-karoo biome (second largest biome, 607 235 km²), of South Africa (Rutherford & Westfall 1986; Palmer & Hoffman 1997) remains sparse and concentrated on a few nature reserves found along the edges of the biome, as evidenced by difficulties experienced by a recent vegetation mapping exercise (Macdonald 1998; Mucina 2000).

Mesas are a general feature of Nama-karoo landscapes (Chapter 2, Study Area). Landscape processes differ dramatically on and off mesas due to their elevation and often steep slopes. While disturbance, particularly grazing pressure, is presumably concentrated largely on the plains and lower slopes of mesas, other processes such as deposition, erosion, run-off of water and soil development vary dramatically over the habitat complex (see Fig. 2.2).

This chapter reports on the classification of the vegetation of the Middelburg study area (Chapter 2) into plant communities. Plant communities and patterns were then compared to previous studies done in the Nama-karoo biome.

5.1.1 The concept of the plant community

The existence of plant communities is one of the major ongoing debates in vegetation science (Noy-Meir & Van der Maarel 1987; Wilson 1991). Some are of the opinion that plant species respond individually to fluctuations in environmental parameters (Gleason 1926; Austin 1985; Austin & Smith 1989). This makes the recognition of communities with clear boundaries difficult, with overlaps between communities being common (Austin 1985). Others support the existence of distinct, recognisable plant communities (Clements 1904; Braun-Blanquet 1932; Keddy 1993; Dale 1994; Mirkin 1994; Palmer & White 1994). This debate between community and continuum concepts was resolved by Austin & Smith (1989) who argued that plant communities are a consequence of landscape patterning, with a patterned

environmental condition such as soil type supporting distinct and homogenous plant communities.

A community can be described as a “system of organisms living together and linked together by their effects on one another and their responses to the environment they share” (Whittaker 1975). Such an assemblage of plant species is distinct from other species assemblages and occurs frequently across the landscape (Kent & Coker 1992). Classification methods aim to group together similar stands of species in discrete entities, where these entities are clearly separated from other groups and entities (Barbour *et al.* 1987).

Communities can be classified by a number of characteristics, such as species dominance, species composition and growth form dominance (Whittaker 1975). There is no single correct way to classify communities, and many different systems have been developed. These include a physiognomic approach, classification by dominant species and classification using different strata (Whittaker 1975).

5.1.2 The Braun-Blanquet classification system

The approach used in this chapter takes the entire floristic composition (Westhoff & Van der Maarel 1973) of the vegetation into account and has been developed by Braun-Blanquet (1932). Data are recorded in a non-random way, samples being selected to be representative of a particular vegetation type (Kent & Coker 1992). Species data (including a full list of species and some indication of their relative importance) are arranged in a table with species as rows and samples as columns (Werger 1974; Whittaker 1975). This raw data table (Kent & Coker 1992) is then re-arranged to group together species that are similar in their distribution (Whittaker 1975). The re-arrangement is repeated until a differentiated table (Westhoff & Van der Maarel 1973; Whittaker 1975; Barbour *et al.* 1987, Kent & Coker 1992) is produced, where species are now arranged in groups (associations) characterised by diagnostic species. The basic unit of the classification system is the association (Braun-Blanquet 1923; Westhoff & Van der Maarel 1973; Werger 1974; Whittaker 1975; Kent & Coker 1992). The association can be described as a plant community type, found by grouping together sample relevés that have species in common (Kent & Coker 1992).

Diagnostic species distinguish between these associations (communities) by their presence in some communities and their absence in others (Whittaker 1975). Diagnostic species can be divided into character species, differential species and constant companions (Braun-Blanquet 1932; Westhoff & Van der Maarel 1973; Whittaker 1975, Barbour *et al.* 1987; Noy-Meir & Van der Maarel 1987). Character species are used to define the association, while differential species are used to define sub-associations and other units below the level of the association (Whittaker 1975). Similar associations can be grouped together to form a higher level of classification called alliance, which can in turn be grouped into orders, and orders into classes (Westhoff & Van der Maarel 1973; Barbour *et al.* 1987). South Africa does not make a distinction between character and differential species, and the general approach is to group the two together under the term differential species (L Mucina, pers. comm.).

Fidelity (faithfulness) is the degree to which a species is concentrated in a given stand and can be expressed by the number of stands outside of the given association that contain the species (Wenger 1974; Braun-Blanquet 1932; Westhoff & Van der Maarel 1973; Barbour *et al.* 1987). A general rule is that if more than 20% of stands outside a chosen association contain a given species, that species can not be used as a characteristic or differential species (Barbour *et al.* 1987). Constancy refers to the number of times a species occurs in a given association (Westhoff & Van der Maarel 1973), and a level of 50% constancy is normally required for differential species (Barbour *et al.* 1987). Fifty percent of the character species of a given association must be present before it can be classified as belonging to that association (Barbour *et al.* 1987).

The Braun-Blanquet approach has the advantage in that it is widely used by ecologists and that different vegetation studies can easily be compared with one another (Whittaker 1975).

5.2 Material and Methods

Chapter 3 provides a detailed description of the sampling methods used and plot layout.

5.2.1 Soil sampling and analysis

Soil samples, consisting of several bulked samples (the soil from open areas in a site were bulked into one soil sample per site for open-canopy, and the same was done for soil from closed-canopy areas) taken from the top layers of soil, were air dried and analysed by the soil analysis laboratories at Elsenberg (Department of Agriculture). Soil was analysed for pH (KCl), resistance, acidity, carbon, Na, P, K, Ca, Mg, Cu, Zn, Mn, B, soil texture, stone, sand, silt and clay (Jones 2000). After soil analysis open- and closed canopy values for the individual parameters were combined to yield one average value per parameter per site.

5.2.2 Data Analysis

5.2.2.1 Classification of vegetation data

The relevés were entered into a database managed by TurboWin1.98 (Hennekens 1996). Data was then exported from TurboWin in CEP format into Megatab 2.0 (Hennekens 1996). Megatab was used to classify the relevés using the program TWINSpan (imbedded within Megatab), after which the relevés were further classified by manual manipulation. Classification of species into classes of diagnostic species and common species was done on the basis of criteria as stated below (5.2.3) and grouped according to the coincidence of these species and clusters of relevés. The final groupings of relevés were interpreted in terms of *communities*, the latter grouped into *community groups*.

5.2.2.2 Species-environmental relationships

A series of ordinations were performed to analyse environmental gradients across the landscape as well as to determine linkages between the distribution of species and environmental variables. Ordination was conducted firstly on the entire data set, thereafter partial data sets were analysed for each of the major communities. Ordination was done using Canonical Correlation Analysis (CCA; Jongman *et al.* 2000), using default options of the program package CANOCO4 (Ter Braak & Smilauer 1998).

5.2.3 Definitions

5.2.3.1 Diagnostic species (differential species)

Diagnostic species are those that differentiate a community from other communities. Ideally such a species should be unique to one, but this was not always the case. If more than 20% of the relevés outside the community contained any given species, such a species was not regarded as a diagnostic species regardless of the densities recorded for that species. However, in communities that lacked diagnostic species, species were sometimes also regarded as diagnostic for a specific community because of their relative dominance in comparison to other communities, or the diagnostic value was linked to the co-occurrence with other species. A species could also be diagnostic in a community by nature of its absence rather than by its presence in the community.

Strong diagnostic species occurred in more than 50% of the relevés and weak diagnostic species in < 50% of the relevés involved, regardless of individual dominance values of the relevant species. Dominance is relative, as some species might not have very high cover values but could still be dominant in a community due to the absence of other potentially more dominant plants. Dominance was given as average cover (of the species at stake) per relevé (of the applicable community), regardless of distribution through the relevés. Dominance was given preference above distribution, so that a species with high dominance in part of the community and a relative absence in other parts of the same community would be ranked higher in the scale of diagnostic species than a species with low dominance values but a slightly wider distribution. Strong diagnostic species and weak diagnostic species were grouped from the most dominant to the least dominant. This was done because sometimes a weak diagnostic species can have a higher total cover value in a community than a strong diagnostic species of low dominance. Species that had high constancy class values (>3) were distinguished as dominant for the specific community and were marked by adding “d” behind the species name in the description of the communities. Weak diagnostic species that occurred in <50% of the relevés in e.g. community Z, but also occurred in more than 50 % of community Y or occurred in community Y at a density higher than in community Z, were not used as diagnostic species for Z.

5.2.3.2 Common species

Common species were species that occurred frequently in a community. Common species for mega-communities/communities could never be narrower in distribution than the mega-communities/communities at stake, e.g. could not be a sub-part of the mega-community/community. Common species could never be diagnostic species.

5.3 Results

A brief framework (5.3.1 & 5.3.2) of community groups and communities is given in the beginning of this section. This is then followed by a detailed description of all community groups and communities (5.3.3). The detailed description starts with the main division in the data (5.3.3.1), followed by Complex A (5.3.3.2) and Complex B (5.3.3.3) with their respective subdivisions.

5.3.1 Outline

A Slopes and Plateaux

A.1 *Felicia filifolia* – *Themeda triandra* Community Group

A.1.1 *Felicia filifolia* – *Dimorphotheca cuneata* Community

A.1.2 *Felicia filifolia* – *Pachypodium succulentum* Community

A.1.3 *Felicia filifolia* – *Eriocephalus africanus* Community

A.2 *Rhigozum obovatum* – *Rhus burchelli* Community Group

A.2.1 *Rhigozum obovatum* – *Maytenus heterophylla* Community

A.2.2 *Rhigozum obovatum* – *Pegolettia baccaridifolia* Community

A.2.3 *Rhigozum obovatum* – *Cenchrus ciliaris* Community

B Plains

B.1 *Aristida adscensionis* – *Eragrostis obtusa* Community Group

B.1.1 *Aristida adscensionis* – *Ruschia intricata* Community

B.1.2 *Aristida adscensionis* – *Adromischus* sp. Community

B.1.3 *Aristida adscensionis* – *Zygophyllum incrustatum* Community

B.1.4 *Helichrysum luciloides* – *Thesium spartioides* Community

B.2 *Eragrostis lehmanniana* – *Eragrostis bergiana* Community Group

B.2.1 *Pentzia incana* – *Eragrostis bergiana* Community

B.2.2 *Eragrostis lehmanniana* – *Eragrostis bicolor* Community

B.2.3 *Eragrostis lehmanniana* – *Rosenia humulis* Community

5.3.2 General Outline

The species-releve matrix (Appendix 5.8.1) was divided into two main groups of communities: Slopes/Plateaux (A) and Plains (B). Slopes/Plateaux (A) was subdivided into Community Groups (CG's) A1 and A2, each constituting of three communities. Plains (B) was subdivided into Community Groups (CG's) B1 and B2, constituting of four and three communities, respectively.

5.3.3 Description

5.3.3.1 Two main groups: Slopes/Plateaux (A) & Plains (B)

Vegetation of Slope/Plateaux (A) was classified as Open Grassy Shrubland, while that of Plains (B) was classified as Open Dwarf Shrubland. Both are different facies of shrubby semi-desert. The environmental variables most strongly correlated with the axes were rocks, bare soil, slope, C and Mn. Communities of the slopes/plateaux were more rocky and had higher values of silt, clay, Bo, Mg, Zn, Mn, Cu and C in comparison with communities on the plains, while the plains communities generally had higher percentages of bare soil, coarse sand, phosphate, Ca, Na, K and Na. The plains communities also had deeper soils, higher resistance and higher pH than slopes/plateaux communities (Fig. 5.1).

Key for ordination diagrams

BARE_SOIL – Bare soil, BO – Boron, C – Carbon, CA – Calcium, CLAYPER – Clay %, COURSAND – Coarse sand, CU – Copper, K – Potassium, MG – Magnesium, MN – Manganese, NA – Sodium, PH_KCL – pH in KCl, PHOSPHAT – Phosphates, RESISTAN – Resistance, ROCKS – Rocks, SILTPER – Silt %, SOIL_DEP – Soil depth, ZN – Zinc. Plateaux and slopes were nominal variables, so that Slopes referred to areas with a slope, while Plateaux referred to areas that were flat.

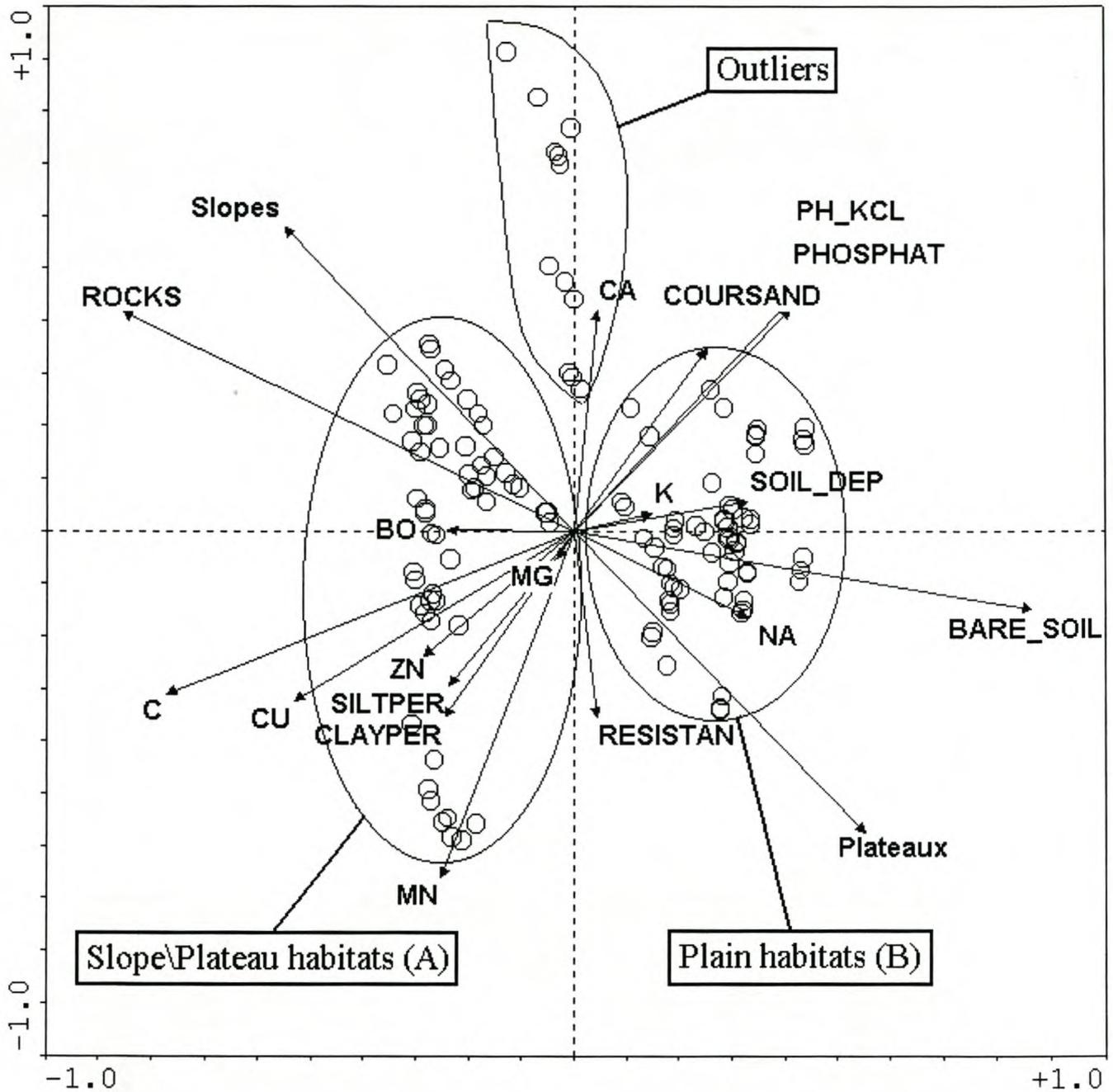


Fig. 5.1 An ordination diagram showing the distribution of sites in relation to available environmental factors for the main division in the data: A) Slopes/Plateau habitats and B) Plains habitats. Eigen values: Axis 1 – 0.735, Axis 2 – 0.544. An identification key for the diagram is provided in 5.3.1.

5.3.3.2 Complex A: Slopes/Plateaux

Community Group A1 (Folminkskop and Tafelberg dolerite plateaux, Tafelberg SE upper and middle slopes) occurred in areas that were relatively high in Na, Zn, Bo, Silt. The soils had higher resistance, status of Mn, Mg, Clay, C, Cu, and bare soil in comparison with CG A2 (all other NW and SE slopes, and the Buffelskop plateau). The environmental variables most strongly correlated with the axes were Na, phosphate, Mn, silt and slope. Exceptions to this were Tafelberg SE upper and middle slopes that were more similar to CG A2 in respect of environmental variables, but were grouped floristically with CG A1 (see Community A.1.3). CG A1 occurs in areas that were higher in Ca, K, coarse sand, pH, phosphate, had more rocks and deeper soils in comparison with CG A1 (Fig. 5.2).

A1 *Felicia filifolia* – *Themeda triandra* Grassy Shrubland

Community Group A1 occurred on Tafelberg plateau, Folminkskop plateau, and Tafelberg SE upper and middle slopes.

Strong diagnostic species: *Felicia filifolia* (d), *Themeda triandra* (d), *Digitaria eriantha* (d) *Helichrysum zeyheri*

Weak diagnostic species: *Pelargonium abrotanifolium* (d), *Eriocephalus africanus* (d), *Wahlenbergia nodosa*, *Pentzia punctata* (d), *Euclea crispa* (d), *Pachypodium succulentum*, *Sutera halimifolia*

Common species (d): *Eragrostis curvula*, *Cymbopogon plurinodes*, *Eustachys paspaloides*, *Felicia muricata*, *Enneapogon scoparius*, *Tragus koelerioides*

This CG was the least impacted by grazing of all the four CGs and the vegetation was in pristine condition. Desirable (palatable) species were common to dominant with undesirable (unpalatable, toxic and spinescent) species occurring at low densities, and soil erosion was minimal.

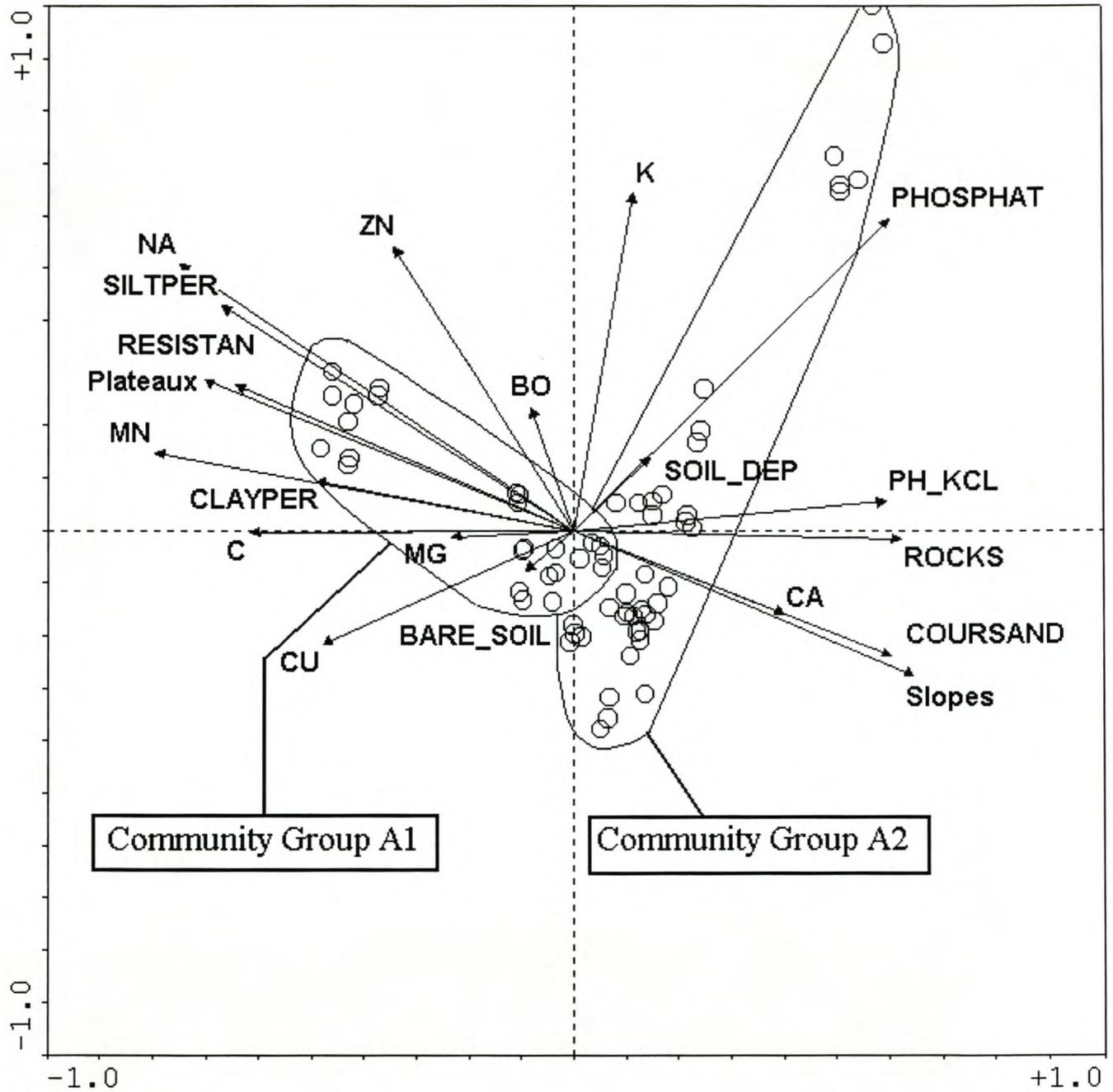


Fig. 5.2 An ordination diagram showing the distribution of sites in relation to the environmental factors assessed for mega-communities A1 and A2. Eigen values: Axis 1 – 0.635, Axis 2 – 0.491. An identification key for the diagram is provided in 5.3.1.

A.1.1 *Felicia filifolia* – *Dimorphotheca cuneata* Shrubby Grassland

This community occurred on Tafelberg plateau, where soils had relatively high status of Na, K, Zn, Mg, Mn, C, Bo and Cu, they were silty and clayey, and showed high level of resistance (Soils had high resistance despite the relatively high levels of Na. Na was, however, not the only salt present in the soil, and resistance was also influenced by levels of Ca and K in the soil) (Fig. 5.3). The environmental variables most strongly correlated with the axes were phosphate, slope, coarse sand, Mn, and silt. Aspect and slope values were absent, as Tafelberg is flat on top. Tafelberg was the highest mesa in the vicinity of the study area, and dolerite caps of Beaufort Group origin, topped both Tafelberg and Folminkskop. Tafelberg plateau and Folminkskop plateau were correlated with the same environmental factors, but the values for Tafelberg were higher than those for Folminkskop. This could be explained by the similarities in geology and soils, but a difference in height (Tafelberg is approximately 200 m higher than Folminkskop).

Strong diagnostic species: *Dimorphotheca cuneata* (d), *Selago saxatilis*, *Diospyros austro-africana* (d), *Bulbine frutescens*, *Crassula obovata* var. *obovata*

Weak diagnostic species: *Ruschia britteniae* (d), *Dianthus basuticus*, *Berkeya pinnatifida*, *Moraea pallida*, etc. (see Appendix 5.8.1)

Common species: *Themeda triandra* (d), *Eragrostis curvula* (d), *Cymbopogon plurinodes* (d), *Tragus koelerioides* (d), *Digitaria eriantha* (d), *Wahlenbergia nodosa*, *Helichrysum zeyheri*, *Eustachys paspaloides* (d), *Felicia filifolia*

Both *Enneapogon scoparius* and *Asparagus striatus* occurred throughout the rest of CG A, but were remarkably absent in this community. This community has not been impacted by domestic herbivores for 40 years, and is grazed by indigenous antelopes such as koedoe (*Tragelaphus strepsiceros*) and reedbuck (*Pelea capreolus*), and rabbits (*Pronolagus rupestris*). The vegetation was in a relatively undegraded condition, and was dominated by highly palatable, desirable grasses.

A.1.2 *Felicia filifolia* – *Pachypodium succulentum* Shrubby Grassland

This community occurred on Folminkskop plateau, on substrates generally more rocky than in Communities A.1.1 and A.1.3. Soil supporting this community were characterised by relatively lower status of Na, K, Zn, Mg, Mn, C, Bo, Cu, lower

resistance, and silt and clay contents as compared to Tafelberg plateau (Community A.1.1). These soil characteristics showed relatively higher values in this particular community as compared to Tafelberg SE slope (Community A.1.3) (Fig. 5.3). The environmental variables most strongly correlated with the axes were phosphate, slope, coarse sand, Mn and silt. Folminkskop has a dolerite cap as does Tafelberg plateau, but is approximately 200 m lower in altitude. There was no aspect or slope, as Folminkskop plateau was flat on top.

Strong diagnostic species: *Pachypodium succulentum*, *Euclea crispa*, *Heliophila suavissima*, *Pentzia punctata* (d)

Weak diagnostic species: *Boophae disticha*.

Common species: *Themeda triandra* (d), *Enneapogon scoparius* (d), *Felicia filifolia* (d), *Cymbopogon plurinodes* (d), *Digitaria eriantha* (d), *Helichrysum zeyheri*, *Eustachys paspaloides*, *Felicia muricata*

Due to the lower elevation, sheep occasionally grazed on the plateau. The impact of grazing is considered to be negligible, as grazing frequency was very low (<10 times a year). The community was, however, grazed regularly by indigenous herbivores such as koedoe, reedbuck, and rabbits. The vegetation was in a relatively undegraded condition, and palatable and desirable plants were common to dominant.

A.1.3 *Felicia filifolia* – *Eriocephalus africanus* Grassy Shrubland

This community occurred on Tafelberg SE slope upper and middle. The environmental variables most strongly correlated with the axes were phosphate, slope, and contents of coarse sand, silt, and Mn. The soils showed a relatively high status of phosphate, coarse sand, Ca, and had more bare soil, and were deeper than those of the dolerite plateau Communities A.1.1 & A.1.2 (Fig. 5.3). Physical attributes of this community had more in common with that of a typical slope, Community A.2.1, than with the plateau communities of Tafelberg and Folminkskop, but floristically the community is similar to the dolerite plateau communities. The overriding effect of moisture might explain this problem, since this community represented the wettest community of all due to the high elevation and the SE-facing aspect.

Strong diagnostic species: *Eriocephalus africanus* (d), *Felicia ovata*

Weak diagnostic species: *Pentzia lanata*, *Crassula cotyledonis*

Common species: *Felicia filifolia* (d), *Eragrostis curvula* (d), *Aristida diffusa*, *Felicia muricata*, *Enneapogon scoparius* (d), *Digitaria eriantha* (d), *Tragus koelerioides*, *Helichrysum rosum*, *Pentzia incana* (d)

The community was also characterised by a complete absence of *Themeda triandra* and *Heteropogon contortus*. The community was grazed by indigenous herbivores such as koedoe, reedbuck, rabbits, and occasionally by domestic herbivores, but more regularly so than Tafelberg plateau (Community A.1.1) or Folminkskop plateau (Community A.1.2). Vegetation was in good condition, with desirable and palatable plants being common to dominant.

A2 *Rhigozum obovatum* – *Rhus burchellii* Grassy Tall Shrubland

Community Group A2 occurred on Folminkskop SE slope upper and lower, Folminkskop NW slope upper and lower, Buffelskop plateau NW and SE, Tafelberg NW slope upper, middle and lower, Tafelberg SE slope lower, Buffels SE plain 1B, Buffelskop SE slope upper and lower, Buffelskop NW slope upper and lower.

Strong diagnostic species (d): *Rhigozum obovatum*, *Rhus burchellii*, *Sporobolus fimbriatus*

Weak diagnostic species: *Cenchrus ciliaris* (d), *Senecio longiflorus* (d), *Gymnosporia buxifolia* (d), *Aloe striata* (d), *Cissampelos capensis*, etc. (see Appendix 5.8.1)

Common species (d): *Enneapogon scoparius*, *Aristida diffusa*, *Heteropogon contortus*, *Eragrostis curvula*

Impact by domestic livestock ranged from negligible to high. Vegetation condition ranged from pristine (upper slopes) to moderately degraded (lower slopes of Buffelskop). Desirable species (highly palatable species) were common to dominant in the pristine areas with undesirable species occurring at low densities. Moderately degraded areas were dominated by less palatable to moderately palatable plants (less desirable), and erosion was minimal.

A.2.1 *Rhigozum obovatum* – *Gymnosporia buxifolia* Grassy Tall Shrubland

This community occurred on Folminkskop SE slope upper and lower, Folminkskop NW slope upper and lower, Buffelskop plateau NW and SE, Tafelberg NW slope upper, middle and lower, Tafelberg SE slope lower. It was a general slope community occurring throughout the entire study area. The soils supporting this shrubland community showed relatively high status of Mn, Mg, C, Cu, Ca and contents of clay in comparison to the communities found on Buffelskop SE and Buffelskop NW slopes (Fig. 5.4). The environmental variables most strongly correlated with the axes were phosphate, Cu, Zn, Na and Mg.

Weak diagnostic species: *Gymnosporia buxifolia* (d), *Senecio longiflorus* (d), *Crassula lanuginosa*, *Hermannia minutiflora*, *Pentzia quinquefida*

Common species: *Eragrostis curvula*, *Aristida diffusa* (d), *Enneapogon scoparius* (d), *Rhigozum obovatum* (d), *Heteropogon contortus* (d)

This slope community was grazed regularly by indigenous herbivores such as koedoe, reedbuck, rabbits, and occasionally by domestic herbivores. Grazing by domestic herbivores occurred much more frequently than in the case of CG A.1, and was concentrated on the lower half of these slopes. Lack of watering points and inaccessibility of the terrain forced animals to stay on the lower half of the slopes. Domestic animals walked down to the watering points on the surrounding plains towards mid-morning. Impact by these domestic herbivores was not considered to be significant as vegetation was in very good condition, with palatable and desirable species common to dominant.

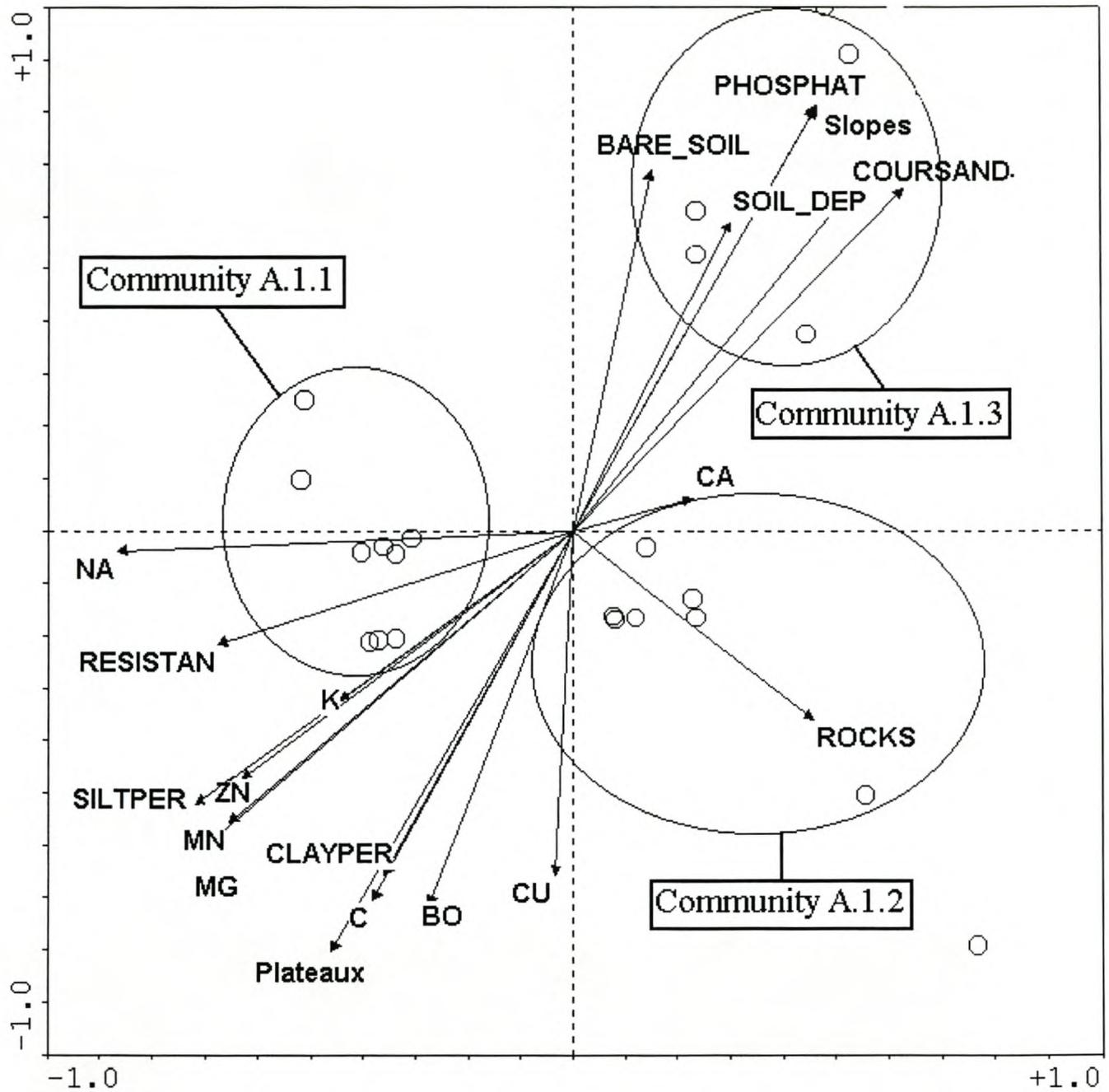


Fig. 5.3 An ordination diagram showing the distribution of sites in relation to available environmental factors for communities A.1.1, A.1.2 and A.1.3. Eigen values: Axis 1 – 0.578, Axis 2 – 0.446. An identification key for the diagram is provided in 5.3.1.

A.2.2 *Rhigozum obovatum* – *Pegolettia baccaridifolia* Tall Shrubland

This community occurred on Buffelskop SE slope, where the soils showed relatively high contents of coarse sand, silt, Na, K, phosphate and Bo, and had high values of pH and resistance (Fig. 5.4). It also had a higher incidence of bare soil and deeper soils in comparison to the Communities A.2.1 and A.2.3. The environmental variables most strongly correlated with the axes were phosphate, Cu, Zn, Na and Mg.

Strong diagnostic species: *Pegolettia baccaridifolia* (d), *Pseudocrossidium crinitum*, *P. replicatum*

Weak diagnostic species: *Chascanum cuneifolium*

Common species: *Rhigozum obovatum* (d), *Felicia muricata*, *Pentzia punctata* (d), *Asparagus burchellii*, *Limeum aethiopicum*, *Helichrysum rosum*, *Selago albida*

The community was grazed regularly by indigenous herbivores such as koedoe, reedbuck and rabbits (less regularly than Tafelberg and Folminkskop), and frequently by domestic herbivores. Buffelskop was more readily accessible for livestock. The impact of domestic herbivores on this community was moderate to high. Buffelskop consisted of sandstone (as opposed to Folminkskop and Tafelberg that are both capped by dolerite), and the slopes were very steep and unstable. Both these factors probably played an important role in shaping this community. Desirable and palatable plants were less frequent and had lower dominance, and vegetation was dominated by a different set of plants in comparison with the dominants on Tafelberg and Folminkskop. Spiny *Blepharis capensis* has the capability to colonise disturbed ground and a tendency to dominate overgrazed patches.

A.2.3 *Rhigozum obovatum* – *Cenchrus ciliaris* Grassy Tall Shrubland

This community occurred on Buffelskop NW slope, upper and lower. The soils were skeletal and showed higher contents of Zn in comparison to the community occupying the SE slopes (Community A.2.2). At the same the soils showed higher content of coarse sand and silt, higher values of pH and resistance, and higher status of Na, K, phosphate and Bo. The bare patches were more common in this community than in the Community A.2.1 (Fig. 5.4). The environmental variables most strongly correlated with the axes were phosphate, Cu, Zn, Na and Mg.

Strong diagnostic species: *Cenchrus ciliaris* (d)

Common species (d): *Rhigozum obovatum*, *Rhus burchellii*

The community was grazed regularly by indigenous herbivores such as koedoe, reedbuck, rabbits (less regularly than Tafelberg and Folminkskop), and was grazed frequently by domestic herbivores. Buffelskop was in theory the same height as Folminkskop, but its height above the surrounding plains was lower, making the mesa relatively lower and more readily accessible to livestock. Impact of domestic herbivores on this community was moderate to high. Buffelskop was mostly comprised of sandstone (as opposed to Folminkskop and Tafelberg that were both capped by dolerite), and the slopes were very steep and unstable. Both these factors probably played important roles in shaping this community. Desirable and palatable plants were less frequent and had lower dominance, and the vegetation was dominated by a different set of plants to those dominant on Tafelberg and Folminkskop.

5.3.3.3 Complex B: Plains

Community group B1 (Tafelberg SE plains, Tafelberg NW plains, Folminkskop SE plain, sampling stations 2, 3 and 4; Fig. 5.5) occurred in two distinct areas – A and B. The soils of area A showed relatively higher resistance and contained more coarse sand than the soils of the area B. The soils of the area B showed relatively higher status of Mn, clay, silt, K, Na, phosphate, Zn and C. Area B also had, on average, higher percentage bare soil and deeper soils. Community Group B2 (Buffelskop NW plain 1, 2, 3, 4; Buffelskop SE Plain 1 & 2; Folminkskop NW Plain 1, 2, 3, 4; Folminkskop SE Plain 1) was supported by soils showing higher status of Bo, Mg, Ca, C, and higher pH, as compared to CG B1. The soils of the CG B2 were more skeletal and showed higher contents of coarse sand (Fig. 5.5). The environmental variables most strongly correlated with the axes were Mn, resistance, phosphate, pH and Ca.

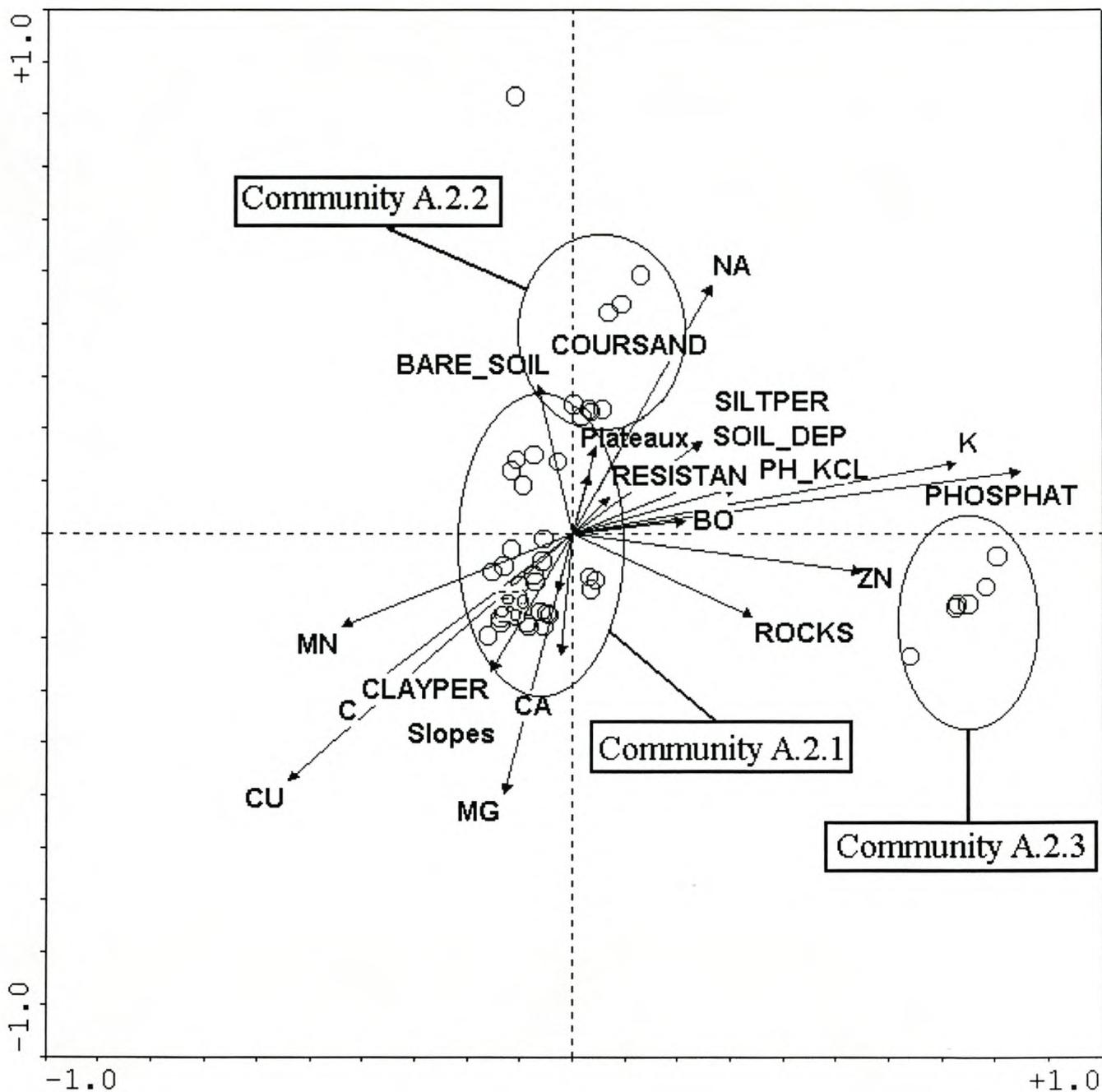


Fig. 5.4 An ordination diagram showing the distribution of sites in relation to available environmental factors for communities A.2.1, A.2.2 and A.2.3. Eigen values: Axis 1 – 0.557, Axis 2 – 0.433. An identification key for the diagram is provided in 5.3.1.

B1 *Aristida adscensionis* – *Eragrostis obtusa* Grassy Dwarf Shrubland

This community group occurred on Tafelberg SE plains, Tafelberg NW plains and Folminkskop SE plain 2, 3, 4.

Strong diagnostic species (d): *Aristida adscensionis*, *Lycium cinereum*, *Eragrostis obtusa*

Weak diagnostic species: *Albuca setosa* (d), *Chloris virgata*, *Geigeria ornativa*

Common species: *Pentzia incana* (d), *Eragrostis lehmanniana* (d), *Tragus koelerioides* (d), *Eriocephalus ericoides* (d), *Aristida diffusa* (d), *Trichodiadema rogersiae*, *Felicia muricata*

This community group was moderately to severely impacted by domestic livestock, and lightly grazed by indigenous animals such as koedoe, springbok (*Antidorcas marsupialis*), and steenbok (*Raphicerus campestris*). Vegetation condition ranged from good to severely degraded. Unpalatable, undesirable plants dominated the vegetation, with desirable species still being common. We have found a very variable evidence for soil erosion.

B.1.1 *Aristida adscensionis* – *Ruschia intricata* Grassy Dwarf Degraded Shrubland

Relevés of this community were made on Tafelberg SE plains (1, 2, 3, 4). The soils supporting this community showed higher resistance, and had more rocks and coarse sand in comparison to Communities B.1.2, B.1.3 and B.1.4 (Fig. 5.6). The environmental variables most strongly correlated with the axes were Bo, soil depth, clay, Mn, silt and bare soil.

Strong diagnostic species: *Ruschia intricata* (d), *Chrysocoma ciliata* (d), *Indigofera sessilifolia* (d), *Monsonia brevirostrata*, *Bulbostylis humilis*

Weak diagnostic species: *Tragus berteroniatus* (d), *Oropetium capense*, *Cyperus usitatus* (d), *Senecio radicans*, *Phymaspermum parviflora*, *Tribulus terrestris*, etc. (see Appendix 5.8.1)

Common species: *Aristida adscensionis* (d), *Pentzia incana* (d), *Eriocephalus ericoides* (d), *Aristida diffusa* (d), *Eragrostis obtusa* (d), *Lycium cinereum* (d), *Drosanthemum duplessiae* (d), *Enneapogon desvauxii*, etc. (see Appendix 5.8.1)

This community was impacted regularly by indigenous herbivores such as springbok, koebe and steenbok and, in the past, was heavily impacted by domestic herbivores. Vegetation was degraded, with unpalatable or undesirable plants dominating. Erosion had taken place to the extent that many plants were growing on pedestals. In the five years prior to this study, Nguni (cattle breed) cattle farming have replaced sheep farming in this community.

B.1.2 *Aristida adscensionis* – *Jamesbrittenia atropurpurea* Grassy Dwarf Shrubland

This community occurred on Folminkskop SE plain 4. The soils had higher levels of Zn, K, Bo, Mg, Na, Cu, C, phosphate, clay, and silt, higher values of pH and were deeper than the soils of the Community B.1.1, but less so than those of the Communities B.1.3 and B.1.4 (Fig. 5.6). The environmental variables most strongly correlated with the axes were Bo, Mn, soil depth, clay, silt and bare soil.

Strong diagnostic species: *Jamesbrittenia atropurpurea*

Common species: *Pentzia incana* (d), *Eragrostis lehmanniana* (d), *Aristida adscensionis* (d), *Albucca setosa* (d), *Ruschia intricata* (d), *Asparagus burchellii* (d), *Plinthus karooicus* (d), *Drosanthemum duplessiae* (d), *Enneapogon desvauxii*

This community was excessively grazed by domestic livestock, as well as indigenous herbivores such as koebe, springbok, and steenbok. The condition of the vegetation was good, but unpalatable or undesirable plants were still common. This community was exceptional for a plains community because of the presence of *Enneapogon scoparius*, usually associated with slopes/plateau habitats. This could possibly be ascribed to increased soil moisture due to close levels of underground water. *Jamesbrittenia atropurpurea* also occurred only in this community. The surface erosion was minimal.

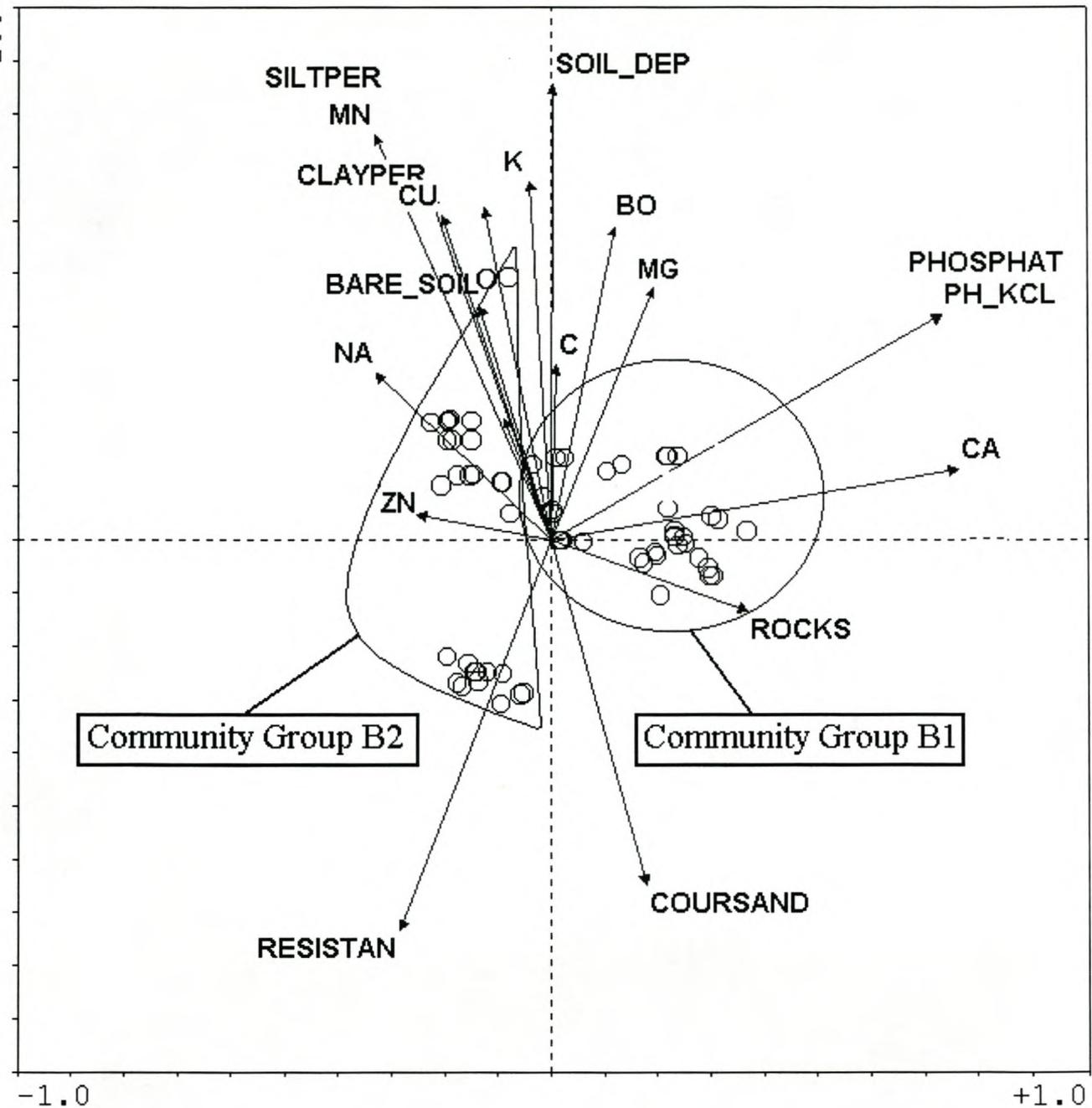


Fig. 5.5 An ordination diagram showing the distribution of sites in relation to available environmental factors for mega-communities B1 and B2. Eigen values: Axis 1 – 0.605, Axis 2 – 0.518. An identification key for the diagram is provided in 5.3.1.

B.1.3 *Aristida adscensionis* – *Zygophyllum incrustatum* Grassy Dwarf Shrubland

Community B.1.3 occurred on Folminkskop SE plain 2 & 3, and Tafelberg NW plain (1, 3, 4). The soils had higher levels of K, Bo, Mg, Cu, C, Na, phosphate, pH, clay, and silt and were deeper soils than soils of Communities B.1.1 and B.1.2. Soils were slightly poorer in these elements in comparison with soils of Community B.1.4 (Fig. 5.6). The environmental variables most strongly correlated with the axes were Bo, soil depth, clay, Mn, silt and bare soil.

Strong diagnostic species: *Zygophyllum incrustatum* (d), *Drosanthemum duplessiae* (d), *Mestoklema elatum* (d), *Berkeya heterophylla*, *Talinum caffrum*

Weak diagnostic species: *Pentzia globosa* (d), *Cynodon dactylon* (d), *Galenia africana*, *Osteospermum leptolobum* (d), etc. (see Appendix 5.8.1)

Common species: *Lycium cinereum* (d), *Aristida adscensionis* (d), *Eragrostis lehmanniana*, *Thesium hystrix* (d), *Pentzia incana* (d), *Eragrostis obtusa* (d), *Albucca setosa*, *Helichrysum luciloides* (d)

The community was impacted by occasional grazing by indigenous herbivores (koedoe, springbok, and steenbok) as well as by excessive grazing by domestic herbivores. Vegetation was degraded and characterised by many denuded areas dominated by unpalatable or undesirable plants. Erosion had taken place to the extent that plants often formed pedestals.

B.1.4 *Helichrysum luciloides* – *Thesium spartioides* Open Dwarf Shrubland

Relevés in this community were made on Tafelberg NW plain 2. The soils showed higher values of K, Bo, Mg, Na, Cu, C, clay, silt, phosphate, pH, and were deeper than those of the Communities B.1.1, B.1.2 and B.1.3, and were distinguished from the Community B.1.3 by lower levels of Zn (Fig. 5.6). The environmental variables most strongly correlated with the axes were Bo, soil depth, clay, Mn, silt and bare soil.

Strong diagnostic species: *Osteospermum leptolobum* (d), *Convolvulus sagittatus*, *Thesium spartioides*

Weak diagnostic species: *Convolvulus boedeckerianus*

Common species: *Helichrysum luciloides* (d), *Lycium cinereum* (d), *Pentzia incana*, *Tragus koelerioides*, etc. (see Appendix 5.8.1)

The community was impacted by occasional grazing by indigenous herbivores (koedoe, springbok, steenbok), as well as excessive grazing by domestic herbivores. Vegetation was degraded with many denuded areas. Erosion had taken place to the extent that plants were on pedestals. This community was slightly impoverished and was also characterised by the complete absence of *Aristida adscensionis*, *Eragrostis obtusa* and *E lehmanniana*, species common throughout the rest of the community group.

B2 *Eragrostis lehmanniana* – *Eragrostis bergiana* Grassy Dwarf Shrubland

Relevés in this CG were made on Folminkskop SE plain 1; Folminkskop NW plain 1, 2, 3, 4; Buffelskop NW plain 1, 2, 3, 4 and Buffelskop SE plain 1, 2.

Strong diagnostic species (all d): *Eragrostis bergiana* and *Blepharis capensis*

Weak diagnostic species: *Zygophyllum gilfillanii* (d), *Pteronia sordida* (d), *Rosenia humilis*, *Gnidia polycephala*, *Psilocaulon junceum*

Common species: *Pentzia incana*, *Eragrostis lehmanniana*, *Tragus koelerioides*, *Enneapogon desvauxii*, *Aristida diffusa*, *Thesium hystrix*, *Lycium cinereum*, etc. (see Appendix 5.8.1)

The community was impacted by occasional grazing by indigenous herbivores (koedoe, springbok, steenbok), as well as excessive grazing by domestic herbivores. This community group represented the most degraded of the four community groups. The high frequency of *Blepharis capensis* (spiny, unpalatable species commonly thriving on disturbed and overgrazed land) was an indication of overutilisation and degradation of this community.

B.2.1 *Pentzia incana* – *Eragrostis bergiana* Grassy Dwarf Shrubland

This community occurred on Folminkskop NW plain 1, 2, 3, 4; Folminkskop SE plain 1; Buffelskop NW plain 1, 3, 4. The soils showed lower status of Mn, Bo, Cu, Mg, K, Na, Zn, Ca, phosphate, bare soil, and higher pH than the soils of the Community B.2.2, but showed higher values of these soil characteristics than those of the Community B.2.3 (Fig. 5.7). The resistance of the soils supporting the Community B.2.3 was higher than that for the Community B.2.1. The environmental variables most strongly correlated with the axes were coarse sand, Mn, silt, clay and Cu.

Strong diagnostic species (d): *Eragrostis bergiana*, *Blepharis capensis*, *Zygophyllum gilfillanii*, *Pteronia sordida*

Weak diagnostic species: *Psilocaulon junceum* (d), *Indigofera zeyheri*, *Melolobium burchellii*, *Polygala asbestina*, etc. (see Appendix 5.8.1)

Common species: *Pentzia incana* (d), *Tragus koelerioides* (d), *Enneapogon desvauxii* (d), *Eragrostis lehmanniana* (d), *Aristida diffusa* (d), *Thesium hystrix* (d), *Aptosimum procumbens*, *Helichrysum luciloides* (d), *Plinthus karoocicus* (d)

The community was impacted by occasional grazing by indigenous herbivores (koedoe, springbok, steenbok), as well as excessive grazing by domestic herbivores. Vegetation was overgrazed and in poor condition with sparse plant cover, while unpalatable or undesirable plants were common to dominant. Shallow soil occurs in pockets, while *Blepharis capensis* was present in high densities.

B.2.2 *Eragrostis lehmanniana* – *Eragrostis bicolor* Grassy Shrubland Community

This community occurred on Buffelskop NW plain 3 & 4. The environmental variables most strongly correlated with the axes were coarse sand, Mn, silt, clay and Cu. Soils contained more Mn, Bo, Cu, Mg, K, Na, Zn, phosphate, Ca, bare soil, and higher pH than the soils of the Communities B.2.1 and B.2.3, and had lower resistance and less coarse sand than the soils of the Communities B.2.1 and B.2.3 (Fig. 5.7).

Strong diagnostic species: *Eragrostis bicolor* (d)

Common species: *Eragrostis lehmanniana* (d), *Lycium cinereum* (d), *Eragrostis bergiana* (d), *Chloris virgata*, *Pentzia incana*

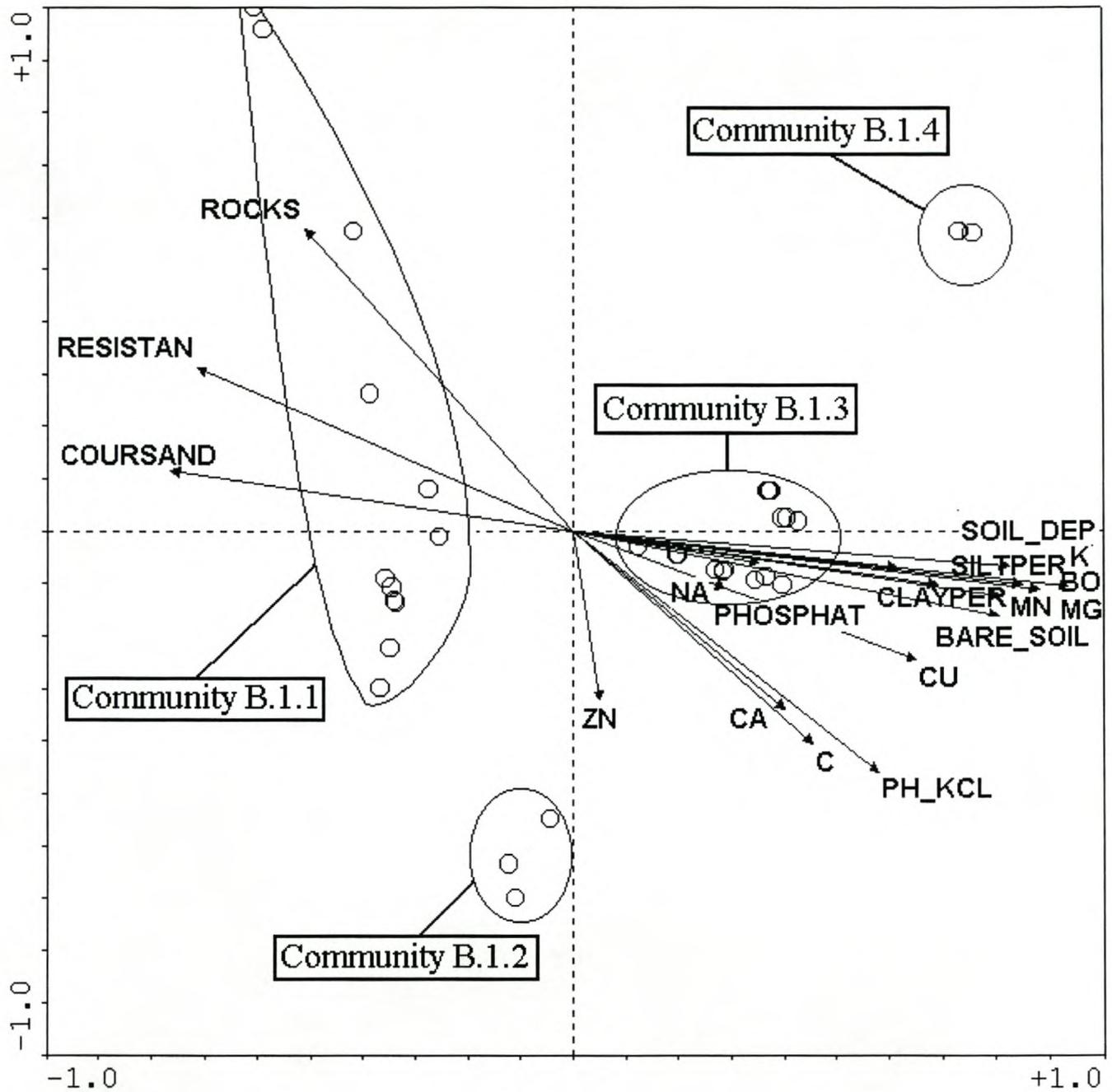


Fig. 5.6 An ordination diagram showing the distribution of sites in relation to available environmental factors for communities B.1.2, B.1.2, B.1.3 and B.1.4. Eigen values: Axis 1 – 0.605, Axis 2 – 0.448. An identification key for the diagram is provided in 5.3.1.

This community was regularly impacted by indigenous herbivores such as koedoe, springbok, steenbok, and heavily impacted by domestic herbivores. Vegetation was degraded with sparse cover and much bare soil. This community was impoverished, possibly as a result of a limited distribution in the landscape and consequent undersampling of the community.

B.2.3 *Eragrostis lehmanniana* – *Rosenia humilis* Shrubby Grassland

This community occurred in Buffelskop NW plain 2. The soils had lower contents of Mn, Bo, Cu, Mg, K, Na, Zn, Ca, phosphate, less bare soil, and lower values of pH than the soils of the Communities B.2.1 and B.2.2, and were relatively higher in percentage coarse sand and resistance (Fig. 5.7). The environmental variables most strongly correlated with the axes were coarse sand, Mn, silt, clay and Cu.

Strong diagnostic species: *Rosenia humilis*

Common species: *Aristida adscensionis* (d), *Pentzia incana*, *Tragus koelerioides*, *Eragrostis lehmanniana*, *Thesium hystrix*, etc. (see Appendix 5.8.1)

This community was regularly impacted by indigenous herbivores such as koedoe, springbok, steenbok, and heavily impacted by domestic herbivores. Vegetation was in an overgrazed, degraded condition and plant cover was sparse. This community was impoverished, possibly as a result of a limited distribution in the landscape that caused undersampling. Species diversity of this community was very low.

5.4 Discussion

5.4.1 Ecological factors

5.4.1.1 Distribution of communities across the landscape

Mesas (plateaux and slopes) are distinctly different in composition compared to the surrounding plains, with no shared communities between mesas and their surroundings. The main division in the Phytosociological Table (see Appendix 5.8.1) also reflected this.

These distinct communities are mainly attributed to a soil-moisture gradient. Shallower, rockier soils of the mesas coupled with very little runoff and naturally higher precipitation due to elevation results in a more mesic habitat in comparison with the plains habitats. Plains have little rock cover, high percentage of bare soils, slightly shallower soils and higher runoff rates than mesas. These factors result in a more xeric habitat. Habitat differences such as these probably existed before the impact of domestic stock introduced by European settlers (Hoffman *et al.* 1997) but overgrazing has probably exacerbated the differences. Overgrazing results in denuded vegetation with larger areas of bare soil than existed naturally in the plains habitats (Fuls 1992). This then results in an increase in xeric micro conditions through the loss of plant cover and water through runoff and more rapid evaporation than would normally occur (Fuls 1992).

Toxic, spinescent and unpalatable plant species are generally not grazed as severely as palatable species and are therefore selected for under high grazing pressure (Milton & Dean 1990; Milton & Hoffman 1994; Milton 1995). This thus results in a change of the dominance structure of plant communities in favour of these undesirable plants.

Tafelberg plateau, Folminkskop plateau and the SE slopes of Tafelberg each have distinct communities, linked to specific environmental factors that play a role in these communities. All other slopes with the exception of Buffelskop are however grouped into one big general slope community, with no distinction between SE and NW slopes. This suggests that aspect and the expected cooler, more moist conditions on SE slopes as

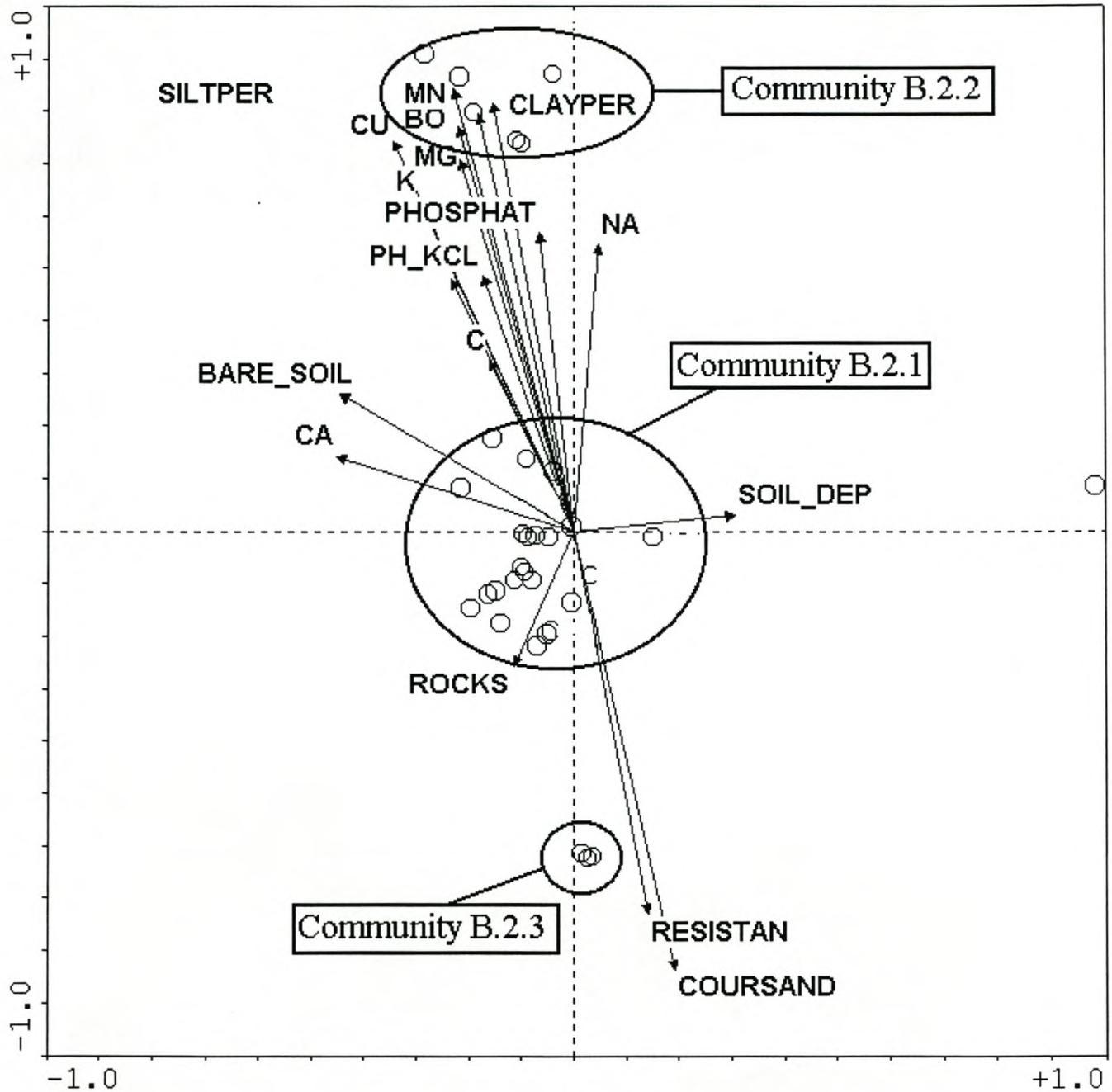


Fig. 5.7 An ordination diagram showing the distribution of sites in relation to available environmental factors for communities B.2.1, B.2.2 and B.2.3. Eigen values: Axis 1 – 0.807, Axis 2 – 0.545. An identification key for the diagram is provided in 5.3.1.

factors determining community composition are overridden by soil type and associated nutrient status. Soils of the SE and NW slopes are both derived from the dolerite cap and dolerite rocks and are characterised by relatively higher levels of C, Cu, Zn, Mn, Mg, Bo, Silt and Clay in comparison with plains habitats.

Buffelskop is the only mesa of the three sampled that is topped by a sandstone layer and not by a dolerite cap. Plant communities on the slopes of Buffelskop are distinct, separate communities that are not linked to any other communities in the study and have distinct soil composition. The slopes of Buffelskop are more arid and less compacted in comparison with those of Tafelberg and Folminkskop. Sandstone absorbs more water than dolerite, and the exceptionally low plant cover and steep sides lead to higher runoff, resulting in a relatively xeric habitat. In xeric sandstone mesas such as Buffelskop, aspect and slope override soil type and associated nutrient status as determinants of community composition.

5.4.1.2 Restoration potential

It has been suggested that mesas could provide sources of seed for the re-colonization, by species in decline, of the degraded surrounding plains habitats (Burke *et al.*, submitted). This study indicated that approximately 28 % of the species were shared between mesas and their surroundings (Appendix 5.8.2). Not all of these shared species can be used in the restoration of degraded vegetation, as many of them are poor colonisers. More species in total occurred only on mesas (45% of species sampled in all plots) in comparison to species that were restricted to plains habitats (26%) or that were shared between mesas and plains habitats (28%)(Appendix 5.8.2). This reflects the larger species pool found on mesas, although alpha diversity on mesas was not significantly higher on mesas compared to their surroundings (Chapter 4, Diversity). Larger mesas such as Tafelberg (450 m above surroundings) shared more species with the surrounding plains than smaller mesas, although the plateau was more distinct than that of smaller mesas (Diversity, Chapter 4).

Species shared between plains and mesa habitats included various valuable grazing species, including generalist species such as *Tragus koeleroides*, *Felicia ovata*, *Felicia muricata*, *Jamesbrittenia tysonii*, *Pentzia incana*, *Selago albida*, *Limeum aethiopicum*, *Fingerhuthia africana*, *Trichodiadema rogersiae* and *Eragrostis obtusa*

that seemingly do not require specific habitat conditions to grow. Highly palatable species such as *Felicia muricata* and *Limeum aethiopicum* occur at higher frequencies on mesas than on plains habitats, a possible consequence of increased grazing pressure on the plains. Species such as these may also have potential to be used in the restoration of surrounding degraded plains.

5.4.1.3 Uniqueness of habitat

Mesas are distinct in composition and can be regarded as islands of one vegetation type in a sea of another vegetation type (plains). Mesa habitats in Middelburg are under-utilized by livestock because of their general inaccessibility (steep slopes, extremely rocky terrain, cliffs and fences) coupled with the absence of natural springs or artificial water points on them. Mesa habitats are not currently threatened by development, but do have a higher conservation status than the surrounding plains due to their relatively undisturbed nature.

Vegetation on the plains in the Queenstown District was, almost entirely, formed by species of subtropical origins, while the temperate element became more important with an increase in altitude (Roberts 1965). This was attributed to a change in microclimate with an increase in altitude. Mountains were found to be grassier in composition with an increase in woody plants in rocky areas due to improved moisture conditions (Roberts 1965). Similar trends were found for the Middelburg study area, with an increase in woody species of temperate affinities on the mesas. Genera such as *Diospyros*, *Euclea*, *Euryops*, *Tarchonanthus*, *Maytenus*, *Carissa* and *Rhus* were restricted to mesa habitats and were absent from all plains in this study.

Plains habitats are used extensively for stock production, and the vegetation is in a state of degradation ranging from light to severe. Toxic, spinescent and unpalatable plants are common to dominant. In severely degraded areas, soil erosion has taken place to the extent that plants occur on pedestals. Less disturbed areas of plains habitat are now restricted to specific locations such as road verges or railway lines where grazing is absent, but for the most part plains habitats have been altered in one way or another through grazing by livestock.

5.4.2 Regional linkages

Plant communities in the Middelburg study area were very similar in composition with the communities identified in other parts of the Nama-karoo (Palmer 1989; Palmer 1991; Rubin & Palmer 1996), and shared many species even with communities along the borders of the Nama-karoo (Roberts 1965; Bezuidenhout 1994; Werger 1973).

Communities identified in the Karoo Nature Reserve (Graaff-Reinet) such as “Grassy Open Shrubland” on dolerite and sandstone derived slopes and ridges, “Open Grassy Shrubland on dolerite upland” and “Shrubland of rocky slopes and ridges” (Palmer 1989) shared many grass species (mainly species from the genera *Themeda*, *Heteropogon*, *Cymbopogon*, *Eragrostis*, *Sporobolus*, *Eustachys*, *Melica*, etc.) and shrub species (mainly species from the genera *Rhus*, *Buddleja*, *Euclea*, *Diospyros*, *Selago*, *Pentzia*, *Euryops*, *Helichrysum*, *Walafrida*, *Hermannia*) with the mesa habitats in Middelburg. Dwarf shrublands for the Karoo Nature Reserve (Palmer 1989) also shared many genera (*Eberlanzia*, *Blepharis*, *Haworthia*, *Pentzia*, *Chrysocoma*, *Felicia*, *Eragrostis*, *Psilocaulon*, *Chloris*, *Tragus*, *Cynodon*) with the dwarf shrublands of the Middelburg District. A similar occurrence of shared species was also found when communities in the Middelburg District were compared with communities of the Camdeboo and Aberdeen plains and surrounding mountains (Palmer 1991) as well as of the Karoo National Park (Beaufort West) (Rubin & Palmer 1996). While communities in the Middelburg study were similar to those reported in the rest of the Nama-karoo, with many shared genera and species, the communities sometimes differed in the specific species occurring in certain areas. This is a consequence of the high beta and gamma diversity typical of southern Africa, and made direct comparisons between communities difficult. A recent vegetation mapping exercise for South Africa (VEGMAP) showed that the vegetation of the mesas in the Middelburg District formed part of Tarkastad Mountain Shrubland (L. Mucina, pers. comm.), while the vegetation of the Middelburg plains formed part of Eastern Karoo Plains Communities (L. Mucina, pers. comm.).

Ecological factors and processes at work in the Middelburg District were very similar to those in the rest of the Nama-karoo. The most important driving force in the Karoo

National Park (Beaufort West) was a topographic moisture gradient (Rubin & Palmer 1996), while soil type was an important factor in the Vaalbos National Park, Northern Cape (Bezuidenhout 1994). The Middelburg study area was strongly influenced by a presumed soil-moisture gradient associated with an increase in elevation from the plains habitats to the higher lying mesa habitats. Degraded shrublands were said to be a consequence of grazing by sheep (Palmer 1989), and both species indicative of disturbance (*Geigeria ornativa*, *Tribulus terrestris* and *Salsola kali*) and normal species (*Pentzia incana*, *Chrysocoma ciliata*, *Felicia muricata* and *Eragrostis obtusa*) were the same as those found in degraded shrublands of the Middelburg District.

5.4.3 Comparison with international arid zones

Plant communities in other arid areas of the world have much in common with the communities identified in the Middelburg District, regardless of annual precipitation often being much lower overseas. Genera shared between the Middelburg District and arid lands from central Saudi Arabia, Egypt (Sinai desert), Niger and Chile (Atacame desert) include *Lycium*, *Convolvulus*, *Cyperus*, *Juncus*, *Scirpus*, *Senecio*, *Medicago*, *Blepharis*, *Sporobolus*, *Hyparrhenia*, *Aristida*, *Indigofera*, *Limeum*, *Euphorbia*, *Tribulus*, *Amaranthus*, *Cucumis*, *Digitaria*, *Cenchrus*, *Commelina*, *Eragrostis*, *Acacia*, *Cadaba*, *Asparagus*, *Themeda*, *Osteospermum*, *Euryops*, *Stachys*, *Salsola*, *Chloris*, *Zygophyllum*, etc. (Moustafa & Zaghoul 1996; Shaltout & Mady 1996; Gutierrez *et al.* 1998; Hegazy *et al.* 1998; Wezel & Boecker 1998). Species such as *Aristida adscensionis*, *Themeda triandra*, *Chloris virgata* and *Hyparrhenia hirta* had a very wide distribution and are common in arid lands from West Africa to the Middle East. Major factors determining the distribution of communities overseas were precipitation, soil texture and altitude (Moustafa & Zaghoul 1996; Shaltout & Mady 1996; Gutierrez *et al.* 1998; Hegazy *et al.* 1998; Wezel & Boecker 1998).

5.5 Final conclusions

Although mesas and plains are similar in alpha diversity (Chapter 4), the communities occurring on these habitats are distinctly different from each other. No communities were shared between mesas and plains habitats. The distribution and composition of communities across the Middelburg landscape were mainly attributed to a soil moisture gradient. Aspect and the expected cooler, moister conditions on SE slopes as factors determining community composition for the dolerite mesas were overridden by soil type and associated nutrient status. In xeric sandstone mesas such as Buffelskop, aspect and slope as determinants of community composition overrode soil type and associated nutrient status. Mesas are distinct in composition and can be regarded as islands of one vegetation type in a sea of another vegetation type. Plant communities in Middelburg were very similar in composition to communities identified in other parts of the Nama-karoo, with many shared genera and species.

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5.8 List of Appendices

5.8.1 Differentiated Table

Differentiated table produced originally in Twinspan, manually manipulated thereafter (see Materials and Methods, Chapter 3). Species data are arranged in a table with species as rows and plots (relevés) as columns. The abbreviations Thornf, Mimosasf, Greyvillef, Buffelsvlf, Buffelspof and Tafelbergf refer to the farms Thorn Springs, The Mimosas, Greyville, Buffelsvlei, Buffelspoort and Tafelberg respectively. Presence of a plot on a farm is indicated by 1.

5.8.2 Distribution of species in different habitats

Species were divided into three different habitats: Mesas, plains, and shared. “Mesas” and “plains” refer to those species found only in either habitat. Shared referred to species that occurred in both mesa and plains habitats.

Appendix 5.8.1 Differentiated Table

Appendix 5.8.2 Distribution of species in different habitats**Species restricted to mesa habitats (Total 89 species)**

<i>A. striatus</i>	<i>H. pulchella</i>
<i>Albuca juncifolia</i>	<i>Haworthia</i> sp.
<i>Albuca</i> sp.	<i>Helichrysum rosam</i>
<i>Aloe striata</i>	<i>Hermannia linearifolia</i>
<i>Asparagus laricinus</i>	<i>Indigastrum parviflorum</i>
<i>Berkheya pinnatifida</i>	<i>Kedrostis africana</i>
<i>Boophane disticha</i>	<i>Kleinia longiflora</i>
<i>Buddleja glomerata</i>	<i>Lantana rugosa</i>
<i>Bulbine frutescens</i>	<i>Lessertia carnosa</i>
<i>C. lanuginosa</i>	<i>Melianthus comosus</i>
<i>C. montana</i>	<i>Melica racemosa</i>
<i>C. obovata</i> var. <i>obovata</i>	<i>Opuntia</i> sp.
<i>C. orbicularis</i>	<i>Oxalis heterophylla</i>
<i>C. perfoliata</i>	<i>P. aridum</i>
<i>C. sp.</i>	<i>P. leptophylla</i>
<i>C. sp. B</i>	<i>P. quinquefida</i>
<i>C. tetragona</i>	<i>P. replicatum</i>
<i>Cadaba aphylla</i>	<i>Pachypodium succulentum</i>
<i>Carissa haematocarpa</i>	<i>Panicum maximum</i>
<i>Cenchrus ciliaris</i>	<i>Pegolettia baccaridifolia</i>
<i>Ceterach cordatum</i>	<i>Pelargonium abrotanifolium</i>
<i>Chascanum cuneifolium</i>	<i>Pellaea calomelanos</i>
<i>Cheilanthes hirta</i>	<i>Pentzia punctata</i>
<i>Chenopodium</i> sp.	<i>Plagiochasma rupestre</i>
<i>Cissampelos capensis</i>	<i>Pleiospilos compactus</i>
<i>Clematis brachiata</i>	<i>Polhillia connatum</i>
<i>Crassula cotyledonis</i>	<i>Polygala ephedroides</i>
<i>Cymbopogon plurinodis</i>	<i>Polygala</i> sp.
<i>Cyperus</i> sp.	<i>Pseudocrossidium crinitum</i>
<i>D. lycioides</i>	<i>R. erosa</i>
<i>D. zeyheri</i>	<i>Rhadamanthus</i> sp.
<i>Dianthus basuticus</i>	<i>Rhigozum obovatum</i>
<i>Dimorphotheca cuneata</i>	<i>Rhus burchellii</i>
<i>Diospyros austro-africana</i>	<i>Ruschia britteniae</i>
<i>Dipcadi</i> sp.	<i>Selago saxatilis</i>
<i>Eriocephalus africanus</i>	<i>Solanum tomentosum</i>
<i>Eriospermum</i> sp.	<i>Stachys linearis</i>
<i>Euclea crispa</i>	<i>Sutera halimifolia</i>
<i>Euryops annae</i>	<i>Sutherlandia frutescens</i>
<i>Eustachys paspaloides</i>	<i>Tarchonanthus camphoratus</i>
<i>F. ovata</i>	<i>Themeda triandra</i>
<i>Fabronia abyssinica</i>	<i>Turbina</i> sp.
<i>Felicia filifolia</i>	<i>Viscum rotundifolium</i>
<i>Gymnosporia buxifolia</i>	<i>Wahlenbergia nodosa</i>
<i>H. minutiflora</i>	

Species restricted to plains (Total 52 species)

<i>Albucca setosa</i>	<i>Urochloa</i> sp.
<i>Aridaria noctiflora</i> ssp. <i>straminea</i>	<i>Zygophyllum incrustatum</i>
<i>Berkheya heterophylla</i>	
<i>Bulbostylis humilis</i>	
<i>C. sagittatus</i>	
<i>Chloris virgata</i>	
<i>Convolvulus boedeckerianus</i>	
<i>Crassula</i> sp.	
<i>Crassula</i> sp. A	
<i>Crassula</i> sp. C	
<i>Cynodon dactylon</i>	
<i>Cyperus usitatus</i>	
<i>Drosanthemum duplessiae</i>	
<i>E. bicolor</i>	
<i>Eragrostis bergiana</i>	
<i>Galenia africana</i>	
<i>Geigeria ornativa</i>	
<i>Gnaphalium confine</i>	
<i>Gnidia polycephala</i>	
<i>Helichrysum lucilioides</i>	
<i>Hermannia pulverata</i>	
<i>Hertia pallens</i>	
<i>Hypertelis</i> sp.	
<i>I. zeyheri</i>	
<i>Indigofera acuticephala</i>	
<i>Jamesbrittenia atropurpurea</i>	
<i>Medicago laciniata</i>	
<i>Melolobium burchelli</i>	
<i>Monsonia brevirostrata</i>	
<i>Nenax microphylla</i>	
<i>Oligocarpus calendulaceus</i>	
<i>Ornithogalum</i> sp.	
<i>Oropetium capense</i>	
<i>Osteospermum leptolobum</i>	
<i>P. sphaerocephala</i>	
<i>Pentzia globosa</i>	
<i>Phyllobolus</i> sp.	
<i>Pseudognaphalium oligandrum</i>	
<i>Psilocaulon junceum</i>	
<i>Pteronia sordida</i>	
<i>Rosenia humilis</i>	
<i>Ruschia intricata</i>	
<i>Salsola</i> sp.	
<i>Salvia verbenaca</i>	
<i>Selago geniculata</i>	
<i>Senecio radicans</i>	
<i>Thesium spartioides</i>	
<i>Tragus berteronianus</i>	
<i>Tribulus terrestris</i>	

Species occurring in both mesa and plain habitats (56 species)

<i>A. diffusa</i>	<i>Selago albida</i>
<i>Adromischus</i> sp.	<i>Senecio cotelydonis</i>
<i>Albuca</i> sp.	<i>Sporobolus fimbriatus</i>
<i>Anacampseros albidiflora</i>	<i>Talinum caffrum</i>
<i>Aptosimum procumbens</i>	<i>Thesium hystrix</i>
<i>Aristida adscensionis</i>	<i>Tragus koelerioides</i>
<i>Asparagus burchellii</i>	<i>Trichodiadema rogersiae</i>
<i>B. mitrata</i>	<i>Zygophyllum gilfillanii</i>
<i>Blepharis capensis</i>	
<i>Chenopodium mucronatum</i>	
<i>Chrysocoma ciliata</i>	
<i>Commelina africana</i>	
<i>Crassula muscosa</i>	
<i>Digitaria eriantha</i>	
<i>E. lehmanniana</i>	
<i>E. obtusa</i>	
<i>E. scoparius</i>	
<i>Enneapogon desvauxii</i>	
<i>Eragrostis curvula</i>	
<i>Eriocephalus ericoides</i>	
<i>Euphorbia brachiata</i>	
<i>F. ovata</i>	
<i>Felicia muricata</i>	
<i>Fingerhuthia africana</i>	
<i>Gazania linearis</i>	
<i>Helichrysum zeyheri</i>	
<i>Heliophila suavissima</i>	
<i>Hermannia filifolia</i>	
<i>Heteropogon contortus</i>	
<i>Hibiscus pusillus</i>	
<i>I. sessilifolia</i>	
<i>Indigofera exigua</i>	
<i>Jamesbrittenia tysonii</i>	
<i>Lepidium africanum</i>	
<i>Limeum aethiopicum</i>	
<i>Lycium cinereum</i>	
<i>Melolobium burchelli</i>	
<i>Mestoklema elatum</i>	
<i>Moraea pallida</i>	
<i>Oxalis commutata</i>	
<i>P. lanata</i>	
<i>Pegolettia retrofracta</i>	
<i>Pentzia incana</i>	
<i>Phymaspermum parvifolium</i>	
<i>Plinthus karooicus</i>	
<i>Polygala asbestina</i>	
<i>Portula</i> sp.	
<i>Pteronia glauca</i>	

6. Concluding remarks

Mesas in arid environments can play an important role in preserving biodiversity and forming refuges for species no longer able to grow in the surrounding plains due to overgrazing and subsequent degradation or to climate change. Plant species on mesas could, in favourable times, serve as potential sources of seeds and propagules for depleted populations on the surrounding degraded plains. Detailed knowledge about the composition of the fauna and flora on mesas and their surroundings are important in the face of predicted global climate change (Anonymous 1998) for southern Africa, and also for purposes of conservation planning and restoration.

This study is a component of a broader umbrella project entitled “Restoration of degraded Nama-karoo rangelands: the role of conservation islands”. The purpose of the project was to assess the role played by isolated mesas in the conservation of biodiversity in Nama-karoo rangelands and to investigate the potential role of mesas as conservation islands to fauna and flora. If the Nama-karoo has spread into vegetation types bordering on it in recent historical times (Acocks 1953), mesas could give us some indication about what the vegetation in the eastern parts of the Nama-karoo used to be like before the impact of domestic livestock. Notwithstanding the fact that these topographical features are unique in themselves, their relative inaccessibility to domestic livestock would imply that their vegetation is more intact than the surroundings plains.

In this study vegetation on and adjacent to three isolated mesas (Tafelberg, Folminkskop and Buffelskop) was studied in the Middelburg District of the Nama-karoo biome, South Africa. Plant species composition and cover values were recorded for transects extending from the SE plains of each mesa across the mesas to the NW plains. Data collected was then used to describe 1) plant diversity and 2) plant communities across the landscape.

6.1 Overview of key questions, results and discussion

6.1.1 Plant Diversity (Chapter 4)

Five key questions were addressed in this chapter: 1) What is the composition of the vegetation like in terms of total species numbers, dominant families and genera? 2)

Are the mesas higher in diversity than the surrounding landscape and are they therefore of special management/conservation value? 3) How do the three mesas differ from one another in terms of diversity? 4) How similar/different are the plateaux, slopes and plains from each other for each of the mesas? and 5) How does plant diversity in Middelburg compare with diversity in other vegetation types?

A total of 353 species were recorded for mesas and their surrounding flatlands in the Middelburg District. These consisted of 61 families and 199 genera. The most diverse families in terms of species diversity were Asteraceae (78 species), Poaceae (36), Crassulaceae (18), Fabaceae (14), Chenopodiaceae (13), Mesembryanthemaceae (13) Hyacinthaceae (10) and Aizoaceae (9). Composition of vegetation in the Middelburg District was typical of Nama-karoo communities, comprising a mixture of grasses, dwarf shrubs and phanerophytes.

Species diversity on mesas was not significantly higher than that of the surrounding plains. This is in contrast to the findings of parallel studies in Namibia where mesas in more arid zones are clearly islands of diversity (Burke 2002). However, in Middelburg more species in total occurred only on mesas (45 %) in comparison to species that were restricted to plains habitats (27 %) or that were shared between mesas and plains habitats (28 %). This compared well with similar findings by Cowling *et al.* (1994) who found that diversity on slopes and flatlands was similar, although more species were sampled in total from slopes habitats. This indicated a greater species pool on slopes habitats (Cowling *et al.* 1994), a possible result of more diverse microhabitats on the slopes associated with rockiness in comparison with the surrounding flatlands. Slightly increased values of diversity on mesas were attributed to increased moisture availability as influenced by higher rock cover, coupled with the effects of aspect. Average diversity across the landscape was strongly influenced by localized pockets of increased and decreased diversity. The most important determinant of diversity in these pockets was moisture heterogeneity, as influenced by factors such as slope, rockiness, soil depth and soil texture, as well as the influence of disturbance and overgrazing.

Mesas in Middelburg were much less distinct from their surroundings in terms of species diversity compared to mesas of similar size in the northern parts of the Nama-

karoo in Namibia (Burke *et al.* 2002). Mesa “islands” in Middelburg were slightly more mesic compared to the matrix of more xeric plains, but the differences in aridity between mesas and their surroundings in the latter areas were far greater in the more arid parts of the Nama-karoo than in Middelburg. Greater differences between mesas and their surroundings led to the mesas being more distinctly different to their surroundings.

No significant differences in average alpha diversity were found between the three mesas, although Tafelberg (450 m above surroundings) had slightly higher values than Folminkskop and Buffelskop (both 200 m above surroundings). These slightly higher alpha diversity values for Tafelberg were attributed to a more diverse microhabitat associated with the larger size of the mesa coupled with increased precipitation due to the higher elevation.

The plains surrounding Tafelberg were on average higher in alpha diversity compared to the plains surrounding Buffelskop and Folminkskop. Patterns of slightly higher and lower alpha diversity levels on the plains were linked to localized overgrazed patches, temporal wetlands, shallow soils and increased rock cover. Grazing history and current management practices were not measured, but overgrazed patches clearly had lower species diversity. Few species were shared between mesas and their surroundings, making it unlikely that the increased diversity found on the plains of Tafelberg was linked to the slightly increased diversity for the mesa compared to the other two mesas.

Dolerite-capped mesas in the Middelburg District (Tafelberg and Folminkskop) showed an increase in average beta diversity with an increase in size, comparing well with similar findings in the northern parts of the Nama-karoo (Burke *et al.* 2002). Bigger mesas had more diverse microhabitats in comparison with smaller mesas, enabling them to support a greater array of species and communities. Buffelskop (sandstone mesa) had abnormally high average beta diversity values for its size. Habitats exceptionally high in diversity (SE slopes) occurring on the same mesa as habitats exceptionally low in diversity (NW slopes and plains) caused average beta diversity values for Buffelskop to be higher than expected.

Buffelskop (sandstone mesa) had much higher average beta diversity compared to Folminkskop (dolerite capped mesa), which was the same height, with comparable environmental conditions. Palmer & Cowling (1994) also found species replacement rates on sandstone to be higher than that on dolerite for comparable environmental conditions. This was caused by the presence of a community that was recently over-utilised by domestic herbivores. Species replacement rates on Buffelskop were relatively high due to the presence of numerous impoverished communities, caused by steep slopes, patches of overgrazing and temporal wetland areas.

Mesas and plains shared few species (28 %). Species shared between the plateau and slopes of a bigger mesa like Tafelberg (450 m above surroundings) were fewer than species shared between the plateau and slopes of the smaller mesas (200 m above surroundings). This suggested that isolation of the plateau became more distinct with an increase in size of the mesa, with bigger mesas supporting more unique vegetation on their plateaux than smaller mesas.

Tafelberg had more species in common with the surrounding plains than did the two smaller mesas. A bigger mesa such as Tafelberg had a more diverse array of microhabitats enabling plains species to occupy certain sites on the slopes of the mesa, while smaller mesas such as Folminkskop and Buffelskop had lower habitat heterogeneity and did not have sites that enable plains species to persist on the slopes of the mesa. This is in contrast to a study in the northern parts of the Nama-karoo where bigger mesas above 240 m were more distinctly different from their surroundings than smaller mesas (< 240 m) (Burke *et al.* 2002).

Average Shannon Wiener alpha diversity indices for Middelburg (2.32) were much higher than those found for the Nama-karoo by Cowling *et al.* (1989), who ascribed a Shannon-Wiener index of 1.8 as an average for the Nama-karoo. Values in Middelburg ranged from 0.69 to 3.2. Higher average alpha diversity for Middelburg could be explained by the increased precipitation experienced by the eastern parts of the Nama-karoo. Species richness in Nama-karoo communities is relatively low in comparison with other biomes in South Africa, especially if its large area is taken into account (Cowling *et al.* 1989). However, although overshadowed by the relatively high diversity of other biomes in South Africa, Nama-karoo communities have a rich

flora for a semi-arid region (Cowling *et al.* 1989). Plant diversity in the Middelburg District would compare favourably with other arid lands of North America and Australia. Communities in the Nama-karoo were found to be similar in patterns and determinants of diversity compared to those from other arid lands such as the New World (Cowling & Hilton-Taylor 1999).

Mesas and their surrounding plains were not significantly different in terms of alpha diversity. However, the composition of the vegetation between these two habitat types was completely different.

6.1.2 Plant community composition (Chapter 5)

Vegetation was divided into plant communities following the approach of Braun-Blanquet (1932). Several key questions were addressed, such as: 1) What plant communities can be identified across the landscape? 2) How do environmental variables such as aspect, slope, substrate, rock cover, soil texture, nutrient availability, soil depth, moisture and altitude influence the composition and distribution of plant species across the landscape? 3) What plants occur on the mesas that do not occur on the flats and *vice versa*? 4) What is the potential of mesas for restoration? 5) Are mesas worthy of special conservation status? 5) How do plant communities in Middelburg compare to communities in the rest of the Nama-karoo biome?

The species-releve matrix was divided into two main groups of communities: Slopes/Plateaux (A) and Plains (B). Slope/Plateaux (A) was classified as Open Grassy Shrubland, while Plains (B) were classified as Open Dwarf Shrubland. Slopes/Plateaux (A) were subdivided into community groups A1 and A2, each consisting of three communities. Plains (B) were subdivided into community groups B1 and B2, consisting of four and three communities respectively. In total 13 plant communities were identified across the landscape.

Mesa and plains communities were distinctly different, with no communities shared between mesa and plains habitats. Both mesas and their surrounding plains play an important role in the conservation of Nama-karoo rangelands. Differences between mesa and plains communities as well as the general distribution of different communities were mainly attributed to a soil-moisture gradient. Similar results were

obtained in other parts of the Nama-karoo biome, with a topographic moisture gradient being the most important driving force in the Karoo National Park (Beaufort West) (Rubin & Palmer 1996) while soil type was an important factor in the Vaalbos National Park, Northern Cape (Bezuidenhout 1994). Shallower, rockier soils of the mesas coupled with very little runoff (due to rockiness and high grass cover) and naturally higher precipitation due to elevation, resulted in a more mesic habitat compared to the plains habitats. Plains had little rock cover, a high percentage of bare soils (likely a result of degradation associated with loss of soil cover), slightly shallower soils and higher runoff rates than mesas. These factors resulted in a more xeric habitat. Habitat differences such as these probably existed before the impact of domestic stock introduced by European settlers but overgrazing has probably exacerbated the differences. Dominance structure of plant communities on the plains has changed in favour of toxic, spinescent and unpalatable plant species due to selective grazing by domestic livestock.

Dolerite mesas such as Tafelberg and Folminkskop had a general slope community shared between the two mesas. Aspect and the expected cooler, moister conditions on SE slopes, as factors determining community composition for the dolerite mesas, were overridden by soil type and associated nutrient status. In xeric sandstone mesas such as Buffelskop, soil type and associated nutrient status were overridden by aspect and slope as determinants of community composition. Buffelskop had distinct SE and NW slope communities, with SE slopes being significantly more diverse than NW slopes.

More species in total occurred on mesas (45 %) in comparison to species that were restricted to plains habitats (27 %) or that were shared between mesas and plains habitats (28 %). The potential to use mesas habitats as sources of seed and propagules for the restoration of degraded plains habitats was thought to be low due to the few species shared between mesas and their surroundings. No plant communities were shared between mesas and their surrounding plains. Some species common to both habitats did not seem to require specific conditions for growth. These generalist species might have some future potential in restoration projects and include desirable (highly palatable) species such as *Eragrostis obtusa*, *Felicia muricata*, *F. ovata*

Fingerhuthia africana, *Jamesbrittenia tysonii*, *Limeum aethiopicum*, *Pentzia incana*, *Selago albida* and *Tragus koeleroides*.

Mesa habitats in Middelburg were under-utilised by livestock because of their general inaccessibility (steep slopes, extremely rocky terrain, cliffs and fences) coupled with the absence of natural springs or artificial water points on them. Mesa habitats were not threatened (at the time of the study) by development, but did have a higher conservation value than the surrounding plains due to their undisturbed nature.

Plains habitats were used extensively for stock production. The vegetation was in a state of degradation ranging from light to severe, possibly a result of past overgrazing (Palmer 1989). Toxic, spinescent and unpalatable plants were common to dominant. Species indicative of overgrazing such as *Geigeria ornativa*, *Tribulus terrestris* and *Salsola kali* (Palmer 1989) occurred frequently. Soil erosion had taken place to the extent that plants occurred on pedestals. Less disturbed areas of plains habitat are currently restricted to specific locations such as road verges or railway lines where grazing is absent, but for the most part plains habitats have been altered in one way or another through grazing by livestock.

Plant communities of the Middelburg study area were very similar in composition to the communities identified in other parts of the Nama-karoo (Palmer 1989; Palmer 1991; Rubin & Palmer 1996), and shared many species even with communities on the border of the Nama-karoo (Roberts 1965; Werger 1973; Bezuidenhout 1994). Grass genera common throughout the Nama-karoo included *Eragrostis*, *Eustachys*, *Cymbopogon*, *Heteropogon*, *Melica*, *Sporobolus* and *Themeda*, while common shrub genera included *Buddleja*, *Blepharis*, *Chrysocoma*, *Diospyros*, *Eberlanzia*, *Euclea*, *Euryops*, *Felicia*, *Haworthia*, *Helichrysum*, *Hermannia*, *Pentzia*, *Psilocaulon*, *Rhus*, *Selago* and *Walafrida* (Palmer 1989; Bezuidenhout 1994; Rubin & Palmer 1996). While the same type of communities occurred in the Middelburg study area that occurred in the rest of the Nama-karoo with many shared genera and species between the two, the communities sometimes differed in the specific species occurring in certain areas. This made direct comparisons between communities difficult. The vegetation mapping of South Africa project showed that the vegetation of the mesas in the Middelburg District formed part of Tarkastad Mountain Shrubland (L Mucina,

pers. comm.), while the vegetation of the Middelburg plains formed part of Eastern Karoo Plains Communities (L Mucina, pers. comm.).

6.2 Shortcomings

Past overgrazing is partly responsible for degraded rangeland today, as the recovery of degraded veld is very slow (Milton & Hoffman 1994). Grazing history and present management practices on the different farms were not measured in any quantitative way in this study, although the effects of overgrazing on certain areas was noted. Some of the farms were subdivided, merged, split or leased by people other than the land owner over the course of their existence, making it difficult to study the effect of past management practices. All the plots established in this study are marked, enabling their revisitation and resampling in the future. It is hoped that by doing so, the effects of current management practices can be elucidated. Mesas were observed to be grazed less intensely than the surrounding plains. This was backed up by observations on higher dung density on the plains habitats compared to the mesas habitats (N Hendricks, pers. comm.).

Specific communities such as plants in drainage lines on the flats, cliff communities, etc. were not included in the collection of data for this study, although species from these communities were sampled when encountered for identification purposes. Species composition, density (not reported on in this thesis) and cover values for communities on the plains, slopes and plateaux were recorded in a subjective way typical of plant phytosociological studies (Kent & Coker 1992).

6.3 Looking to the future

6.3.1 Degraded plant communities – further degradation, stability or recovery?

Vegetation on the plains in the Middelburg District had clearly been affected by more than 200 years of grazing by domestic livestock, primarily sheep. A high density of unpalatable, undesirable, toxic, spinescent plants or species indicative of disturbance were common to dominant especially on the plains. The occurrence of species such as these was lower on the mesas, primarily because they were protected from grazing by their natural inaccessibility and lack of watering points. Species that are continually at a disadvantage due to intense grazing reproduce less successfully in comparison to species that are not grazed or protected from grazing (Milton 1992).

Long-term, continuous, selective grazing can lead to an increase of species that are protected from grazing and a decrease of desirable species. Overgrazing also accelerates soil erosion through a reduction of plant cover and trampling of the soil (Fuls 1992).

Long-term changes (50 years) are mostly said to be irreversible, while medium term changes are reversible or permanent depending on the duration of the disturbance and the amount of soil lost (Roux & Theron 1987). Marked changes in vegetation composition take place at a slow rate (decades) (Roux & Theron 1987). Evidence for the continual degradation of karoo veld is often debatable with some areas being in a better condition than 60 years ago (Hoffman & Cowling 1990). Resilience of karoo rangelands is a controversial issue (Milton & Dean 1999) with some arguing that loss of certain perennial plant species from communities reduces resilience of such a community following drought and thus lowers sustainable animal production (Milton & Dean 1999). Other authors suggest that resilient plants are favoured by high stocking rates, enabling the vegetation to recover faster following drought and disturbance (Milton & Dean 1999). Replacement of perennial plant communities by annual plant communities could make the availability of fodder less stable, linked to increased and reduced yield in wet and dry periods respectively (Milton & Dean 1999). However, Hoffman *et al.* (1999) showed that the number of domestic livestock that ephemeral plant communities can support on degraded land did not decrease over time, indicating that ephemeral plant communities might be unstable in the short term but resilient and stable in the long term (Milton & Dean 1999).

Productivity (based on average ranch size and livestock numbers) in the eastern Cape has declined over the last 100 years, and more so than in the more mesic savanna vegetation of the Gauteng, Limpopo, North-West and Mpumalanga Provinces (formerly the Transvaal Province) and the KwaZulu/ Natal Province (formerly the Natal Province) (Milton & Dean 1995). Results from this study suggest that the plains are at present more degraded in comparison with the mesa habitats, but it is impossible to conclude whether or not rangelands have stabilised given current stocking rates and climatic conditions. Many farmers in the Middelburg District today are not able to make a living on land they inherited from their fathers, and most of the farmers on whose land I worked currently own two properties. This could

possibly indicate that the vegetation is degrading further, but at a rate so slow that at present farmers would not even realize it. The plots used in the vegetation survey reported on in this thesis are all of a permanent nature, enabling us to go back and resample the vegetation again in the future. This should shed some light on whether or not rangelands are at present degrading even further, or whether the vegetation has stabilized.

6.3.2 Future restoration of degraded rangelands – necessity and feasibility

Severely overgrazed bare patches often have difficulty recovering due to an unfavourable microhabitat in which seed production, germination and seedling survival was severely hampered (Fuls 1992) or in which soil loss and altered soil conditions prevented the recruitment of perennial plants (Milton & Hoffman 1994). Depleted seed banks of perennial plant species (Jones 2000), inadequate seed production by defoliated plants and competition from established unpalatable plants can further reduce passive recovery of overgrazed rangeland (Milton & Hoffman 1994).

Once these semi-arid and arid rangelands have reached a certain state of degradation it is unlikely that they will recover through the withdrawal of livestock alone (Fuls & Bosch 1991; Milton & Hoffman 1994). Severely overgrazed rangelands might only recover through active intervention such as soil reclamation and re-seeding (Milton & Hoffman 1994). Less degraded vegetation might be able to improve by resting after key rain events and seed set coupled with rotational grazing at recommended stocking rates (Milton & Hoffman 1994).

Recovery of degraded veld can often exceed the lifetime of the owner, discouraging many farmers from trying to rehabilitate their land. At the same time farmers are dependant on the natural environment for a living, and few farmers can afford to rest large tracts of land for extended periods of time (Milton *et al.* 1994). The irony is that it is often the wealthy farmers with good land that have the resources to improve their land, while many farmers with more degraded veld cannot afford, financially, to rest their veld for extended periods of time (Milton *et al.* 1994). Mesas in the Middelburg District do have potential albeit limited as sources of seed and propagules for the surrounding plains due to the few species shared between them and their degraded

surroundings. This study identifies that highly palatable species such as *Eragrostis obtuse*, *Felicia ovata*, *F. muricata*, *Fingerhuthia africana*, *Jamesbrittenia tysonii*, *Limeum aethiopicum*, *Pentzia incana* and *Selago albida* occurred in both mesa and plains habitats and might have some potential in restoring degraded land. Various restoration practices have been used by farmers in the Middelburg District with varying success. These include brush packing, ploughing, stone packing and limited reseeding.

Restoring degraded rangeland in the Middelburg District ranged in costs from R150/ha to R1312/ha, depending on which restoration method was being used (Esler & Kellner 2000; Esler *et al.* 2002). A combination of ripping the soil, fertilizing it with old manure, sowing seed and packing *Acacia* branches was found to be the most effective, but also most expensive (R1312/ha) method used (Esler & Kellner 2000; Esler *et al.* 2002). Ripping the soil was one of the most inexpensive methods (R160/ha) but not as effective as methods where rip was combined with the sowing of seed (Rip and seed = R350/ha). However, on a large scale and short term most farmers would not be able to afford costly restoration techniques such as these (Esler & Kellner 2000; Esler *et al.* 2002). It is proposed that government cost sharing for restoration should be examined as an alternative (Esler & Kellner 2000; Esler *et al.* 2002). Restoration programs normally make use of commercially obtained seed. However, local seed sources could possibly prove to be better adapted to their specific environments.

6.3.3 Relics of natural vegetation in a changed environment

The eastern parts of the karoo are said by some to have been a stable and extensive grassland before the colonization of the land by European settlers and their associated domestic livestock (De Klerk 1947; Acocks 1953). Acocks hypothesized that the karoo is expanding into more productive grassland habitats to the north and east (Acocks 1953). According to Acocks, the false upper karoo supposedly represents the most spectacular of all vegetation changes in SA, and "the conversion of 51 800 square km of grassveld into eroded karoo can only be regarded as a national disaster" (Acocks 1953). Other authors have questioned the extent to which the karoo has spread into other vegetation types, warning that much of the publications on vegetation change have appeared during or after extended droughts (Hoffman &

Cowling 1990). It was the overriding assumption of the broad project that mesas in the Middelburg District (part of the false upper karoo) might represent a more relictal natural vegetation type more representative of vegetation composition and condition before the impact of domestic livestock due to their natural inaccessibility and general unsuitable conditions (steep slopes without watering points) for livestock production. The assumption was that this would have given us some indication of what vegetation used to be like before the alteration of the vegetation through selective grazing. However, it is important to remember that mesas have probably been different by default even before the arrival of domestic livestock, and that sheep do graze mesas to a limited extent.

The presence of highly palatable grazing species such as *Digitaria eriantha*, *Eragrostis curvula* and *Themeda triandra* in railway lines and other protected areas on the plains in and around the study area could possibly indicate that these grasses had a much wider distribution in historical times than they do now. Woody species from the genera *Carissa*, *Diospyros*, *Euclea*, *Euryops*, *Maytenus*, *Rhus* and *Tarchonanthus* have probably been restricted to mesas even in historical times. Some palatable species such as *Felicia muricata*, *Felicia ovata*, *Limeum aethiopicum* and *Sporobolus fimbriatus* often occur inside other less palatable plants where they are protected from grazing (personal observation). Palatable shrubs such as these possibly had a wider distribution on the plains in the Middelburg District in historical times than they do at present.

Impoverished communities on the plains (e.g. Community B.2.3 – NW plain 2 Buffelskop) might originally have formed part of more general plains communities (Community B.1.1). Overgrazing, trampling and erosion have degraded communities like these so much that the original natural community is virtually unrecognizable today. High percentages of bare soil, denuded vegetation and lack of diagnostic (differential) species characterize communities such as these.

6.3.4 Future recommendations for sustainable use

Rangelands must be maintained at a step one level (step one meaning that the growth of forage plants could be restored by altering the grazing season/stocking intensity/animal type; no changes in secondary productivity, fauna, and soil) by

livestock reduction in dry years (Milton *et al.* 1994). The degraded condition of many rangelands today is the result of overgrazing and high stocking rates in the past. Farmers should assess their land on a regular basis that fits in with their grazing system (Milton *et al.* 1998). Assessment should precede movement of livestock to a rested camp and stocking rates should be adjusted according to the condition of the vegetation in the specific camp (Milton *et al.* 1998). Vegetation should be rested on a regular basis to give plants the chance to recover and seedlings the opportunity to establish especially after rain events. Areas denuded of vegetation (known as “brak kolle”) are of no value to the farmers and are at risk of future erosion through wind and water. Several farmers in the Middelburg District have attempted restoring these patches by ploughing, brush packing, stone packing and various other restoration techniques. Vegetation cover has been noted to increase on such ploughed areas, although most of the species that germinated following ploughing had been unpalatable grasses and annuals such as *Aristida adscensionis* (steekgras). Cover such as this could help stop erosion, while even species said to be unpalatable might be palatable at some stage of their life cycle. It is recommended that farmers invest in buying some seed of palatable grass or shrub species to sow in these denuded areas at the beginning of the rainy season, combined with the common practice of ploughing and resting of the camp at stake during germination of the seed. Seeds are expensive to buy and some species might be difficult to obtain, but even a limited amount of reseeded could be of great value to restore degraded vegetation and depleted natural seedbanks. Species occurring naturally on the farms that have seed that can be harvested easily (such as *Eriocephalus ericoides*, *Pentzia incana*, *Digitaria erianthra*) should also be considered as potential sources of seeds.

6.4 Future research

Above ground vegetation composition will be compared to present seed bank composition and densities for mesas and their surroundings in the Middelburg District. Seed banks of perennial species were found to be depleted on the degraded plains habitats in comparison to that of ephemeral species (Jones 2000), a possible result of selective florivory by domestic livestock (Milton 1995).

The density of dung as an indicator of habitat preference will be correlated with the composition and palatability of above ground vegetation. More dung was found in

the degraded plains habitats (N. Hendricks, pers. comm.) in comparison with the mesas habitats.

This study only reports on data collected from the SE and NW slopes and plains and plateaux of the mesas. However, data on species composition, density and cover was also recorded for the NE and SW slopes and plains of the mesas. Diversity and plant communities on the NE and SW slopes will be analyzed using the same methods as in the present study.

All the plots in the present study are of a permanent nature and clearly marked. These plots will be re-sampled in the future. Re-sampling the vegetation the future would provide a valuable long-term data set and enable us to comment on aspects of stability and degradation on the long run.

Most of the farms in the study area are commercial sheep farms. However, one of the farmers converted to cattle farming (Nguni cattle) about 7 years ago, and that farm has now been turned into a game farm. Re-sampling plots from this farm in future and comparing them with re-sampled plots from sheep farms could provide information on the recovery rate of degraded vegetation in the absence of grazing by sheep, and the impact of game farming on the condition of the vegetation.

6.5 Conclusions

The Braun-Blanquet classification system (Braun-Blanquet 1932) has proved to be an effective method to describe plant communities in the semi-arid Nama-karoo biome. Several studies on Nama-karoo vegetation have made use of the Braun-Blanquet classification system and have all used the same basic programs (such as Canoco and Megatab) for vegetation analysis (Palmer 1989, Palmer 1991, Bezuidenhout 1994, Rubin & Palmer 1996). This enables researchers to make comparisons between different vegetation studies.

Mesas in the Middelburg District contribute to overall biotic diversity, and play a role as drivers of ecological processes in the Nama-karoo landscape. In a sea of degraded plains habitats mesas are refugia for certain plants and animal species, with limited potential for restoration of the degraded surroundings. This study contributes valuable data on species diversity and community composition across a Nama-karoo

landscape, adding to the karoo database as an understudied part of South Africa's flora. Mesa habitats are worthy of conservation especially in the event of predicted climate changes.

6.6 References

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