Effects of domestic livestock on the vegetation of the Knersvlakte, South Africa

Diploma thesis

submitted by

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February 2009

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ABSTRACT

The vegetation of the Knersvlakte, which is part of the southern African Succulent Karoo Biome and known for its high diversity and endemism, has been subjected to domestic livestock grazing for centuries. In the course of establishing a conservation area there, it became relevant to assess the suitability of alternative future landuse practices from a conservation point of view. In this study, I investigated the effects of grazing on the vegetation of the Knersvlakte in terms of diversity and species composition of plant communities as well as plant size and reproduction of selected species and endozoochorous dispersal. Data were sampled on four largely adjacent farms, one of which was ungrazed, one moderately and two intensively grazed. Plant community and population data were collected on 27 quartz and 24 non-quartz plots, representing the two major habitat types of the region. Within each of the 1000 m² plots, 100 subplots of 400 cm² size were sampled and analysed for diversity and compositional changes. Endozoochorous dispersal was assessed by the seedling-emergence method from domestic and wild herbivore dung, sampled on the plots.

ANOVAs revealed that the species richness and abundance of endemic species on quartz fields was only slightly reduced through grazing. An association of plant strategy type and grazing intensity could not be detected, as abundance of annuals seemed to be mainly driven by rainfall which seemed to have varied spatially in the year of investigation. Ordination and fidelity analyses indicated that the species composition differed between grazing intensities and that the ungrazed and moderately grazed plots both contained unique locally endemic habitat specialists. Reproduction of *Drosanthemum schoenlandianum* and *Argyroderma fissum* was increased through moderate grazing, which in the case of *D. schoenlandianum* was ascribed to overcompensation for experienced biomass losses. The low number of seedlings on the moderately grazed plots was attributed to lower rainfall on the respective farm. The germination experiment revealed that dispersal of Aizoaceae was facilitated by endozoochory through domestic livestock, whereas Fabaceae mainly germinated from wild herbivore dung. From the nature conservation point of view, either the ungrazed or the moderately grazed plots showed the most favourable status in most of the parameters. In the Knersvlakte, both ungrazed areas and moderately grazed areas therefore seem to be important for the conservation of the existing plant diversity, vegetation pattern and their underlying processes.

Keywords: biodiversity, compositional shift, endozoochory, herbivory, intermediate disturbance hypothesis, Namaqualand, nature conservation

1 INTRODUCTION

The conservation of the biosphere with its diversity of ecosystems and their characteristic plant and animal species is one of this century's main challenges. The degradation of land in the consequence of its overexploitation by men through, for instance, agriculture, mining, overgrazing, or contamination has rapidly changed our environment during the past centuries (MEA 2005). Recent climate change effects are further aggravating the situation. Particularly, arid and semi-arid regions are now threatened by an acceleration of these processes, as they are predicted to suffer the highest increase in temperature and change in rainfall pattern due to climate change (BATES *et al.* 2008). The degradation of land impedes the provision of ecosystem goods and services, which are of great importance regionally for the well-being of local people (e.g. food and fuel production, water regulation, cultural identity) as well as globally (e.g. carbon sequestration, nutrient cycling) (MEA 2005). Therefore, it is crucial to identify and mitigate the main sources of degradation.

South Africa hosts an exceptionally high level of biodiversity and endemism (VAN JAARSVELD *et al.* 1998). Due to its unique flora and its - especially for a semi-arid area - high diversity and endemism, the Knersvlakte has been recognized as one of the areas with the highest conservation priority in South Africa (HILTON-TAYLOR & LE ROUX 1989; DESMET *et al.* 1999). The nature conservation management authority of the Western Cape Province, CapeNature, is now in the process of establishing a conservation area, which is 'a geographically defined area where conservation of important biodiversity is needed in order to ensure sustainable benefits' (ENVIRONMENTAL AFFAIRS & TOURISM RSA 2005). At the moment, the prospective Knersvlakte Conservation Area has a size of 62,000 ha. By incorporating more farms, CapeNature aims for an ultimate size of 113,500 ha (Elbé Cloete, personal communication 2008). As CapeNature has to make decisions about future conservation management, a deeper understanding of the effects of livestock on the vegetation is needed.

Processes leading to degradation and the loss of biodiversity in arid and semi-arid environments have often been attributed to overuse by domestic livestock (WASER & PRICE 1981; AYYAD & ELKADI 1982; WEST 1993; COWLING & HILTON-TAYLOR 1994; FLEISCHNER 1994; HILTON–TAYLOR 1994). MILTON *et al.* (1994) describe degradation as a stepwise process, which is 'increasingly difficult and costly to reverse'. This process starts with a reduction in abundance of palatable plants, which causes changes in the demography of their

populations. When, in a next step, plant species fail to recruit, this again leads to losses of productivity and species. Step three includes the reduction of perennial plant cover, which causes accelerated erosion and increasing temperature fluctuation on the soil surface. Ephemeral and weedy species benefit from the reduced competition and flourish after major rains (MILTON *et al.* 1994). A vegetation dominated by annuals, however, is more susceptible to environmental stochasticity and therefore more likely to experience a complete failure in production (GILLSON & HOFFMAN 2007). This could not only be fatal for the livestock, but can also accelerate erosion processes.

The compositional shift from plant communities dominated by perennial plant species on moderately grazed land to those dominated by annuals under high grazing intensities has been recorded as typical for many arid areas (AYYAD & ELKADI 1982; NOYMEIR *et al.* 1989; OLSVIG-WHITTAKER *et al.* 1993; MILTON *et al.* 1994; ANDERSON & HOFFMAN 2007).

These negative effects of grazing are described for overutilisation through livestock (WASER & PRICE 1981; FLEISCHNER 1994; MILTON *et al.* 1994; TODD & HOFFMAN 1999; KRAAIJ & MILTON 2006). On the other hand, light and moderate grazing often affects the vegetation positively, particularly with regard to biodiversity (NAVEH & WHITTAKER 1979; AYYAD & ELKADI 1982; OLSVIG-WHITTAKER *et al.* 1993; ECCARD *et al.* 2000). This effect is predicted by the well-known intermediate disturbance hypothesis, which states that species richness and diversity are highest when disturbance is of intermediate intensity and frequency (GRIME 1973; CONNELL 1978).

Herbivores can induce a compositional shift of the vegetation through selective consumption of vegetative as well as generative organs. In the presence of interspecific competition, this can result in the decrease or even elimination of some species and the dominance of others (MILTON 1994). A first indicator for the impairment of a population can be reduced vitality (e.g. size) of individual plants. When feeding on flowers and fruits, herbivores can affect the respective species negatively by reducing the reproductive fitness (TODD 2000; MILTON & WIEGAND 2001). However, due to consumption of ripe fruits, herbivores can also have a positive effect on the population by means of endozoochoric dispersal, although this has been described as very rare for the Namaqualand (VAN RHEEDE VAN OUDTSHOORN & VAN ROOYEN 1999).

Over the last about 150 years, almost the entire Knersvlakte has been used as rangeland for sheep and goats. Formerly, the land was inhabited by !KhoiKhoi pastoralists practicing transhumant land use for about 2000-1600 years BP (BOONZAIER *et al.* 2000). Besides the

presence of domestic animals, wild ungulates (e.g. antelopes, elephants and black rhinoceroses) used to roam the country but have been drastically decimated since the intensification of livestock farming (HOFFMAN & ROHDE 2007). The floristic composition of the Knersvlakte today with its high contribution of endemic plant species is mainly based on the pronounced small-scale heterogeneity of abiotic soil characteristics (SCHMIEDEL & JÜRGENS 1999). However, the role of herbivory in evolutionary adaptation processes should not be underestimated (DESMET 2007). It is essential for the conservation of existing patterns of diversity to also preserve the underlying processes. The complete exclosure of domestic animals in the course of establishing a protected area might change the unique flora of the Knersvlakte by removing an important driver for the dynamics and the rejuvenation of the vegetation.

The aim of this study was to examine the effects of grazing on the vegetation of the Knersvlakte. To achieve this aim, the following research questions were addressed:

- Does grazing affect plant communities in terms of species composition, strategy types and diversity, with particular respect to endemic taxa?
- Does grazing affect the plant size and reproduction of selected perennial plant species?
- How does domestic livestock, in comparison to indigenous herbivores, contribute to seed dispersal by endozoochory?

The results obtained from this study could assist the management authority of the Knersvlakte Conservation Area with the decisions about appropriate future land use management.

2 METHODS

2.1 Study area

The Knersvlakte (30°27'–32°05' S, 17°46'–19°06' E) is an extensive peneplain stretching from the Matsikamma mountains in the South to the Namaqualand Rocky Hills (near Bitterfontein) in the North. The eastern boundary is formed by the Bokkeveld Escarpment; the western part (Sandveld) lies adjacent to the Atlantic Ocean. The altitude ranges from 50 to 600 m above sea level (VAN WYK & SMITH 2001). The Knersvlakte comprises an area of 13,500 km² and forms the southernmost part of the Namaqualand, which is part of the Succulent Karoo Biome (RUTHERFORD & WESTFALL 1994; MILTON *et al.* 1997). According to CONSERVATION INTERNATIONAL (2008), the Succulent Karoo is one of only two arid regions besides the horn of Africa among the 34 internationally recognised biodiversity hotspots. According to MYERS *et al.* (2000), it is even the only arid one of 25 global hotspots.

Due to its high number of endemics with more than 150 vascular plant species (VAN WYK & SMITH 2001), the Knersvlakte is often referred to as a centre of endemism and diversity (HILTON-TAYLOR 1996; JÜRGENS 1997; VAN WYK & SMITH 2001) also known as Vanrhynsdorp Centre (NORDENSTAM 1969; HARTMANN 1991; HILTON-TAYLOR 1994). The semi-arid climate is determined by a relatively predictable winter rainfall with an average of 116 mm per annum (mainly falling in May-August), occasionally supplemented by fog and dew (MUCINA *et al.* 2006). Temperatures are ranging from 5-10°C in winter to 30-35°C in summer (MUCINA *et al.* 2006).

One characteristic of the Knersvlakte is the frequent occurrence of quartz fields covered with quartz gravel by up to 100%. These quartz gravels have derived from weathered quartz veins running through parental material of limestone, shale and phyllites (SCHMIEDEL & JÜRGENS 1999). These conditions create a unique habitat with a distinct flora dominated by succulent nanochamaephytes (succulent dwarf shrubs < 5 cm; SCHMIEDEL & JÜRGENS 1999), mainly Aizoaceae. This type of habitat is further referred to as 'quartz'. Another typical habitat type consists of base-rich sandy to loamy soils without quartz gravel cover. These habitats are inhabited by the zonal vegetation mostly consisting of microchamaephytes (shrubs 5-15 cm; SCHMIEDEL & JÜRGENS 1999) and macrochamaephytes (shrubs 15-50 cm; SCHMIEDEL & JÜRGENS 1999). This habitat is further referred to as 'non-quartz'.

2.2 Study sites

In order to investigate the effects of different grazing intensities on the vegetation, four farms with three different grazing intensities were selected. These farms are located in the prospective Knersvlakte Conservation Area (Figure 1).

Criteria for the selection of the sites of investigation were the following:

- Appropriate grazing intensities
- Location in the Knersvlakte Conservation Area
- Livestock grazing still ongoing practice (except for the non-grazed farms)

These criteria led to the selection of following farms (Figure 1):

- Hoogstaan and Rooiberg: intensive grazing (‘high’)
- Ratelgat: moderate grazing (‘moderate’)
- Quaggaskop: no grazing (‘no’)

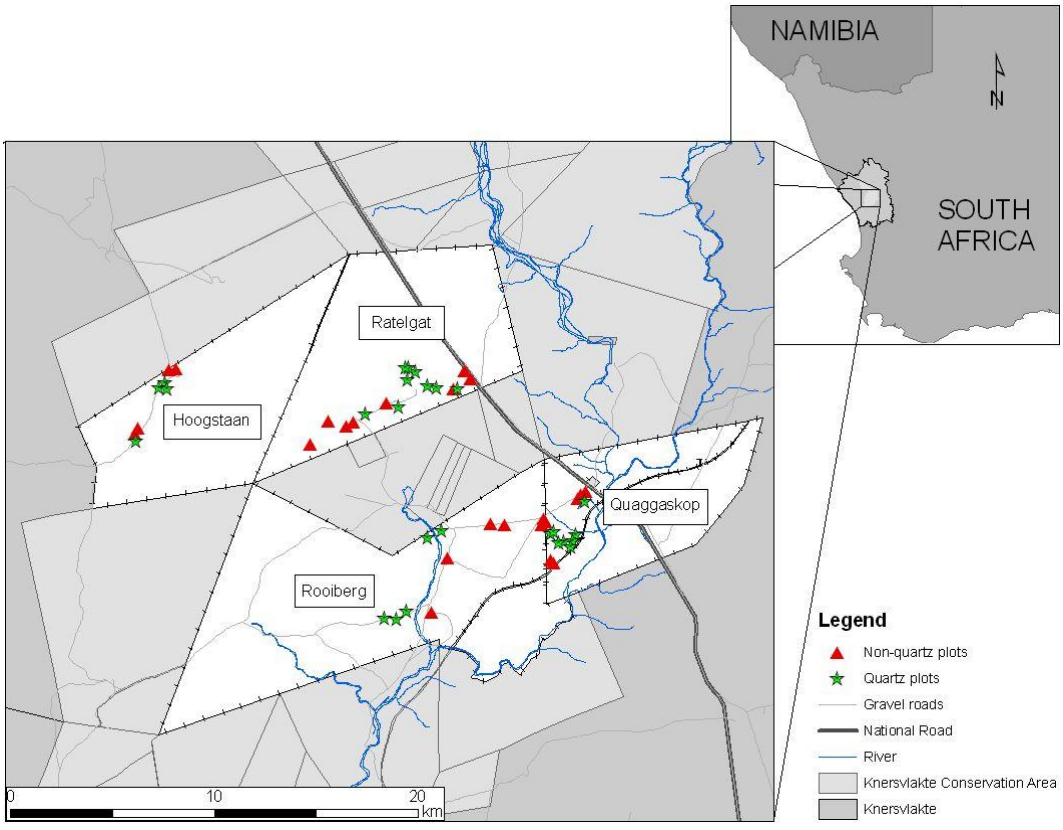


Figure 1: Study area. Investigated farms are printed in white and labelled with their names (crossed lines = farm borders). Grazing intensities: Quaggaskop: no grazing; Ratelgat: moderate grazing; Hoogstaan and Rooiberg: intensive grazing. Shapefiles of farms, rivers and roads kindly provided by CapeNature.

The selected farms are situated close to the N7, 30 to 50 km north of Vanrhynsdorp and about 30 km east of the Atlantic Ocean. The farm **Hoogstaan** covers an area of 6,000 ha. It is in private property with a grazing intensity of about 10 ha per SSU (small stock unit after ESLER *et al.* 2006). **Rooiberg** is located south of Hoogstaan with a size of 11,500 ha. For the last 20 years it has been state land used informally by several settlers for sheep and goat farming. At the time of the study, there were eight different herders each using different sections of the farm. Since about a third of the farm area has not recently been used for grazing, the present stock numbers only apply to the used parts which comprise about 7,000 ha (Elbé Cloete, personal communication 2007). This corresponds to a grazing intensity of 12 ha per SSU. From 1984-1987 the farm Rooiberg was also used for military training which obviously excluded grazing but caused a high level of degradation making the land less suitable for grazing.

Ratelgat covers an area of about 7,000 ha and had been private property until 1999. For many years, it had only very sporadically been used for farming until it was assigned to the Griqua developmental trust in 2000 in line with the land restitution process. Since 2000 it has been moderately grazed with a grazing intensity of about 17 ha per SSU. Being owned by the Griqua Development Trust, the farm is also used for traditional celebrations as well as for tourism.

The farm **Quaggaskop** covers an area of about 5,000 ha and is situated west of Rooiberg. It is private property and contains one section that is known to be the only piece of land in the Knersvlakte with no grazing for the past 40 years (Ute Schmiedel, personal communication 2007). This part comprises approximately 1,500 ha. It has been partly used as a plant nursery (for seed harvest) and for tourism with a walking trail providing information about succulents.

For selected pictures of the four different farms please refer to Appendix 1a-d for quartz plots and Appendix 2a-d for non-quartz plots.

2.3 Sampling design

The data were collected for a period of three months from the beginning of August to the beginning of November 2007. Altogether 51 plots (for GPS coordinate see Appendix 3) were set up at homogenous sites representative for the respective farm. Each grazing intensity (no, moderate, high) was represented by eight replicates on non-quartz and nine replicates on quartz habitats. Due to logistical limitations the plots could only be set up in the vicinity (10-

1000 m distance) of gravel farm roads. Each plot was 20 m by 50 m in size and contained 100 subplots. These measured 20 cm by 20 cm and were arranged in a regular grid as shown in Figure 2.

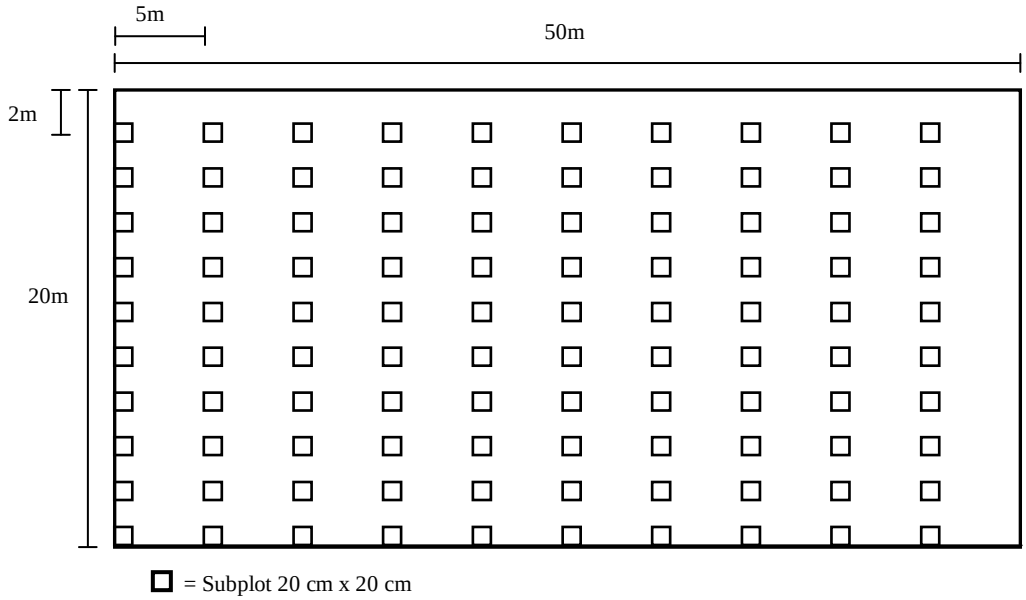


Figure 2: Schematic design of a plot, containing 100 subplots. For the subplots, recorded parameters were microhabitat, microtopography, vascular plant species identity and abundance, developmental stage of each individual as well as size and number of reproductive organs of the adult individuals of perennial species.

For each subplot, the following parameters were recorded:

Microhabitat: the microhabitat of the subplot was determined using following categories expressed as proportion of quartz cover:

- High quartz cover: more than two thirds of the surface were covered with quartz gravel.
- Medium quartz cover: between one and two thirds of the surface were without quartz cover.
- Low quartz cover: up to one third of the surface was covered with quartz.

Microtopography: for the topography of the subplots three categories were used:

- Flat: difference between highest and lowest point less than 1 cm.
- Medium: difference between highest and lowest point between 1 and 5 cm.
- Hilly: difference between highest and lowest point more than 5 cm.

Species: the identity and abundance of vascular plant species rooting in the subplots was determined using a field guide (LE ROUX 2005) or collected for later identification by U. Schmiedel (University of Hamburg). Unidentified individuals recognized as taxonomic units were given field names or determined on family or genus level (see Appendix 4). Nomenclature follows GERMISHUIZEN & MEYER (2003) except for the Aizoaceae which were classified according to HARTMANN (2002). The term 'mesemb' refers to the former family Mesembryanthemaceae (Aizoaceae subfamilies Ruschioideae and Mesembryanthemoideae *sensu* HARTMANN 2002).

Developmental stage: all vascular plant individuals were classified into three developmental stage classes:

- Seedling: only cotyledons have emerged.
- Juvenile: more leaves than the cotyledons have grown, but the individual is not mature yet and does not exhibit the shape of an adult.
- Adult: species-specific habit with or without reproductive organs.

Size: for adult chamaephytes and phanerophytes the volume was measured by the following dimensions:

- Height: height of the plant from ground surface to highest living part.
- Length: longest diameter.
- Width: longest diameter orthogonal to length.

Number of reproductive organs: reproductive organs (flowers for plants with single flowers, inflorescences for other plants, or fruits) of chamaephytes and phanerophytes (RAUNKIAER 1934) were counted.

2.4 Soil analysis

For the analysis of soil parameters, one mixed soil sample from 1-11 cm soil depth was collected on each plot (after removal of the top crust layer) and air dried. The soil was sieved (mesh wide: 2 mm) to prepare for the following analyses (conducted in the laboratory at the University of Hamburg).

For pH measurement, a subsample of 10 g was suspended in 25 ml $CaCl_2$ (0.01 $mol \cdot l^{-1}$) for one hour and then measured with a pH-meter (model CG837 from Schott with an electrode

BlueLine 28 ph-P) for five minutes (VAN REEUWIJK 1995). The electrical conductivity was determined with an electrode (LF197, WTW) immersed in a suspension of 10 g soil and 25 ml bidistilled water (VAN REEUWIJK 1995). For the estimation of carbonate content, a HCl test (AG BODEN 2005) was conducted: A few drops of hydrochloric acid (10%) were poured on a small soil sample (approximately 1 g). Carbonate content was estimated and grouped according to AG BODEN (2005) by making use of the visually and acoustically perceptible reactions that take place during the generation of carbon dioxide.

2.5 Germination experiment

To assess the extent domestic and wild herbivores contribute to plant dispersal via endozoochory, a germination experiment with dung was carried out. On every plot and its immediately adjacent areas, dung of domestic (sheep, goats or donkeys) or indigenous herbivores (mainly antelopes) was collected on the day of vegetation sampling where available. The animal species the dung originated from was visually determined using the field guide of STUART & STUART (2000). All available dung was collected and sorted by animal type and plot, and subsequently air dried.

In June 2008, the dung was suspended overnight in tap water in a glass bottle (ca. 10 g of dry dung in a 50 ml bottle, or less according to the sampled size). The next day the moist dung was applied onto a sterilized sand/peat mixture (1:1 volume ratio) in plant pots (10 cm x 10 cm x 10 cm) in the greenhouse in Hamburg. The temperature span of about 25-40 °C was maintained by airing and heating, and regular water supply was ensured by an automatic droplet irrigation system. For six weeks, the seedlings were determined and counted twice a week until the number of additionally emerged seedlings was less than 1% of the number accumulated until then.

As seedlings were numerous, only a few representatives of every morphologically distinguishable group (morpho-type) were transplanted and cultivated further, the rest was removed. All individuals were given numbers and classified according to morpho-types for later identification. As this grouping of dicotyle seedlings into ‘morpho-types’ analogous to species level turned out to be inconsistent, seedlings not surviving to further stages were merely classified into ‘mesemb’, and ‘non-mesemb’, as the mesemb seedlings (i.e., Aizoaceae subfamilies Ruschioideae and Mesembryanthemoideae *sensu* HARTMANN 2002) have very distinct features and can easily be distinguished from other dicotyle seedlings. Species were

determined using the field guide of LE ROUX (2005) and by expert knowledge (Ute Schmiedel, University of Hamburg). For further analyses, data for domestic or wild herbivore dung, respectively, were pooled per plot. Each sample, therefore, contained data for one plot and animal group.

2.6 Data analyses

Inferential statistics were conducted with STATISTICA 8.0 (STATSOFT INC. 2007). Normal distribution and homogeneity of variance were assessed visually as recommended by QUINN & KEOUGH (2002). Data with heterogenic variances or strongly departing from normal distribution were transformed using log or arcsin transformation, depending on which of the transformations achieved the best approximation to homogeneity of variances (QUINN & KEOUGH 2002).

In the following, I discriminate between analyses at community level and those at the population level. Analyses at community level include diversity and abundance measures as well as species composition analyses. Analyses at population level focus on plant size, reproduction and number of seedlings for populations of particular species.

2.6.1 Community level: diversity measures

For the analysis at community level, I used several parameters for abundance and diversity measurements. Plot data represent cumulated subplot data of the respective 20 m x 50 m plot and are not to be confused with data obtained by an inventory of the whole plot. Since the identification of seedlings on the species level was impossible in most cases, I did not include them for the statistical analysis of the parameters described in the following:

1. **Individuals**: number of individuals per plot.
2. **Endemic individuals**: number of individuals of locally endemic species per plot. Locally endemic species in this case are those species only occurring in the Knersvlakte. Only species with a known distribution were included. For a complete list see Appendix 5.
3. **Perennial individuals**: number of individuals of above ground perennial species (i.e. chamaephytes, phanerophytes after RAUNKIAER 1934) per plot.

4. **Annual individuals**: number of individuals of annual species.
5. **Plot species richness**: number of species per plot.
6. **Mean species richness**: average number of species of all subplots per plot.
7. **Plot evenness**: Shannon-Evenness *E* of a plot's vegetation, which is a measurement of the heterogeneity of the species' abundances (HILL 1973).
8. **Plot/subplot ratio**: The ratio of plot species richness (see 5) and average number of species of all subplots (see 6) per plot. This is used as a measure of β-diversity, where high numbers indicate high diversity (WHITTAKER 1960).
9. **Endemic species richness**: species richness per plot for endemic species described under 2.
10. **Endemic evenness**: Shannon evenness *E* (see 7) per plot for local endemic species described under 2.
11. **Perennial species richness**: species richness of perennial species described under 3 per plot.
12. **Perennial evenness**: Shannon evenness (see 7) per plot for species described under 3.
13. **Annual species richness**: number of annual species per plot.

Differences between habitats:

To verify differences between quartz and non-quartz habitats, I performed analyses of variance (ANOVAs) for each parameter (1-13) as well as for pH and conductivity. I chose the use of an ANOVA in this case, as it keeps the number of applied tests down and still gives the same results as a t-test (DYTHAM 2003). For differences in carbonate content, I performed the non parametric Mann-Whitney-U test since ranked data were used (STATSOFT INC. 2007).

Differences between grazing intensities:

As a first step of comparing the effects of different grazing intensities, I conducted ANOVAs for the parameters 1-13 with the Tukey's HSD post-hoc test (level of significance: $p<0.05$).

To take into account potentially confounding effects of environmental data, I performed Analyses of Covariance (ANCOVA) with soil pH as well as with electrical conductivity as linear predictors.

2.6.2 Community level: species composition

Ordination

For the visual analysis of differences in species composition between habitats, I conducted a DCA with the species abundance data (excluding seedlings) of all plots using CANOCO 4.5 (TER BRAAK & ŠMILAUER 2002). Those species lacking identification and for which the possibility of an overlap with an identified species could not be ruled out, were excluded. Those were the following 'species': 'Annual', 'Asteraceae spec.', 'Dicotyle', 'Mesemb', 'Monocotyl' and 'Poaceae spec.' as well as unknown species. To analyse habitats separately, I conducted DCAs and PCAs according to the recommendation of LEYER & WESCHE (2007). For gradients shorter than 4 SDs obtained by a DCA, I additionally conducted a PCA.

Fidelity measures

To test the fidelity of the species to the vegetation units (habitats, grazing intensities), I determined phi coefficients (CHYTRÝ *et al.* 2002) for each species/vegetation unit association. The phi coefficient is a measure of association between two categories (in this case species and vegetation unit) and its values range from -1.00 to 1.00. The value 1.00 indicates that species and vegetation unit are completely faithful (CHYTRÝ *et al.* 2002).

For each vegetation unit, species were grouped into categories according to their phi values (CHYTRÝ 2007):

1. Highly diagnostic species: phi ≥ 0.50, indicates a high fidelity to the vegetation unit.
2. Diagnostic species: $0.25 \leq$ phi < 0.50, indicates a moderate fidelity to the vegetation unit.

3. Positively associated non-diagnostic species: $0.00 \leq \text{phi} < 0.25$, indicates a low fidelity to the vegetation unit.
4. Negatively associated non-diagnostic species: $\text{phi} < 0.00$, indicates no fidelity to the vegetation unit.

The Fisher's exact test was used to test whether the observed distribution of co-occurrences of species and vegetation units within the data set was significantly ($p<0.05$) different from the frequency expected if such occurrences were distributed randomly. Such a significant co-occurrence of species is further referred to as 'significant accumulation'. The Fisher's exact test was conducted using STATISTICA (STATSOFT INC. 2007).

2.6.3 Population level: plant size

For the analyses of the effects of grazing on the size of selected species, I chose perennial species (chamaephytes and phanerophytes, see Appendix 4) that were unambiguously identified by species name or field name and were present as adults on at least three plots of each grazing intensity. For the statistical analysis, I conducted ANOVAs to test for differences between grazing intensities with the geometric mean (arithmetic mean of natural logarithms) of the volumes per plot as response variable. This was done for each of the selected species.

2.6.4 Population level: reproduction

For the analyses of the effects of grazing on the number of reproductive organs, I used a similar approach as described for the plant size (2.6.3.). However, the criteria for the selection of species were further constrained by the presence of reproductive organs. Since I intended to focus more on the effects of grazing on the number of reproductive organs than on their presence or absence, I only included individuals carrying reproductive organs in the analysis.

For the statistical analysis I conducted ANOVAs for each selected species to test for differences between grazing intensities with the geometric mean of reproductive organs per plot as response variable.

For a combined analysis including all of the selected species, I standardised the species values by dividing the log transformed numbers of the reproductive organs of each individual by the

species' mean. I averaged the values for each species and conducted an ANOVA to test for differences between grazing intensities.

2.6.5 Population level: number of seedlings

For the analyses of the effects of grazing on the germination of seedlings, I did not differentiate between species but rather analysed (i) all seedlings (ii) seedlings of the family Aizoaceae and (iii) seedlings not belonging to the family Aizoaceae. As the data were Poisson-distributed and log transforming was impracticable due to high numbers of zeros, I applied Generalized Linear Modeling (GLM) with log-link for the analyses of seedling numbers.

GLMs model relations of response and predictor variables similarly to general linear models, but have the advantage of wider application ranges of distributions. The general linear models are based on linear relations between response and predictor variable, whereas GLMs also model other (e.g. log-linear) relations (MCCULLAGH & NELDER 1983). This makes them especially attractive for count data frequently showing Poisson distributions. GLMs are not always appropriate as a practical alternative of ANOVAs, as in common software packages like STATISTICA (STATSOFT INC. 2007) a post-hoc test is not implemented. Because of this disadvantage, I preferred ANOVAs using transformed data in the previous analyses. In the case of seedling numbers with a high percentage of zeros, a log transformation was only possible by first adding an arbitrary number to the data. Thus, an ANOVA seemed inappropriate (WILSON 2007).

With the mean number of above mentioned seedling groups per subplot and plot I conducted a GLM to look for differences between habitat types, grazing intensities, microhabitat (expressed as quartz cover) and microtopography on subplot level. For this I conducted GLMs with the mean seedling frequencies per subplot, category (in the latter two cases) and plot. For overdispersed data (variance is greater than mean) I used the Pearson's chi^2 correction implemented in STATISTICA (STATSOFT INC. 2007).

3 RESULTS

For the raw data please refer to the electronic appendices (attached CD-ROM). The contents of the electronic appendices are listed in Appendix 6.

3.1 General characterisation of the plots

In total, 175 vascular plant species were recorded with 16,563 individuals (10,343 adults, 2,607 juveniles and 3,613 seedlings), of which 133 species could be clearly identified at species level. 14 species were identified unambiguously by field name (only two of them with unknown genus or family) and 22 species were determined at family or genus level without unambiguous species identification (see Appendix 4). 124 species were found on intensively grazed as well as on ungrazed plots and 105 on moderately grazed plots. The most abundant species on the 27 quartz plots were *Argyroderma deleatii* (732 individuals) and *Foveolina dichotoma* (610 individuals) and the most abundant families were Aizoaceae (with 2,526 individuals) and Asteraceae (with 1,179 individuals). On the 24 non-quartz plots, the species *F. dichotoma* (2,196 individuals) and *Rhynchopsidium pumilum* (868 individuals) were most abundant. Like on the quartz plots, the families Asteraceae (5,292 individuals) and Aizoaceae (1,318 individuals) occurred most frequently. For a list of the ten most abundant species recorded on quartz and non-quartz plots, see Appendix 7 and for the most abundant families (> 10 individuals per family), see Appendix 8. The three most abundant species of each grazing intensity and their percentage contribution are illustrated in Appendix 9.

Of the 133 clearly identified species, 40 are endemic to the Knersvlakte and 32 of these 40 endemic species belong to the family Aizoaceae (see Appendix 5). Additionally, two species (*Argyroderma* spec., *Monilaria* spec.) only identified as belonging to the respective genus were considered as endemic, since in both cases all occurring species of these genera are endemic to the Knersvlakte. Prevailing growth forms were chamaephytes and therophytes (Appendix 10).

3.2 Community level: biodiversity

3.2.1 Habitat types

The two habitat types differed significantly in most of the tested biodiversity parameters (Table 1) as well as in their soil properties (Table 2). Non-quartz plots had a higher total number of individuals and species, but lower numbers of endemic individuals and species. Non-quartz plots contained more annual but less perennial individuals than quartz plots. The species richness of annuals was higher on non-quartz plots than on quartz plots, but the perennial species richness did not differ between the habitat types. Evenness of total species composition did not differ significantly, but evenness of endemic as well as of perennial species composition was higher on non-quartz than on quartz plots. The soils of quartz plots had lower and more varying pH values and higher conductivity than non-quartz plot soils. Carbonate content was higher in non-quartz soils.

Table 1: Summary of the ANOVA results for the parameters 1-13 for differences between quartz and non-quartz plots; df=49; *N*=51; [1]results for log transformed data.

	Parameter	Non-quartz		quartz		p-value
1	Individuals	330	± 197	186	±116	**0.002**[1]
2	Endemic individuals	34	±12	75	±42	**<0.001**[1]
3	Perennial individuals	74	±18	123	±73	**0.005**[1]
4	Annual individuals	237	±193	56	±72	**<0.001**[1]
5	Plot species richness	31	± 6	23	±6	**<0.001**
6	Mean species richness	1.66	± 0.62	1.14	±0.47	**0.002**
7	Plot evenness	0.42	± 0.17	0.46	±0.12	0.335
8	Plot/ subplot ratio	21	±6	22	±7	0.439
9	Endemic species richness	6	± 2	8	±3	**0.013**
10	Endemic evenness	0.71	± 0.12	0.58	±0.15	**0.001**
11	Perennial species richness	15	± 3	15	±5	0.874
12	Perennial evenness	0.62	± 0.11	0.49	±0.14	**<0.001**
13	Annual species richness	12	± 3	6	±3	**<0.001**

Table 2: Means ±SD or medians (*) of environmental data for the habitat types; *N*=51; *p*-values were obtained by [1]ANOVA and [2]Mann-Whitney-U test.

Parameter	Non-quartz *n*=24		Quartz *n*=27		*p*-value
pH	7.67	± 0.47	6.33	± 1.31	**<0.001**[1]
Conductivity [µS cm^{-1}]	2554	± 2117	4836	± 2405	**<0.001**[1]
Carbonate content (ordinal scale with range of 1-7)	3*		1*		**<0.001**[2]

3.2.2 Grazing intensities

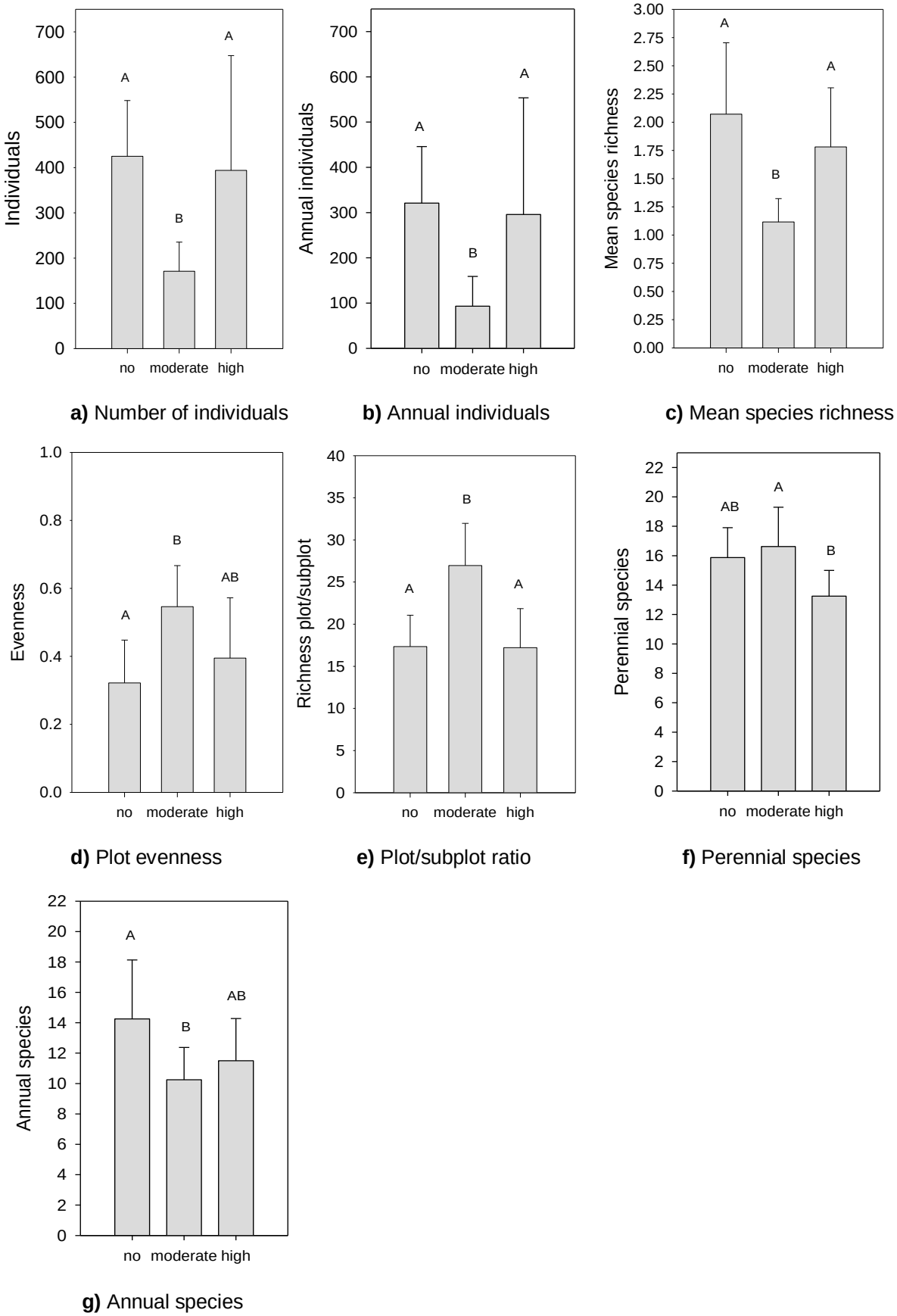
In this section, I present the results regarding differences in biodiversity parameters between the three grazing intensities. As habitat types differed in most of the tested parameters (compare 3.2.1), I conducted the following analyses separately for quartz and non-quartz plots. For a complete list of the respective tests including mean, standard deviation and *p*-values, see Table 3 (non-quartz) and Table 4 (quartz).

Non-quartz plots:

The number of individuals, annual individuals as well as the mean species richness on non-quartz plots was significantly lower on moderately grazed than on ungrazed and intensively grazed plots (see Figure 3a-c). Plot evenness, however, was lowest on ungrazed plots and highest on moderately grazed plots (Figure 3d). Similarly, the plot/subplot ratio of species richness was highest on moderately grazed plots and significantly lower on ungrazed as well as on intensively grazed plots (Figure 3e). Differences in plot species richness were insignificant, but a trend of ungrazed plots having the highest number of species could be detected. The perennial species richness was highest on moderately grazed plots and lowest on intensively grazed plots (Figure 3f). Ungrazed plots contained the highest and moderately grazed plots the lowest number of annual species (Figure 3g). ANCOVAs, both with pH and conductivity as covariates, though, yielded marginally insignificant differences in annual species richness.

Table 3: Summary of the ANOVA and ANCOVA results for the parameters 1-14 for differences between grazing intensities for non-quartz plots and their means ± SD; df=21, *N*=24; *n*=8; p-values printed in bold indicate significant differences; [1]results of log transformed data.

	Parameter	No (mean ± SD)		Moderate (mean ± SD)		High (mean ± SD)		p-value ANOVA	p-value ANCOVA (pH)	p-value ANCOVA (conductivity)
1	Individuals	425	± 123	171	±64	394	±254	**0.001**[1]	**0.002**[1]	**0.002**[1]
2	Endemic individuals	29	± 14	35	±8	37	±14	0.443[1]	0.443[1]	0.290[1]
3	Perennial individuals	81	±25	69	±14	73	±15	0.512[1]	0.643[1]	0.794[1]
4	Annual individuals	321	±125	93	±66	296	±258	**0.003**[1]	0.004[1]	0.005[1]
5	Plot species richness	35	± 7	29	±4	29	±3	0.061	0.080	0.101
6	Mean species richness	2.07	± 0.63	1.12	±0.21	1.78	±0.52	**0.001**	**0.001**	**0.002**
7	Plot evenness	0.32	± 0.13	0.55	±0.12	0.39	±0.18	**0.016**	**0.012**	**0.025**
8	Plot/subplot ratio	17	±4	27	±5	17	±5	**<0.001**	**<0.001**	**0.001**
9	Endemic species richness	7	± 2	7	±1	5	±2	0.096	0.102	0.099
10	Endemic evenness	0.78	± 0.11	0.66	±0.16	0.71	±0.07	0.160	0.158	0.145
11	Perennial species richness	16	±2	17	±3	13	±2	**0.014**	**0.017**	**0.012**
12	Perennial evenness	0.61	±0.09	0.64	±0.11	0.61	±0.13	0.762	0.817	0.794
13	Annual species richness	14	±4	10	±2	12	±3	**0.043**	0.060	0.071



a) Number of individuals **b)** Annual individuals **c)** Mean species richness

d) Plot evenness **e)** Plot/subplot ratio **f)** Perennial species

g) Annual species

Figure 3 a-g: Comparisons of grazing intensities (no, moderate, high) for non-quartz plots for parameters with significant ANOVA results; error bars represent standard deviations; different letters above error bars indicate significant differences according to Tukey's test.

Quartz plots:

Only the number of perennial and annual species as well as the annual species richness showed significant differences in the ANOVA and both ANCOVAs (Figure 4 a-c). Ungrazed plots contained the highest number of annual and perennial individuals as well as annual species.

Following parameters differed significantly for ANOVA as well as ANCOVA with pH as covariate but not for ANCOVA with conductivity as covariate: ungrazed sites contained significantly more individuals and had higher mean species richness than moderately as well as intensively grazed sites (Figure 4 d+e). The number of endemic individuals was highest on ungrazed plots and lowest on intensively grazed plots with significant differences between the two extremes (Figure 4 f).

Table 4: Summary of the ANOVA and ANCOVA results for the parameters 1-13 for differences between grazing intensities for quartz plots and their means ±SD; df=24; *N*=27; *n*=9; *p*-values printed in bold indicate significant differences; [1]results of log transformed data.

	Parameter	No (mean ± SD)		Moderate (mean ± SD)		High (mean ± SD)		p-value ANOVA	p-value ANCOVA (pH)	p-value ANCOVA (conductivity)
1	Individuals	279	± 108	118	±51	162	±117	**<0.001**[1]	**0.0091**[1]	0.172[1]
2	Endemic individuals	100	± 42	73	±38	52	±33	**0.041**[1]	**0.036**[1]	0.170[1]
3	Perennial individuals	187	±82	105	±46	78	±36	**0.001**[1]	**0.001**[1]	**0.028**[1]
4	Annual individuals	89	±48	11	±9	68	±105	**0.012**[1]	**0.048**[1]	**0.045**[1]
5	Plot species richness	26	± 6	21	±6	22	±7	0.282	0.383	0.164
6	Mean species richness	1.51	± 0.41	0.92	±0.30	1	±0.47	**0.009**	**0.017**	0.225
7	Plot evenness	0.41	± 0.10	0.51	±0.11	0.46	±0.14	0.19	0.47	0.666
8	Plot/subplot ratio	18	±5	24	±7	24	±8	0.086	0.059	0.811
9	Endemic species richness	9	± 3	9	±3	6	±3	0.177	0.233	0.109
10	Endemic evenness	0.56	± 0.12	0.54	±0.14	0.63	±0.19	0.438	0.348	0.446
11	Perennial species richness	16	±4	17	±5	14	±7	0.451	0.639	0.324
12	Perennial evenness	0.41	±0.13	0.51	±0.11	0.55	±0.14	0.073	0.085	0.280
13	Annual species richness	8	±2	4	±2	5	±3	**0.001**	**0.008**	**0.012**

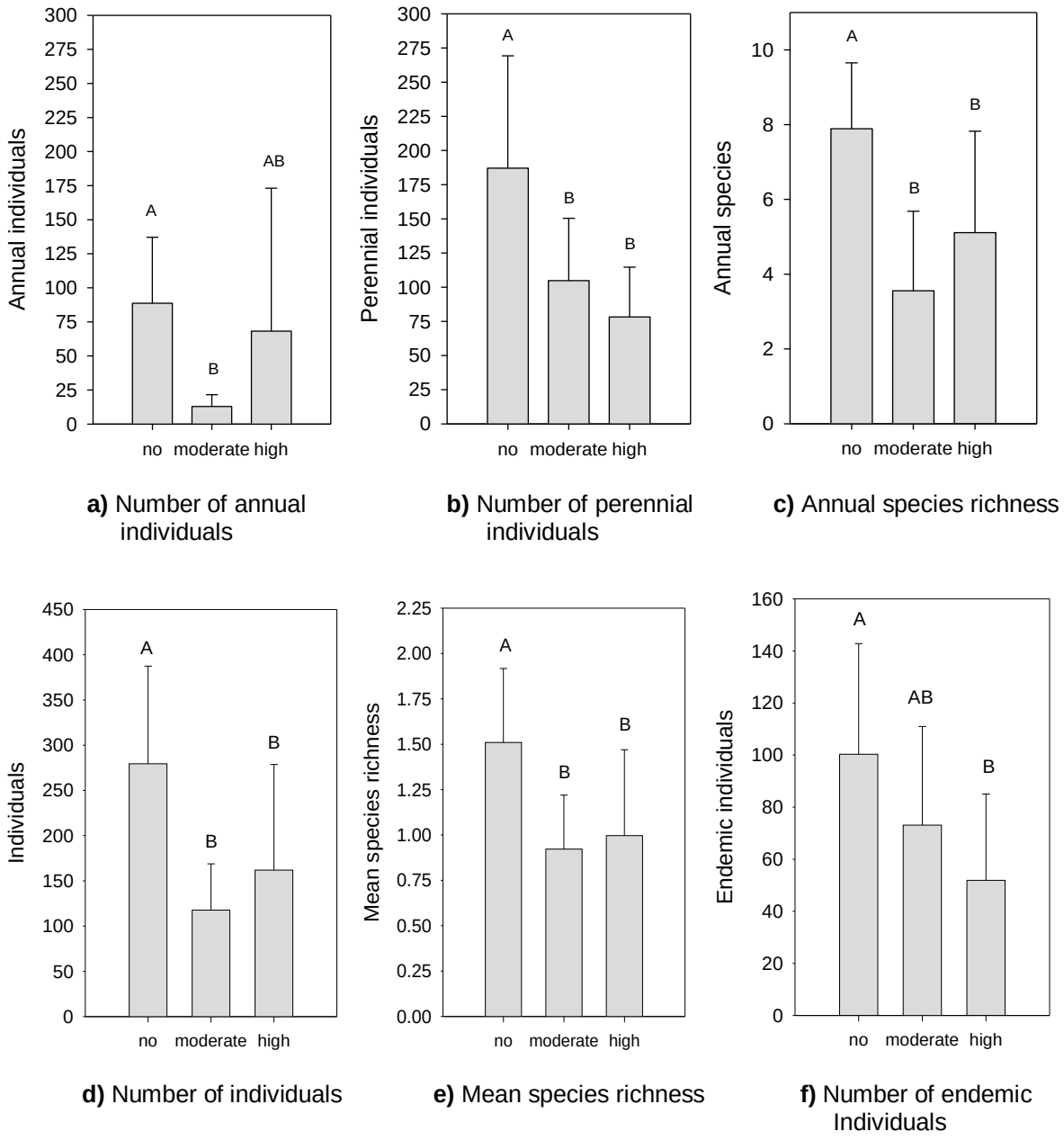


Figure 4 a-f: Comparisons of grazing intensities for quartz plots for parameters with significant ANOVA results; error bars represent standard deviations; different letters above error bar indicate significant differences according to Tukey's test.

3.3 Community level: species composition

Ordination

The visual analysis of habitat differences in species composition by means of a DCA showed a clear pattern (see Figure 5): the species composition differed between quartz and non-quartz plots along the first axis and was more heterogeneous within quartz plots than within non-quartz plots. The quartz plots were spread along the first and the second axis whereas the non-

quartz plots were clumped. The environmental parameters (pH, conductivity and carbonate content) correlated with the first axis, while conductivity also correlated with the second axis (Table 5).

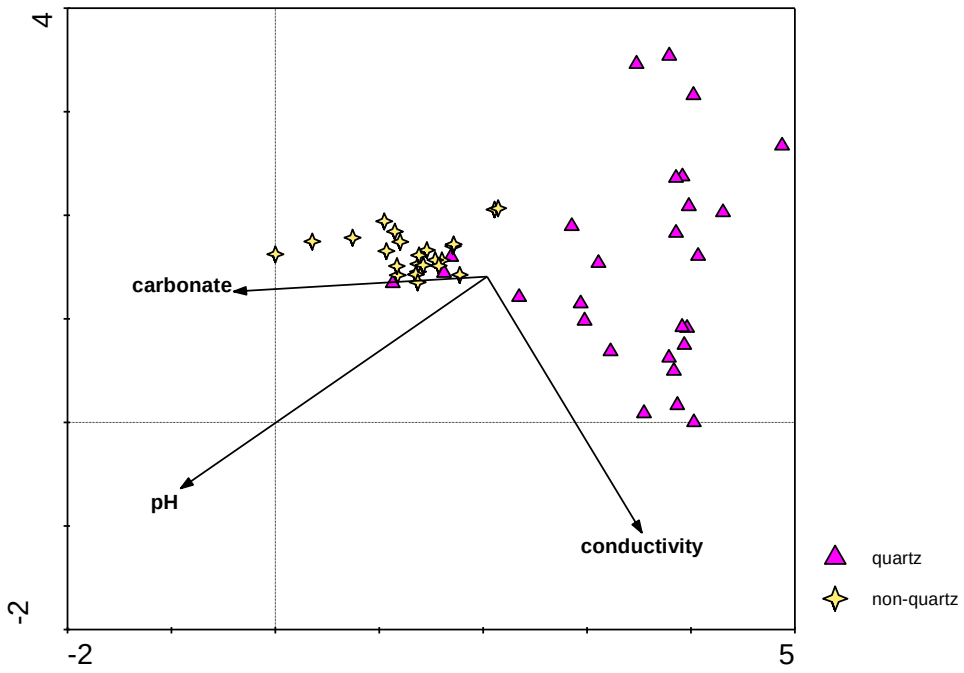


Figure 5: DCA of all plots based on plant species and their abundance; different symbols/colours represent different habitat types (see legend); arrows indicate correlations of environmental data with the axes; eigenvalues 1st axis: 0.710, 2nd axis: 0.472 (total: 7.954); length of gradient (1st axis): 4.878.

Table 5: Pearson Correlations (*r*) of environmental data and first two axes of the DCA (Figure 5).

	1st axis	**2nd axis**
pH	-0.618	-0.114
Conductivity	0.462	-0.576
Carbonate contents	-0.577	0.185

Focusing only on quartz plots regarding differences between farms and therefore grazing intensities, the DCA showed even higher correlations of environmental variables with the axes (Figure 6; Table 6). The species composition of the plots showed the following pattern: the plots on Ratelgat (moderate grazing) as well as those on Quaggaskop (no grazing) were clustered; the separation of the two plot groups seems to be partly due to soil pH with Ratelgat plots arranged at lower pH values than Quaggaskop plots. Rooiberg and Hoogstaan (both high grazing intensity) plots did not clearly differ, but were visibly separated from Quaggaskop and Ratelgat plots along the second axis. This separation seems to be partly due

to soil electrical conductivity with Quaggaskop and Ratelgat plots showing higher conductivity values than the plots on the other two farms.

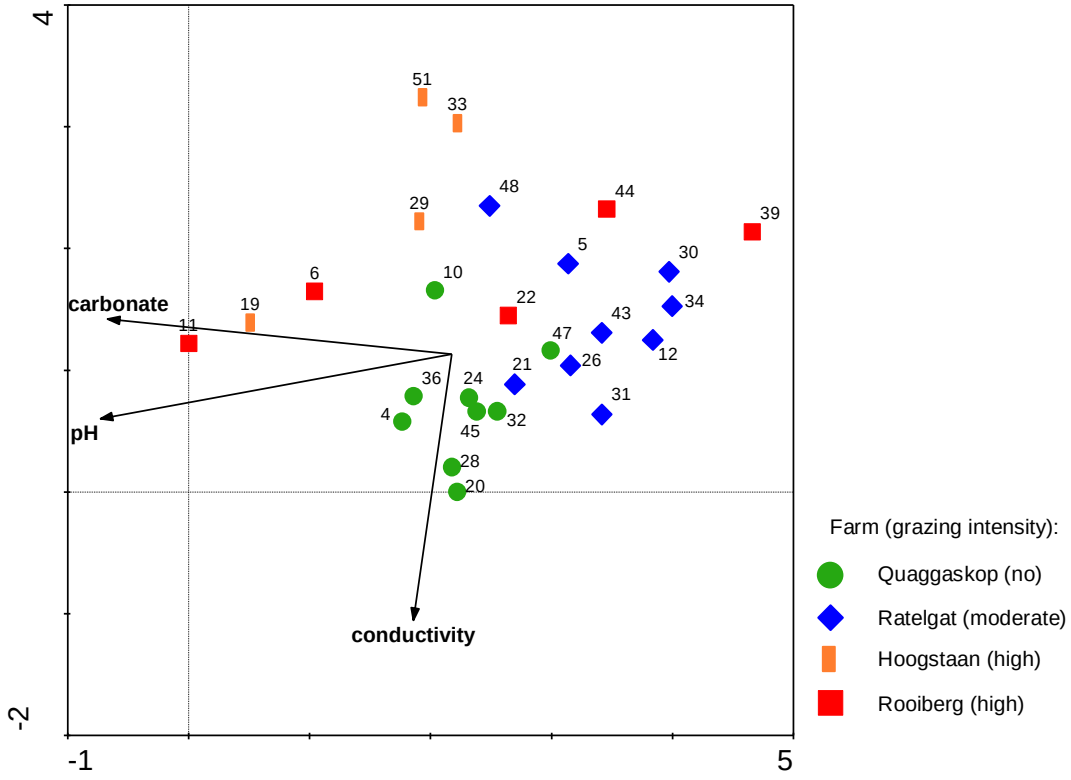


Figure 6: DCA of quartz plots based on plant species and their abundance; different symbols/colours represent different farms with their respective grazing intensities (see legend); numbers next to symbols represent plot numbers (for a complete list see Appendix 3); arrows indicate correlations of environmental data with the axes; eigenvalues: first axis = 0.593; second axis = 0.393 (total 6.202); length of gradient (first axis): 4.659.

Table 6: Pearson correlations (*r*) of environmental data and first two axes of DCA (Figure 6).

	1st axis	**2nd axis**
pH	-0.760	-0.171
Conductivity	-0.095	-0.622
Carbonate contents	-0.740	0.061

A DCA of the non-quartz plots (gradient length of 1st axis: 3.114, graph not shown) did not show any clear patterns in the comparison of farms (grazing intensities), which was already evident in the DCA of all plots (Figure 5). The Pearson correlations of environmental gradients with the first two axes were negligible (r<0.25).

Fidelity measures

When comparing the floristic composition of the habitat types by means of the Fisher's exact test, it turned out that 17 species (eleven endemics among them) were significantly accumulated on quartz plots and 29 (four endemics) on non-quartz plots (compare Appendix 4). According to phi-values, only one species (*Drosanthemum schoenlandianum*, an endemic species) was highly diagnostic for non-quartz plots and no species for quartz plots.

When comparing the grazing intensities of quartz plots, the analysis showed that seven species (three of them endemic) were significantly accumulated according to Fisher's exact test and four (one of them endemic) highly diagnostic according to phi-values on ungrazed plots. On moderately grazed plots, three species (one endemic) accumulated and one, an endemic species, was highly diagnostic. On intensively grazed plots, two species were accumulated (one endemic) and one, an endemic species, was highly diagnostic (Table 7).

On non-quartz plots, five species (none of them endemic) were significantly accumulated according to Fisher's exact test, one of them was highly diagnostic according to phi-values on ungrazed plots. On moderately grazed plots, four species (two of them endemic) were accumulated and two were highly diagnostic (one of them endemic). One (non-endemic) species was accumulated on intensively grazed plots, whereas no species was highly diagnostic (Table 7). For the results of all species, compare Appendix 4.

Table 7: Species that were significantly accumulated at one of the three grazing intensities (quartz and non-quartz separately) according to Fisher's exact test. C=chamaephyte, G=geophyte, T=therophyte; endemic species are printed in bold; *highly diagnostic species according to phi values (see also Appendix 4).

Grazing intensity	Quartz	Growth form type	Non-quartz	Growth form type
No	***Argyroderma delaetii****	C	*Crotalaria meyeriana*	C
	Cephalophyllum framesii	C	*Gazania lichtensteinii*	T
	*Crotalaria meyeriana**	C	*Lachenalia framesii**	G
	Mesembryanthemum guerichianum	T	*Senecio abruptus*	T
	*Mesembryanthemum longistylum**	T	*Senecio arenarius*	T
	Oophytum nanum	C		
	*Senecio arenarius**	T		
Moderate	***Antimima watermeyeri****	C	***Antimima solida****	C
	Tetragonia fruticosa	C	*Crassula expansa* ssp. *pyrifolia**	C
	Ursinia nana	T	*Othonna protecta*	C
			Ruschia bolusiae	C
High	*Gazania lichtensteinii*	T	*Galenia sarcophylla*	C
	*Sarcocornia xerophila**	C		

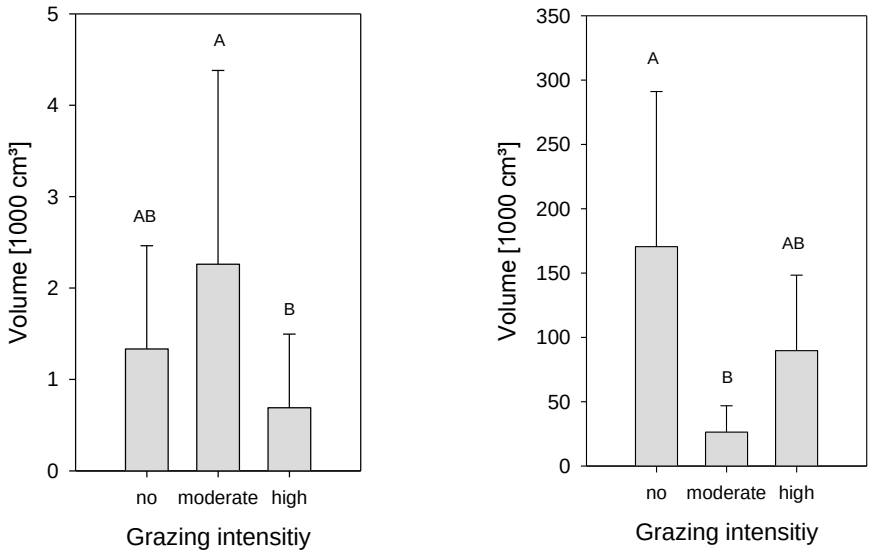
3.4 Population level: plant size

In total, twelve perennial species were present as adults on at least three plots of each grazing intensity and included in the assessment of plant size (Table 8). As these species were not homogenously distributed across habitat types, a corresponding statistical analysis for the comparison of habitat types was not suitable.

Differences in the volumes (geometric means per plot) were significant for the species *Argyroderma fissum* and *Lampranthus otzenianus*. *A. fissum* had the largest volumes on plots with moderate grazing and the smallest on plots with high grazing intensity, whereas *L. otzenianus* was biggest on ungrazed plots and smallest on moderately grazed plots (Table 8; Figure 7). For all other species the volume did not differ significantly between grazing intensities (Table 8).

Table 8: Summary of the ANOVA results for volumes (geometric means per plot) for differences between grazing intensities and their arithmetic means ±SD [dm³]; N_p: number of plots (replicates); n_i: number of individuals; *p*-values printed in bold indicate significant differences.

Species	No (mean ± SD)		Moderate (mean ± SD)		High (mean ± SD)		N_p	n_i	*p*-value ANOVA
Argyroderma fissum	1.3	± 1.1	2.3	± 2.1	0.7	± 0.8	27	143	**0.022**
Cephalophyllum framesii	15.8	± 20.0	11.0	± 9.9	9.7	± 10.6	26	103	0.536
Drosanthemum diversifolium	5.6	± 4.3	7.4	± 5.7	7.5	± 8.8	35	262	0.978
Drosanthemum globosum	8.5	± 8.4	26.9	± 22.9	11.6	± 9.4	16	47	0.540
Drosanthemum spec. 1 ('glossy')	22.7	± 17.2	32.1	± 26.8	37.6	± 41.6	15	43	0.895
Drosanthemum pulverulentum	26.4	± 20.6	21.3	± 17.9	16.4	± 14.3	29	143	0.276
Drosanthemum schoenlandianum	3.2	± 2.5	3.7	± 3.3	2.6	± 2.7	27	174	0.199
Lampranthus otzenianus	170.4	± 120.6	26.5	± 20.6	89.5	± 58.8	15	54	**0.041**
Malephora purpureo-crocea	15.7	± 9.7	21.6	± 30.4	10.5	± 12.0	22	65	0.844
Phyllobolus nitidus	24.6	± 20.4	8.9	± 1.4	21.8	± 16.4	10	29	0.576
Ruschia bolusiae	67.9	± 78.7	58.9	± 50.4	130.1	± 160.0	15	36	0.545
Zygophyllum cordifolium	5.3	± 5.7	8.3	± 12.5	4.5	± 4.5	18	38	0.865



a) *Argyroderma fissum* **b)** *Lampranthus otzenianus*

Figure 7: Comparisons of grazing intensities for significant differences in volume (arithmetic means) for the species *Argyroderma fissum* (**a**) and *Lampranthus otzenianus* (**b**); error bars represent standard deviation; different letters above error bars indicate significant differences in geometric mean according to Tukey's test.

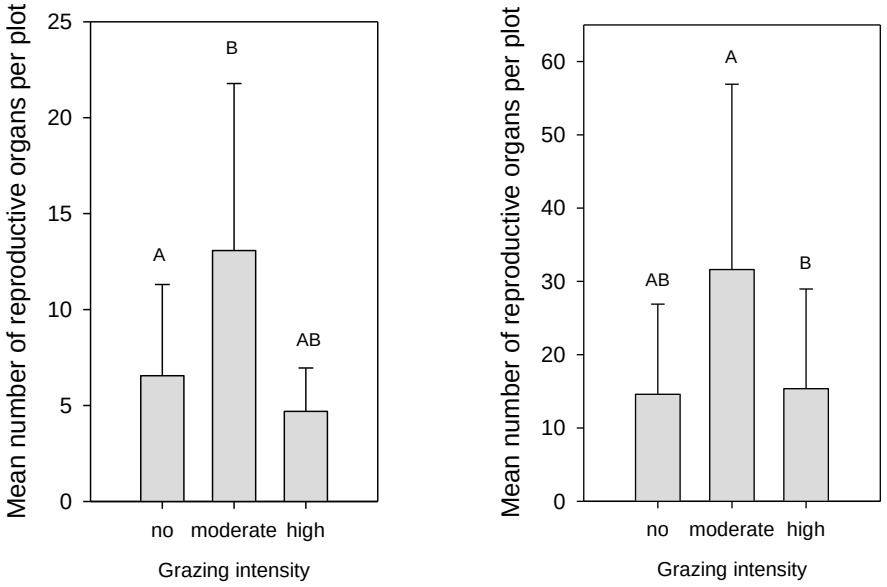
3.5 Population level: reproduction

In total, seven perennial species were present as individuals carrying reproductive organs on at least three plots of each grazing intensity and were included in the reproduction assessment. For the same reason as mentioned under 3.4, a statistical analysis for the comparison of habitat types was not suitable.

Both, *Argyroderma fissum* and *Drosanthemum schoenlandianum* individuals had the highest number of reproductive organs on moderately grazed plots (Figure 8, Table 9). *D. diversifolium*, *D.* spec. 1 ('glossy') and *Malephora purpureo-crocea* showed the same trend (Table 9).

Table 9: Summary of the ANOVA results for numbers of reproductive organs (geometric means of plot data) for differences between grazing intensities and their arithmetic means ±SD; N_p: number of plots (replicates); n_i: number of individuals; *p*-values printed in bold indicate significant differences.

Species	No (mean ± SD)		Moderate (mean ± SD)		High (mean ± SD)		N_p	n_i	*p*-value ANOVA
Argyroderma fissum	6.56	± 4.75	13.07	± 8.71	4.70	± 2.26	25	104	**0.030**
Drosanthemum diversifolium	15.35	± 4.80	36.17	± 38.56	29.81	± 26.00	31	143	0.525
Drosanthemum spec. 1 ('glossy')	148.20	± 148.12	454.70	± 461.01	205.10	± 215.08	13	37	0.667
Drosanthemum pulverulentum	38.56	± 26.51	41.94	± 33.22	52.95	± 40.55	27	89	0.893
Drosanthemum schoenlandianum	14.60	± 12.30	31.62	± 25.30	15.36	± 13.60	26	138	**0.048**
Lampranthus otzenianus	125.93	± 109.73	98.58	± 91.30	90.48	± 149.78	13	40	0.488
Malephora purpureo-crocea	16.28	± 18.80	22.63	± 27.12	7.92	± 5.90	20	49	0.837



a) *Argyroderma fissum* **b**) *Drosanthemum schoenlandianum*

Figure 8: Comparisons of grazing intensities for significant differences in numbers of reproductive organs (arithmetic means) for the species *Argyroderma fissum* (**a**) and *Drosanthemum schoenlandianum* (**b**); error bars represent standard deviations; different letters above error bars indicate significant differences in geometric mean according to Tukey's test.

The combined analysis of the species' means of the standardised numbers of reproductive organs per plot confirmed this trend of highest numbers on moderately grazed plots. The difference between the grazing intensities was marginally insignificant with p=0.050 (see also Figure 9). As one plot (Plot no. 39, see Appendix 3) did not contain any of the species, only 50 plots were included in this analysis.

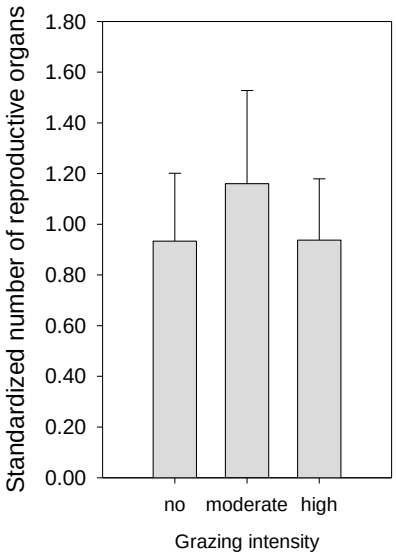


Figure 9: Comparisons of grazing intensities for differences in species' means of standardised numbers of reproductive organs per plot for all selected species; *N*=50 plots; error bars represent standard deviations. Note that the values represent the natural logarithms of the numbers of reproductive organs per individual.

3.6 Population level: number of seedlings

3.6.1 Habitat types

The two habitat types differed significantly in abundance of Aizoaceae seedlings per subplot (averaged per plot): on quartz plots more than twice as many Aizoaceae seedlings occurred as on non-quartz plots (Table 10, Figure 10). The total numbers of seedlings and the numbers of other seedlings did not differ significantly between habitat types (Table 10).

Table 10: Mean numbers (±SD) of seedlings per subplot for the two habitat types and GLM results; *p*-values printed in bold indicate significant differences.

	Quartz (mean ± SD)		**Non-quartz (mean ± SD)**		***p*-value GLM**
	***n*=27**		***n*=24**		
Number of seedlings	0.82	± 0.79	0.57	± 0.63	0.223
Number of Aizoaceae seedlings	0.68	± 0.67	0.29	± 0.23	**0.004**
Number of non-Aizoaceae seedlings	0.14	± 0.32	0.26	± 0.48	0.285

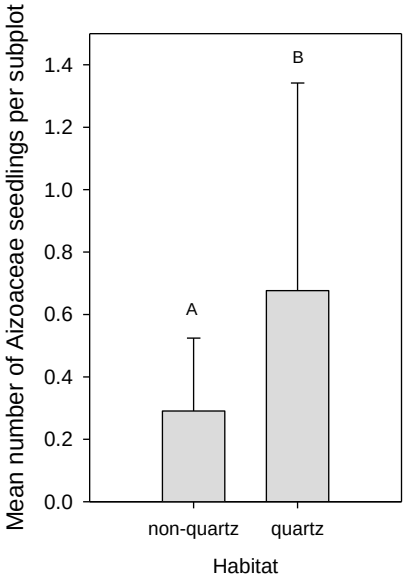


Figure 10: Comparisons of habitat types for mean numbers of Aizoaceae seedlings per subplot; *N*=51 plots; error bars represent standard deviations; different letters above error bars indicate significant differences in geometric mean according to GLM.

3.6.2 Grazing intensities

When quartz and non-quartz plots were combined, the results for the three grazing intensities did neither differ in total number of seedlings nor when differentiating between Aizoaceae and non-Aizoaceae seedlings. When only the quartz plots were taken into account, the numbers of Aizoaceae seedlings differed significantly between grazing intensities (Table 11). The highest number of seedlings occurred on ungrazed and the lowest on moderately grazed plots (Figure 11).

Table 11: Mean numbers (±SD) of seedlings per subplot for the three grazing intensities and GLM results; *p*-values printed in bold indicate significant differences.

	No (mean ± SD)		**Moderate (mean ± SD)**		**High (mean ± SD)**		***p*-value GLM**
	***n*=17**		***n*=17**		***n*=17**		
Number of seedlings	0.84	± 0.70	0.43	± 0.42	0.83	± 0.93	0.155
Number of Aizoaceae seedlings	0.69	± 0.64	0.31	± 0.34	0.48	± 0.56	0.110
Quartz: number of Aizoaceae seedlings	1.08	± 0.65	0.31	± 0.43	0.64	± 0.71	**0.048**
Non-quartz: number of Aizoaceae seedlings	0.26	± 0.24	0.32	± 0.23	0.30	± 0.26	0.976
Number of non-Aizoaceae seedlings	0.15	± 0.27	0.10	± 0.16	0.34	± 0.61	0.143

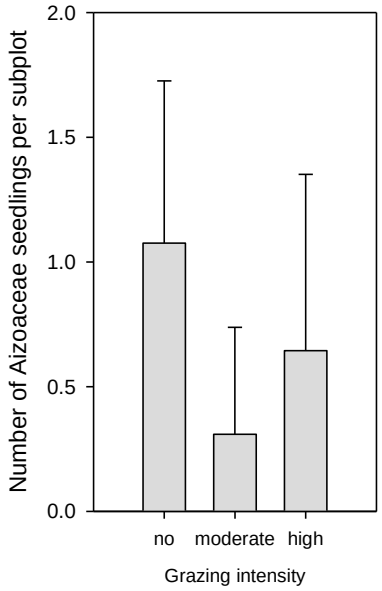


Figure 11: Comparisons of grazing intensities on quartz plots for mean numbers of Aizoaceae seedlings per subplot; *N*=27 plots; error bars represent standard deviations; *p*=0.048 (GLM).

3.6.3 Microhabitat

The three microhabitat categories of quartz cover densities differed significantly in their total numbers of seedlings and highly significantly in their numbers of Aizoaceae seedlings (Figure 12). No differences in the numbers of non-Aizoaceae seedlings could be detected between the categories of quartz cover densities (Table 12).

Table 12: Mean numbers (±SD) of seedlings per subplot for the three microhabitat categories of quartz cover densities and GLM results; *p*-values printed in bold indicate significant differences.

	Low (mean ± SD)		**Medium (mean ± SD)**		**High (mean ± SD)**		***p*-value GLM**
	***n*=46**		***n*=39**		***n*=30**		
Number of seedlings	0.46	± 0.57	0.34	± 0.58	0.87	± 0.98	**0.006**
Number of Aizoaceae seedlings	0.26	± 0.32	0.21	± 0.39	0.74	± 0.85	**<0.001**
Number of non-Aizoaceae seedlings	0.18	± 0.40	0.13	± 0.32	0.13	± 0.31	0.714

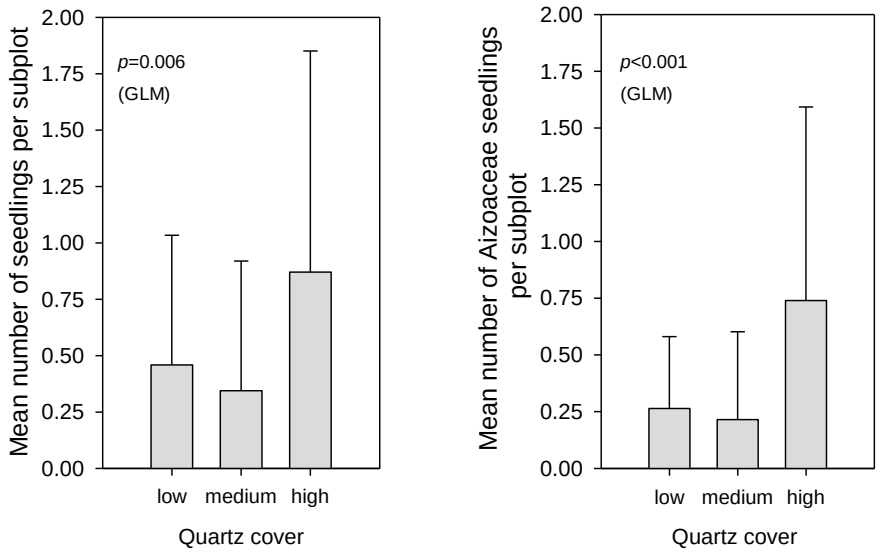


Figure 12: Comparisons of microhabitat categories of quartz cover densities for mean numbers of total (left) and Aizoaceae (right) seedlings per subplot; *N*=51 plots; error bars represent standard deviations.

3.6.4 Microtopography

The three microtopography categories differed significantly in their numbers of Aizoaceae seedlings in which the highest number of seedlings occurred on flat surfaces (<1 cm between highest and lowest point, see Table 13, Figure 13).

Table 13: Mean numbers (±SD) of seedlings per subplot for the three categories of microtopography and GLM results; *p*-values printed in bold indicate significant differences.

	Flat (mean ± SD)		**Medium (mean ± SD)**		**Hilly (mean ± SD)**		***p*-value GLM**
	***n*=51**		***n*=51**		***n*=43**		
Number of seedlings	0.77	± 0.79	0.53	± 0.65	0.53	± 0.80	0.182
Number of Aizoaceae seedlings	0.57	± 0.61	0.32	± 0.38	0.29	± 0.53	**0.014**
Number of non-Aizoaceae seedlings	0.19	± 0.39	0.21	± 0.44	0.24	± 0.51	0.866

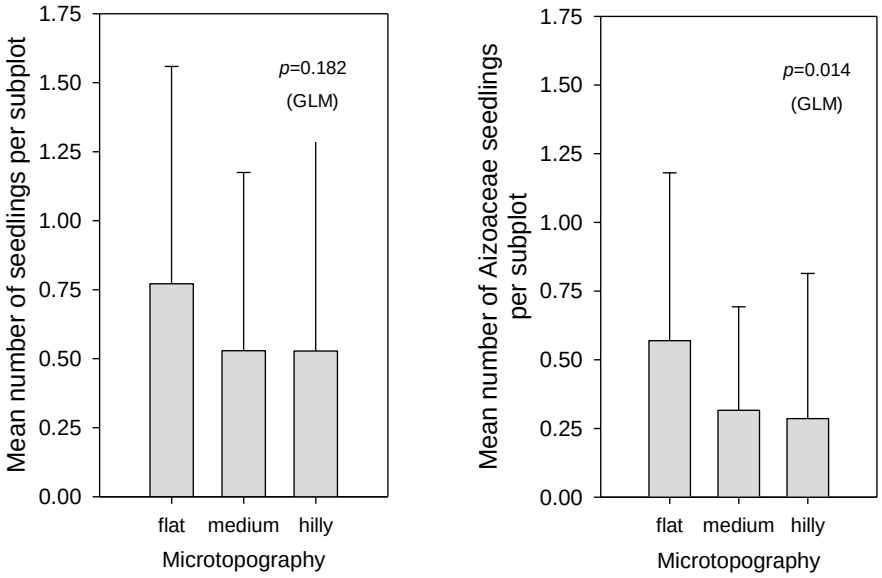


Figure 13: Comparisons of microtopography categories for mean numbers of total (left) and Aizoaceae (right) seedlings per subplot; *N*=51 plots; error bars represent standard deviations.

3.7 Germination experiment

Altogether 1.472 kg dung was sampled (domestic: 1.281 kg; wild: 0.191 kg). The seedlings began to emerge on the forth day after the dung was watered. On the sixth day, already two thirds of the altogether 1,077 seedlings were counted and after 25 days, 96% had emerged. From the 29 samples of domestic animal dung, 953 seedlings germinated (744 seedlings · kg^{-1}) with a mean of 31.8 ± 53.2 seedlings per sample (range 0-213). From the eight samples of dung from wild herbivores, 124 seedlings emerged (649 seedlings · kg^{-1}), with a mean of 15.5 ± 26.0 (range 1-77).

Of the 54 distinguished morpho-types, 42 could be assigned unambiguously to taxa (species, genus or family level) from nine different families. Of the morpho-types, 38 emerged exclusively from domestic livestock dung and four only from dung of wild herbivores. For a complete list of taxa and their seedling abundances, see Appendix 11.

The spectrum of the endozoochorously dispersed flora was in good agreement with the standing vegetation the samples were drawn from. In both cases, the Aizoaceae family was dominating, on species as well as individual level. In particular, the high abundance of the endemic *Drosanthemum schoenlandianum* in the dung of domestic livestock compares well with its high abundance in the vegetation of the plots.

The Asteraceae, although in the endozoochorous flora represented by seven different identified taxa, were less frequent among the seedlings germinated from dung than in the established vegetation. The Poaceae, Fabaceae, Brassicaceae and Chenopodiaceae were important families among both, seedlings emerged from dung and the standing vegetation on the plots, although the proportion of Chenopodiaceae was clearly higher among seedlings compared to standing vegetation. Crassulaceae and Oxalidaceae, though abundant in the standing vegetation, did not emerge at all from dung. The seedlings from dung of domestic and wild herbivores differed mainly in the proportion of mesembs. While individuals of this Aizoaceae subgroup constituted two thirds of all seedlings from domestic animal dung, they made up only 4% of the individuals from wild mammal dung. In contrast, the Fabaceae were highly abundant in wild herbivore dung (19%) but germinated only sporadically from domestic animal dung. Chenopodiaceae was an abundant family in dung of both animal groups. For an overview of the abundances of families, see Figure 14.

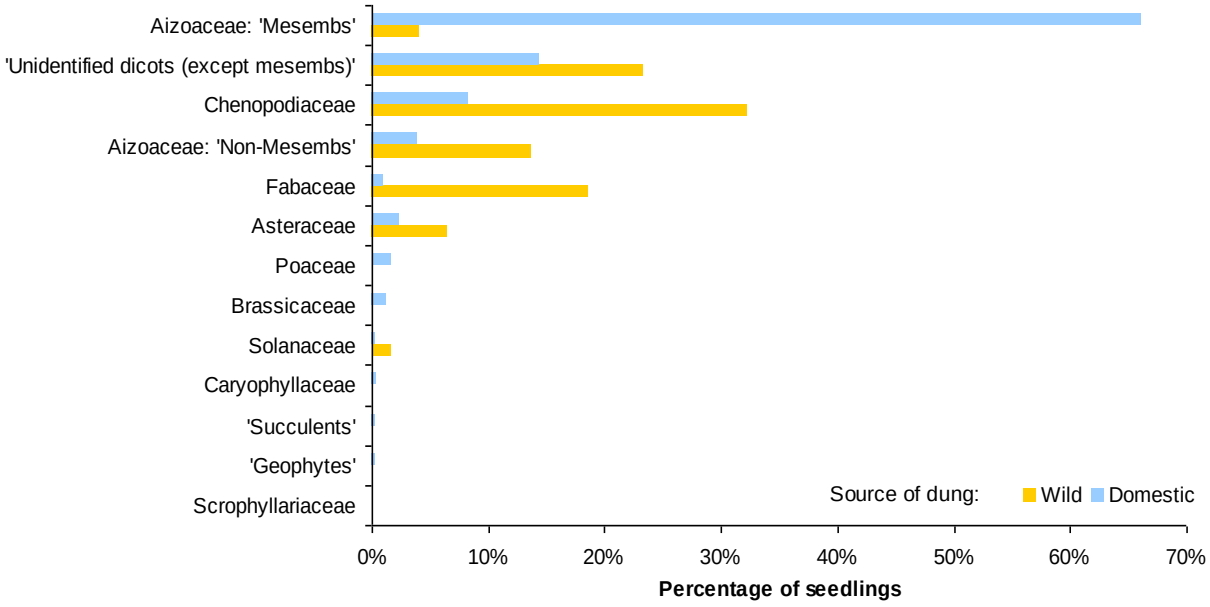


Figure 14: Percentage of seedlings of the families emerged from domestic and wild herbivore dung. The percentage values relate to the respective dung type. Names with quotation marks represent non-taxonomic groups of taxa with similar seedling morphology. The notation ‘mesembs’ refers to the subfamilies Mesembryanthemoideae and Ruschioideae of the family Aizoaceae; ‘Aizoaceae: non-mesembs’ refers to the subfamilies Aizoideae and Tetragonioideae.

4 DISCUSSION

4.1 Effects of grazing on the community level

Abundance of plant individuals and strategy types

The abundance of plant individuals showed different patterns for quartz and non-quartz plots. The similar pattern of total and annual individuals on non-quartz sites, and the fact that no difference in the abundance of perennial species was detected, suggests that the number of individuals was mostly determined by the number of annuals. For the ungrazed farm, this is supported by the extremely high proportional abundance of the annual Asteraceae species *Foveolina dichotoma* on non-quartz plots (compare Appendix 9). Similarly, on the two intensively grazed farms, the three most abundant species (*Rhynchopsidium pumilum*, *Foveolina dichotoma* and *Helichrysum* spec. 2 'succulent') are also annual Asteraceae and accounted for half of the total number of individuals on the farm. In contrast, the three most abundant species recorded for the moderately grazed farm made only a relatively smaller contribution to the abundance.

By contrast, the abundance pattern on quartz plots was determined by both annuals and perennials, both of which were most abundant on ungrazed plots. Since the most abundant species on ungrazed and moderately grazed plots were endemic chamaephytes and, additionally, the number of endemic individuals was lowest on intensively grazed plots, it seems as if a high grazing intensity represses the abundance of endemics in favour of non-endemic species.

As the abundance of annuals did not significantly increase with grazing intensity on quartz as well as on non-quartz plots and was even lowest on the moderately grazed farm Ratelgat, the hypothesis that predicts shifts from a vegetation dominated by perennials to one dominated by annuals in reaction to grazing pressure (WEST 1993; MILTON & HOFFMAN 1994; GRIME 2001; DESMET 2007) could not be supported. Other factors than grazing intensity could be responsible for this pattern, like spatially differing rainfall patterns or soil properties such as water storage capacity or nutrient availability (GILLSON & HOFFMAN 2007). In a study that was conducted across the nearby Kamiesberg mountain range (Leliefontein area) with higher average annual rainfall, though, ANDERSON & HOFFMAN (2007) did not find an increase in cover of annuals in response to higher grazing pressure either. They attributed this to the low

rainfall in the year of data collection. Similarly, HENDRICKS *et al.* (2005) did not find differences in growth form in response to grazing pressure in the Richtersveld National Park. They also argued that precipitation was the most likely cause for the abundance of therophytes and ascribed the contrasting results of TODD & HOFFMAN (1999) to the same fact. The latter researchers detected an increased cover of annuals due to grazing pressure in a fence line contrast study in the Leliefontein area. These findings substantiate the impression that a shift from a vegetation dominated by perennials to one dominated by annuals in the course of intensified grazing pressure in the Namaqualand only applies if precipitation is high enough for annuals to grow in high abundances. As rainfall varies annually, studies about the effects of grazing should be conducted over several years with focus on the abundance of perennial species.

In summary it can be said that effects of grazing on plant abundance were detected only for quartz plots. A shift in strategy type composition could not be ascribed to grazing pressure; neither on quartz nor on non-quartz plots.

Plant diversity

On non-quartz fields, the moderately grazed plots contained the lowest number of species per subplot (400 cm², 'mean species richness'). This would indicate a negative effect of moderate grazing but not of intensive grazing on species richness, which is contrary to most other studies (e.g. NAVEH & WHITTAKER 1979; AYYAD & ELKADI 1982; OLSVIG-WHITTAKER *et al.* 1993; ECCARD *et al.* 2000) and the intermediate disturbance hypothesis (GRIME 1973; CONNELL 1978). This, as well as the relatively highest β-diversity and evenness on moderately grazed plots, can be explained by the very low number of therophytes on moderately grazed plots in comparison to the other grazing intensities. Smaller plants, e.g. due to grazing by animals or difference in growth forms, provide space for more individuals and species (OKSANEN 1996) and therefore increase mean species richness of subplots. This also explains the low evenness of the ungrazed and intensively grazed plots, as these small therophytes are mainly individuals of a few species (especially *Foveolina dichotoma*). The high β-diversity on the non-quartz plots of the moderately grazed farm can be explained by the different dispersal types of the low abundant Asteraceae, which make up most of the annual plants, and the proportionally high abundant Aizoaceae, which represent most of the perennial plants. The short-distance ombrohydrochorous dispersal of the Aizoaceae is an important factor that is responsible for their patchy, heterogenous distribution (PAROLIN

2006). In contrast, the less abundant Asteraceae species are mainly wind-dispersed, which enables their seeds to travel longer distances, particularly in the Knersvlakte with its strong winds. Therefore, highly abundant Asteraceae species are generally more homogeneously distributed than Aizoaceae and have a homogenising effect on the vegetation.

In contrast to non-quartz fields, on quartz fields, the ungrazed plots contained the highest average number of species per subplot as well as the highest total plant species richness on plot level (insignificant trend). Moreover, the number of annual species was also significantly highest on ungrazed plots. This pattern of species richness on quartz plots corresponds to the intermediate disturbance hypothesis if the conditions on the ungrazed farm are described as 'intermediate disturbed'. Although sheep have been excluded on Quaggaskop for about 40 years, the farm is, like the others, still accessible to wild animals like springbok (*Antidorcas marsupialis*) or duiker (*Cephalophus monticola*). The browsing of these animals could be responsible for a disturbance that would be 'intermediate' in terms of the intermediate disturbance hypothesis. Moreover, the pattern of species richness is in concordance with the loss of biodiversity in MILTON *et al.*'s (1994) second step of their model of arid rangeland degradation: loss of species due to failure in recruitment. It appears as if particularly the establishment of annuals was impeded on quartz fields due to extreme habitat conditions like high salinity. However, these results indicate a negative effect of grazing on the total and endemic species richness on quartz fields.

No significant difference in evenness or β-diversity was detected for quartz plots between the different grazing intensities. However, a trend could be observed for the ungrazed plots to have the lowest β-diversity. This, in turn, can be attributed to the high number of therophytes and their homogenising effect on the vegetation.

Taking all plots together, the total number of recorded species per grazing intensity (n=17) was the same for the ungrazed farm as for the two intensively grazed farms together, although the same number of plots on the ungrazed farm was set up on a much smaller area than those with high grazing intensity. Similarly, the plots on the moderately grazed farm were also arranged further apart than those on the ungrazed farm Quaggaskop, but contained less species (compare Figure 1). Therefore, the species on the grazed farms seem to have a less patchier distribution, possibly due to the relative increase of disturbance-adapted species on the expenses of less grazing-tolerant species (DESMET 2007). This can be interpreted as a sign of a degradation process. Another reason for this homogenisation could be the facilitated dispersal by means of domestic livestock zoochory.

Species composition

On non-quartz plots, the pattern of the DCA indicated no differences in species composition between the grazing intensities. However, the analysis of fidelity measures showed that the ungrazed farm contained the highest number of highly diagnostic and significantly accumulated species on non-quartz plots. These species turned out to be non-endemic therophytes or geophytes (with the exception of the chamaephyte *Crotalaria meyeriana*). On moderately grazed non-quartz plots, however, all accumulated species were chamaephytes, two of them being endemic (i.e. *Antimima solida*, *Ruschia bolusiae*). Thus, the diagnostic species of the moderately grazed plots are of high value from the conservational point of view. On intensively grazed plots, the only accumulated species was *Galenia sarcophylla*, which is known as a disturbance indicator (Ute Schmiedel, personal communication 2009). No highly diagnostic species were found in sites with high grazing intensity, which substantiates the hypothesis of a floristic homogenisation on degraded rangeland.

On quartz plots, the number of diagnostic species also decreased with increasing grazing intensity. The number of endemics among these species showed the same trend. In contrast to the non-quartz sites, the tendency of more perennial diagnostic species on moderately grazed plots could not be detected for quartz plots. The intensively grazed plots contained only two accumulated species. One of them, the halotolerant, endemic chamaephytous species *Sarcocornia xerophila* (Ute Schmiedel, personal communication 2009), was highly diagnostic and only occurred on intensively grazed quartz plots. The other one, *Gazania lichtensteinii*, a non-endemic therophyte, did also occur on other farms and was even accumulated on ungrazed non-quartz plots, which make it a less important indicator species for the high grazing intensity.

The DCA ordination of the quartz plots showed two separate clusters for the plots on the ungrazed and moderately grazed farms, respectively. The two intensively grazed farms did not show a clustering but were separated from the other two farms. This DCA ordination as well as the results of the highly diagnostic and accumulated species indicate a high floristic variability between all quartz plots as well as between the different farms and grazing intensities. This is in concordance with SCHMIEDEL (2002), who identified 67 obligate quartz field species for the entire Knersvlakte. Only four of them covered the total quartz field area whereas the distribution of the other species was recorded only for restricted parts of the area. This patchiness was ascribed to the strong radiation experienced by ancestors of modern taxa (SCHMIEDEL 2004).

The ungrazed farm Quaggaskop and the moderately grazed farm Ratelgat host a number of locally endemic habitat specialists, on both, quartz and non-quartz plots. The few accumulated and highly diagnostic species on the intensively grazed farms were not endemic to the Knersvlakte. This gives both the farms Quaggaskop (no grazing) and Ratelgat (moderate grazing) and their grazing regimes a higher conservation significance.

Role of environmental parameters

On non-quartz plots, the recorded environmental parameters did neither significantly alter most of the effects of grazing when used as covariates in the ANCOVAs, nor explained a DCA pattern. This suggests that the effects found for non-quartz plots were due to grazing and not biased by the measured soil properties. Nevertheless, it does not exclude stronger effects of other parameters, such as small-scale rainfall pattern, spatial distance (BERTRAM 2006; PAROLIN 2006) micro-climate, or soil properties, other than the recorded, that have been shown to influence vegetation patterns in the Succulent Karoo (ELLIS & WEIS 2006).

On quartz plots, the soil properties showed an effect on the diversity, abundance and species composition. In the DCA, conductivity and pH correlated highly with the axes and contributed to the visible clustering of plots. These results are in line with SCHMIEDEL & JÜRGENS (1999) and SCHMIEDEL (2002), who also found a strong impact of both parameters on species composition. While species abundance and diversity of the quartz plots were not influenced by the inclusion of soil pH, soil salinity (electrical conductivity) did affect mean species richness and the number of total and endemic individuals. This indicates a higher importance of soil salinity than of grazing pressure for abundance and diversity patterns of species on quartz plots. As salinity amplifies the effects of drought by lowering the osmotic potential in the soil (CAMPBELL & REECE 2005), it can be speculated that the abundance and diversity of plant species on quartz fields is mainly determined by soil water availability.

4.2 Effects of grazing on the population level

Plant size

The majority of the species was not affected in size by the grazing regime. Only two of the species (*Argyroderma fissum* and *Lampranthus otzenianus*) responded to moderate grazing with converse responses (*Argyroderma fissum* was highest in volume on moderately grazed

plots whereas *Lampranthus otzenianus* showed the opposite effect). As only two of twelve species, both being unpalatable plants (Ute Schmiedel, personal communication 2009), showed significant but converse effects and no overall trend could be detected, the ecological meaning of the results is unclear. In a study in the Great Karoo, MILTON (1994) detected a decrease of canopy area for highly palatable species, an increase for unpalatable species and no effect for moderately palatable species. The contradictory results of my study suggest that other factors like water and nutrient availability may play a more important role in the growth of the individuals of the investigated species than grazing.

Reproduction

The production of flowers and fruits was increased by moderate grazing but not by intensive grazing in two of the seven studied species, namely *Argyroderma fissum* and *Drosanthemum schoenlandianum*. A combined analysis across all seven species showed a trend towards the same effect. An explanation could be that injury caused by moderate grazing or trampling stimulates the production of flowers. Therefore, the plant overcompensates for the experienced losses by producing even more flowers (MCNAUGHTON 1983). This mechanism has been demonstrated for other African species, for example the dwarf shrub *Indigofera spinosa* (OBA *et al.* 2000) and *Acacia drepanolobium* (GADD *et al.* 2001) and could also apply for *D. schoenlandianum* which seems to be a palatable species, as its seeds were very frequently found in dung (compare 3.7). However, with higher grazing pressure, the increased production of flowers might be insufficient for overcompensating the more severe losses.

TODD & HOFFMAN (1999) as well as MILTON (1994) found a significant decrease in flowering or seed set in response to heavy grazing in two different palatable plant species, whereas an unpalatable species was not affected. A decrease in reproduction due to grazing could not be detected in my study, although a further increase in grazing intensity might lower the number of flowers and eventually impede reproduction. However, as not all species showed the same trend in reproduction, it is likely that responses to grazing are different across different species. *A. fissum*, however, is known to be unpalatable to stock and there was no indication in the field that this plant was grazed at all. Thus, the detected increase of flowers of this species does not seem to be related to grazing. Considering the likewise higher volume of *A. fissum* individuals on the moderately grazed farm Ratelgat, a more likely explanation is that the plants grow better on this farm in response to more suitable habitat conditions and therefore carry more flowers and fruits.

Unfortunately, information about the palatability of the studied plants is lacking, as in previous studies about the palatability of Karoo plant species, most Knersvlakte endemic species were not included (VAN BREDA & BARNARD 1991; DU TOIT 2002; ESLER *et al.* 2006). For a better comparability to other studies (e.g. MILTON 1994; TODD & HOFFMAN 1999), the knowledge about the palatability value of plant species in the Knersvlakte should be extended.

Number of seedlings

The number of seedlings generally tended to be lowest on the moderately grazed farm (significant only for the family Aizoaceae on quartz plots). This is in line with the relatively low abundance of therophytes on the same sites. Basically, the abundance of annuals as well as that of seedlings is dependent on water supply. It suggests that the low seedling numbers on the moderately grazed farm can be rather explained by local differences in precipitation than by the different grazing intensities. This suggestion is supported by the personal judgement of local people who reported less rain on Ratelgat than on other farms in 2007 (Cecil le Fleur, personal communication 2007), although such a spatially heterogeneous rainfall pattern would be unusual for the winter rainfall region of Namaqualand (DESMET 2007). Based on these results it can be assumed that grazing and trampling have a weaker effect on seedling numbers than other environmental drivers like rainfall.

Similarly, MILTON (1994) did not find an effect of grazing on seed numbers during a study in the Great Karoo. In a study in the Paulshoek area, RIGINOS & HOFFMAN (2003) found that the recruitment of seedlings of *Ruschia robusta* and *Cheridopsis dendiculata*, both belonging to the Aizoaceae, was limited by seeds rather than by abundance of adult plants. However, this limitation was only detected for heavily grazed sites, which suggests that only very intensive grazing affects germination and abundance of seedlings. The grazing intensities investigated in the Knersvlakte, even on the farms with relatively intensive grazing, were apparently not high enough to affect seedling recruitment.

The presence of a quartz cover had a highly significant positive effect on the total number of seedlings found per subplot, which is mainly due to the effect of Aizoaceae seedlings. It is in concordance with the result that revealed higher abundance of Aizoaceae seedlings on quartz plots than on non-quartz plots on a plot level (0.1 ha) and suggests a strong influence of quartz cover on seedling recruitment. The soil between the quartz stones is less exposed to solar radiation and is therefore generally cooler (SCHMIEDEL & JÜRGENS 2004) and moister

(Charles Musil, unpublished data) than the soil without quartz cover. As water uptake is essential for germination, the quartz habitat seems to better fulfil germination requirements for Aizoaceae seedlings than the non-quartz habitat.

As small depressions in the surface, generated, for instance, by sheep footprints, can act as seed and water traps, they are expected to contain many seeds and accumulate water. One could therefore predict an accumulation of seedlings on surfaces with more pronounced microtopography. This prediction was not confirmed, as the number of seedlings was not higher on more heterogeneous surfaces. Aizoaceae seedlings were even recorded most frequently on plane surfaces (compare Figure 13). However, the measured effect could have been biased by other factors. For instance, a correlation between quartz cover and topography cannot be ruled out, since, subjectively, the topography on quartz fields was more homogenous than on non-quartz fields.

4.3 Contribution of domestic and wild herbivores to seed dispersal

Presence and absence of species in the endozoochorous flora is determined *inter alia* by three factors. First, the seeds have to be eaten by the animal. This can either happen deliberately due to high palatability or by accident (e.g. due to close vicinity to a palatable plant) (PAKEMAN *et al.* 2002). Second, the seeds have to survive the digestive system (COSYNS *et al.* 2005). Third, necessary dormancy breaking and germination requirements have to be fulfilled (MALO 2000).

The high abundance of mesemb seedlings, germinated from domestic animal dung, indicates a relatively high importance of endozoochory by domestic livestock for the dispersal of some species of this taxon. In particular the endemic *Drosanthemum schoenlandianum* emerged in high abundance and can therefore expected to be rather palatable. Mesembs usually show short-distance ombrohydrochorous dispersal, a specific adaptation to abiotic environmental conditions like fine-scale habitat variation (ELLIS & WEIS 2006) and intra-annual rainfall patterns (PAROLIN 2006). Domestic animals like sheep and goats, however, can carry seeds as far as they move in 24-36 hours, which is about the retention time in the digestive system of sheep (HUSTON *et al.* 1986). Domestic animals can act therefore as important dispersal vectors of endozoochorous plants. The high abundance of mesemb seedlings, germinated from domestic animal dung, could indicate a high palatability of some species of this group. The fact that wild herbivore dung does not show the same frequency of mesembs among the

emerging seedlings could be due to more selective feeding of indigenous mammals as it has been recorded for e.g. duiker (KIGOZI 2003) and steenbok (DU TOIT 2008). It shows that the importance of domestic livestock as endozoochorous dispersal vectors for these taxa does not necessarily apply to wild herbivores. This means that the species composition of plant communities might be affected differently in response to grazing of domestic or indigenous herbivores.

The low abundance of the usually anemochorous Asteraceae among the seedlings indicates a minor importance of endozoochory for their dispersal. As the family was not completely absent from the seedling flora, the inability to survive the digestive system can basically be ruled out and either low palatability or a high incidence of seed dormancy can be suggested. The high frequency of Fabaceae seedlings in the endozoochorous flora of wild herbivores is in line with the results of other studies that show an important influence of ungulates in general on the dispersal of *Acacia* seeds in an African Savanna (REID & ELLIS 1995; MILLER 1996). The very low presence of few and the absence of most species of the standing vegetation diagnostic to quartz (like *Argyroderma delaetii*, *A. fissum* and *Cephalophyllum spissum*) among the seedlings can be explained by the low height of these species (usually < 15 cm) or their unpalatability (Ute Schmiedel, personal communication 2009), which may have prevented them from being browsed. The complete absence of Crassulaceae species is probably due to their unpalatability, which is characteristic for many members of this family (KELLERMAN *et al.* 1996).

In comparison to the only other study about endozoochorous mammalian dispersal conducted in the Karoo (MILTON & DEAN 2001), the present study yielded five times as many seedlings per kg dung. In the mentioned study, the mesembs also constituted a big part of the emerged individuals, though, similarly to the present study, the proportion was higher among seedlings emerged from dung of sheep than of wild herbivore. Also consistent with my study, MILTON & DEAN (2001) found that mesembs were less abundant among seedlings emerging from dung of wild herbivores like antelopes, but the proportion of fleshy-fruited species (e.g. Fabaceae, Asteraceae) was higher compared to domestic animal dung.

The results suggest that domestic livestock facilitates the dispersal of mesembs and therefore give the primarily short-distance dispersed plants the opportunity to occasionally disperse across long distances.

4.4 Discussion of applied methods

Selection of farms

For the data collection, I selected four farms representing three different grazing intensities. The reasons for the small number of farms were the selection criteria. Most farms belonging to the Knersvlakte Conservation Area had been heavily grazed for centuries, but in the course of establishing the Conservation Area, livestock had been removed during the past several years. These farms had been lying fallow for up to five years and were therefore unsuitable for this study. The investigated part of the farm Quaggaskop is the only piece of land in the Knersvlakte without any grazing of domestic livestock for several decades (about 40 years). Due to this small number of farms, the generalisation of some of the results beyond the study area might be questionable. The selected farms, however, are located in the centre of the Conservation Area and make up a large part of the area of highest concern (Elbé Cloete, personal communication 2007). Therefore, the results obtained for these farms can be regarded as representative and applicable for the Knersvlakte Conservation Area, as was the main concern in this study.

Plot design

I separated the 51 investigated plots into the habitat types "quartz" and "non-quartz" as well as the three grazing intensities, so that the number of replicates for each grazing intensity was eight for non-quartz and nine for quartz plots. Although a higher number of replicates might have been desirable, the applied replication is still in line with the recommended minimum of six replicates per treatment required for standard statistical analyses (QUINN & KEOUGH 2002).

The applied design of subplots instead of the complete sampling of plots allowed for the investigation of plant-microhabitat-interactions (as I used, for example, in the analyses of seedling numbers) and the capture of spatial patterns of vegetation and habitat at the plot level (for instance, small-scale accumulation of species in relation to intra-plot variation of the microhabitat). The latter was not investigated in this thesis, but may still be analysed. It also enabled me to sample a larger area with less effort and therefore allowed for a higher sample size, as mentioned by RUXTON & COLEGRAVE (2006). The plot size of 20 m x 50 m was chosen as it is frequently used in biodiversity assessment and monitoring in the area (e.g. by

BIOTA Southern Africa, SCHMIEDEL & JÜRGENS 2005). However, regardless of the possibilities deriving from this plot design, smaller plots could have increased the sample size with an unchanged sampling effort.

Sampling of population data

The measurements of plant size and the counting of reproductive organs were conducted for all adult individuals of perennial plants. This was done to include as many species as possible in the analysis. This highly time consuming effort could have been reduced by exclusively focussing on a few selected species. The sampling of these selected species could then have been extended to a larger area for the benefit of higher statistical power. MILTON (1994) as well as TODD & HOFFMAN (1999), for instance, restricted their studies to a few species of known palatability. As data about palatability values of many species in the Knersvlakte are scarce, this selection criterion could not be applied without risking misleading conclusions. A study about abundance patterns of frequently occurring plant species or feeding behaviour of sheep or goats (like, for example, HENDRICKS *et al.* 2002 in the Richtersveld National Park) could have provided an indication with regard to the adequate selection of focal species.

Dung sampling and germination experiment

My study was one of the first about endozoochorous dispersal in the Succulent Karoo and can be seen as pioneer work for the Knersvlakte in this regard. The only other comparable studies in South Africa were carried out at the Succulent-Nama-Karoo interface (MILTON & DEAN 2001) and in the Renosterveld (SHIPONENI & MILTON 2006). As the role of endozoochory was unknown and many mesembs were regarded as unpalatable (Ute Schmiedel, personal communication 2007), this study aimed at obtaining a first insight into the general practicability of a respective study in the Knersvlakte. Thus, the design was more of qualitative than of quantitative nature (as to answer the question, which species, if any, are endozoochorously dispersed). At the beginning of the data collection, I intended to limit the dung collection to the proper plot areas. As on some plots, this would have led to insufficient sample size due to lack of dung, I extended the sampling to an undetermined area surrounding the plot. As my study revealed that there are many endozoochorously distributed species with even a high number of mesembs, and that the applied methods were practical, further studies could use a more systematic sampling approach. The dung could be sampled, for example,

along transects that are narrow enough to be able to survey the full width and long enough to get a sufficient amount of dung as it was done by SHIPONENI & MILTON (2006). They additionally sampled over a longer period of time to account for differences in flowering times. With such a design, larger samples and a wider range of species could be included, which would allow for more quantitative analyses.

As neither a key nor a field guide for the identification of seedlings was available in the literature for the Knersvlakte, most of the emerged seedlings could not be identified more closely than to the family level before they died off. Due to these restrictions, the results obtained from this experiment can only serve as an indication for those species that could be clearly identified. For a more comprehensive analysis it would be advisable to first compile an identification key for seedlings. However, as no such key exists to date and information about the endozoochorous dispersal of the species of the Knersvlakte is scarce or even nonexistent, the results of my study serve as a first step to bridge this gap.

4.5 Conclusions and implications for nature conservation

The study revealed that the vegetation of the Knersvlakte is a complex system affected by multiple impact factors, where different vegetation parameters showed different responses to grazing pressure. The abundance, diversity and composition of species as well as reproduction and growth of some frequently occurring perennial species were only secondarily affected by grazing. The main drivers of vegetation and population dynamics in the Knersvlakte seem to be slight spatial variations in rainfall and soil properties. Despite its minor role, grazing showed effects on some parameters (e.g. species abundance on quartz plots, number of diagnostic species and production of flowers in *Drosanthemum schoenlandianum*). From the nature conservation point of view, most analyses resulted in favour of either the ungrazed or the moderately grazed plots, and both systems hosted unique locally endemic habitat specialists.

Therefore, neither a complete ban nor an overall homogenous application of grazing is advisable when aiming at the conservation of the existing vegetation pattern with its unique flora and high endemism. The nature conservation management should consequently consider implementing both the exclusion of domestic livestock on some and the maintenance of a controlled, moderate grazing intensity on other parts of the conservation area, which would also comply with the growing request for farm land by previously disadvantaged communities. Further studies should aim at evaluating whether the effects of moderate domestic livestock grazing can also be generated by indigenous game.

ACKNOWLEDGEMENTS

Fist of all I want to thank Dr. Ute Schmiedel, who supervised my thesis and introduced me into the very special and intriguing flora and local characteristics of the Knersvlakte. Thank you for your strong support (technically and mentally), your cordiality and fairness and the many encouraging words. I am very grateful for your patience with my never-ending questions, your time and the several inspiring discussions.

Special thanks also go to my first evaluator Prof. Dr. Kai Jensen, who taught me a large part of the necessary plant ecological skills and was able to win me for the subject of vegetation ecology. Thank you for your willingness to evaluate my thesis and your valuable comments and advice.

I want to thank my second evaluator Prof. Dr. Norbert Jürgens who gave me the opportunity to make this great experience of taking part in the BIOTA Africa project and going to South Africa for my diploma thesis.

Thanks to Dr. Jürgen Dengler for his help with statistical questions, his critical comments and all his time. I learned a lot about the art of scientific writing from him.

Britta Bösing I want to thank for going along with me the long way. The shared responsibility in the field and the company during the last 1 ½ years have made the hard times much easier to bear and the good times even better to enjoy. It was great having you as a companion!

Many thanks go to Elbé Cloete with CapeNature, who initiated the study, supported us in the field, organised our accommodation and was always concerned about our well-being. Dankie vir alles!

Thanks to Henri Combrink, who was always ready to help with anything on the farm and kept us company in his free time. I enjoyed your company and the evenings at the fire.

For their help with the fieldwork I want to thank Wynand Pieters, Gerda Kriel, Mariana Beukes-Joseph, Henry Cloete, Jona Luther-Mosebach, Matthias Hoffmeister and, of course, Witja Pitz. I am very grateful for your commitment and your valuable suggestions. Baie dankie!

Thanks to Cecil le Fleur and the Griqua community, Buys Wiese and Marietjie van der Merwe as well as the herders on Rooiberg for their hospitality and the permission to work on their farms.

Many thanks to Tessa Oliver for the friendly reception, heartily welcome and support in organisational matters.

I am very grateful to Wiebke Hanke, Jens Oldeland, Dirk Wesuls and Niels Dreber. Thank you not only for helping me with the many questions concerning data analysis but also for making me feel like ‘home’ in the working group.

Thanks to the participants of the Paper-Writing-Seminar (Jürgen, Ute, Manfred, Niels, Dirk, Jens O., Wiebke H., Anna, Jona, Inga, Wiebke M., Magda, Jens D., Oliver, Tene; I hope, I didn’t forget anyone…) for your valuable comments and inspiring discussion and the whole working group Systematik for the warm welcome and friendly atmosphere, Imke Oncken and Karen Dehn for their help in the lab and Dr. Ingo Homburg for his assistance with organisational concerns.

Thanks a lot to Gesine Engels, Frauke Müller, André Jankowski and Imke Fähnders for proofreading and constructive comments and Kristin Ludewig for the inspiring talks on the numerous walks through the Botanical gardens.

Thanks to the working group Angewandte Pflanzenökologie for always making me feel welcome and for the room in the greenhouse, and to Marion Klötzl for her kind and friendly help with the seedlings.

The field work has been funded by BIOTA Africa, the Deutsche Kakteen Gesellschaft e.V. and the DAAD. Permits were kindly granted by the Department of Nature Conservation in South Africa and the Amt für Gesundheit und Verbraucherschutz.

And, finally, I would like to express my deep gratitude to my beloved family, in particular my parents, for financially and mentally supporting me all the years throughout my studies. Thank you for never losing confidence in me!

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ABBREVIATIONS

ANCOVA: analysis of covariance

ANOVA: analysis of variance

BP: before present

DCA: detrended correspondence analysis

df: degree of freedom

GLM: generalized linear modelling

PCA: principle component analysis

SD: standard deviation

SSU: small stock unit

WGS 84: World Geodetic System 1984

APPENDICES

Appendix 1a-d: Selected pictures of quartz plots of the four investigated farms. For a complete list of plots, please refer to Appendix 3.

a) Hoogstaan (intensive grazing),
20.09.2007; Plot 19

b) Rooiberg (intensive grazing),
02.10.2007; Plot 22

c) Ratelgat (moderate grazing),
16.10.2007; Plot 34

d) Quaggaskop (no grazing),
12.10.2007; Plot 32

Appendix 2 a-d) Selected pictures of non-quartz plots of the four investigated farms. For a complete list of plots, please refer to Appendix 3.

a) Hoogstaan (intensive grazing), 13.09.2007; Plot 13

b) Rooiberg (intensive grazing), 23.08.2007; Plot 8

c) Ratelgat (moderate grazing), 27.08.2007; Plot 9

d) Quaggaskop (no grazing), 05.09.2007; Plot 16

Appendix 3: Habitat and soil characteristics and GPS data of the plots (reference system: WGS84).

Plot	Latitude	Longitude	Farm	Habitat	Grazing Intensity	pH	Conductivity [µS·cm^{-1}]	Carbonate content
1	-31.34354764	18.60397741	Ratelgat	non-quartz	moderate	7.94	950	0,5-2%
2	-31.33897671	18.47421885	Hoogstaan	non-quartz	high	7.90	1162	2-4%
3	-31.33980327	18.47128317	Hoogstaan	non-quartz	high	7.81	2100	<0,5%
4	-31.41154164	18.63944694	Quaggaskop	quartz	no	7.68	3720	0%
5	-31.34026461	18.57984826	Ratelgat	quartz	moderate	3.77	981	0%
6	-31.41011604	18.59105855	Rooiberg	quartz	high	7.38	3990	0%
7	-31.40476369	18.63611966	Quaggaskop	non-quartz	no	7.13	1636	0%
8	-31.40705296	18.61298427	Rooiberg	non-quartz	high	8.15	680	0,5-2%
9	-31.34793037	18.59634385	Ratelgat	non-quartz	moderate	7.98	2800	<0,5%
10	-31.41211026	18.6505942	Quaggaskop	quartz	no	6.88	5500	<0,5%
11	-31.41328909	18.58494714	Rooiberg	quartz	high	8.21	5200	>10%
12	-31.34754413	18.58895436	Ratelgat	quartz	moderate	5.69	2200	0%
13	-31.36520245	18.45755428	Hoogstaan	non-quartz	high	7.74	2320	0,5-2%
14	-31.40760952	18.63553762	Quaggaskop	non-quartz	no	8.41	5650	>10%
15	-31.34020829	18.60162243	Ratelgat	non-quartz	moderate	6.67	647	0%
16	-31.39437684	18.65254819	Quaggaskop	non-quartz	no	7.98	380	2-4%
17	-31.40614503	18.63715097	Quaggaskop	non-quartz	no	7.85	3270	4-7%
18	-31.35424026	18.56685966	Ratelgat	non-quartz	moderate	6.74	3000	2-4%
19	-31.34544664	18.469356	Hoogstaan	quartz	high	7.98	2580	>10%
20	-31.41489306	18.64904791	Quaggaskop	quartz	no	6.84	9100	0%
21	-31.35923185	18.55784878	Ratelgat	quartz	moderate	7.11	6690	<0,5%
22	-31.44555473	18.57581958	Rooiberg	quartz	high	7.50	5640	0%
23	-31.40750223	18.61887708	Rooiberg	non-quartz	high	7.64	638	0%
24	-31.41531148	18.6452432	Quaggaskop	quartz	no	5.45	5940	0%
25	-31.39294988	18.65466043	Quaggaskop	non-quartz	no	8.26	9320	0,5-2%
26	-31.34645917	18.58503699	Ratelgat	quartz	moderate	4.83	3350	0%
27	-31.3624666	18.55245754	Ratelgat	non-quartz	moderate	8.17	1761	7-10%
28	-31.41477638	18.64906803	Quaggaskop	quartz	no	7.58	8580	0%
29	-31.34735771	18.46669927	Hoogstaan	quartz	high	7.71	2660	0%
30	-31.33887389	18.57646868	Ratelgat	quartz	moderate	4.32	1063	0%
31	-31.33875989	18.57551113	Ratelgat	quartz	moderate	6.44	5390	0%
32	-31.41066589	18.64068478	Quaggaskop	quartz	no	7.69	9410	0,5-2%
33	-31.3478043	18.47022504	Hoogstaan	quartz	high	7.32	3980	0%
34	-31.34417527	18.57638419	Ratelgat	quartz	moderate	4.07	3070	0%
35	-31.3959513	18.6512433	Quaggaskop	non-quartz	no	7.29	2980	<0,5%
36	-31.39723741	18.65421653	Quaggaskop	quartz	no	6.78	7970	0%
37	-31.36453324	18.5491772	Ratelgat	non-quartz	moderate	7.93	3460	2-4%
38	-31.42199957	18.59401837	Rooiberg	non-quartz	high	7.75	3310	4-7%
39	-31.4485856	18.56587663	Rooiberg	quartz	high	4.26	4290	0%
40	-31.37212702	18.53326678	Ratelgat	non-quartz	moderate	7.98	958	2-4%
41	-31.44597449	18.58670801	Rooiberg	non-quartz	high	7.28	6730	<0,5%
42	-31.42430493	18.64058688	Quaggaskop	non-quartz	no	7.53	797	>10%
43	-31.34784722	18.59823078	Ratelgat	quartz	moderate	5.46	742	0%
44	-31.44900271	18.57142478	Rooiberg	quartz	high	5.25	4650	0%
45	-31.41718232	18.64799649	Quaggaskop	quartz	no	6.37	7120	0%
46	-31.42325618	18.63952875	Quaggaskop	non-quartz	no	7.55	2580	<0,5%
47	-31.41538792	18.6427474	Quaggaskop	quartz	no	5.46	6010	0%
48	-31.35610842	18.57204974	Ratelgat	quartz	moderate	6.64	6610	0%
49	-31.36216083	18.54150206	Ratelgat	non-quartz	moderate	7.32	2200	<0,5%
50	-31.36787795	18.45611796	Hoogstaan	non-quartz	high	6.98	1967	4-7%
51	-31.37080424	18.45639825	Hoogstaan	quartz	high	6.12	4130	0%

Appendix 4: Species list, with growth form types after RAUNKIAER (1934), families and number of plots where species are present as adults or juveniles on the different vegetation units; C=chamaephyte, G=geophyte, H=hemicryptophyte, P=phanerophyte, T=therophyte; asterisks indicate significant differences (Fisher's exact test); red marks: highly diagnostic species; orange marks: diagnostic species; yellow marks: positively associated non-diagnostic species; [1]species recorded only as seedlings.

					quartz				non-quartz			
Species	**Growth form type**	**quartz**	**non-quartz**	**total**	**no**	**moderate**	**high**	**total**	**no**	**moderate**	**high**	**total**
Aizoaceae												
Amphibolia saginata (L.Bolus) H.E.K. Hartmann	C	1	1	2	0	0	1	1	0	0	1	1
Antimima excedens (L.Bolus) Klak	C	4	8	12	1	3	0	4	4	2	2	8
Antimima intervallaris (L.Bolus) H.E.K. Hartmann	C	1	1	2	1	0	0	1	0	0	1	1
Antimima solida (L.Bolus) H.E.K. Hartmann	C	7	4	11	4	3	0	7	0	4*	0	4
Antimima watermeyeri (L.Bolus) H.E.K. Hartmann	C	10*	0	10	2	7*	1	10	0	0	0	0
Argyroderma crateriforme (L.Bolus) N.E.Br.	C	5*	0	5	3	1	1	5	0	0	0	0
Argyroderma deleatii C.A. Maass	C	15*	0	15	9*	4	2	15	0	0	0	0
Argyroderma fissum (Haw.) L.Bolus	C	22*	9	31	9	7	6	22	4	4	1	9
Argyroderma framesii L.Bolus ssp. *framesii*	C	2	0	2	0	0	2	2	0	0	0	0
Argyroderma pearsonii (N.E.Br.) Schwantes	C	10*	0	10	5	1	4	10	0	0	0	0
Argyroderma spec.	C	1	0	1	0	1	0	1	0	0	0	0
Aridaria noctiflora (L.) Schwantes ssp. *noctiflora*	P	2	5	7	0	2	0	2	1	2	2	5
Aridaria serotina L.Bolus	P	2	1	3	1	1	0	2	0	1	0	1
Brownanthus corallinus (Thunb.) Ihlenf. & Bittrich	C	2	1	3	0	0	2	2	0	0	1	1
Caulipsolon rapaceum (Jacq.) Klak	G	3	4	7	1	1	1	3	1	1	2	4
Cephalophyllum caespitosum H.E.K. Hartmann	C	1	1	2	1	0	0	1	1	0	0	1
Cephalophyllum framesii L. Bolus	C	14	13	27	8*	4	2	14	6	4	3	13
Cephalophyllum parvibracteatum (L.Bolus) H.E.K. Hartmann	C	8*	1	9	3	3	2	8	0	1	0	1
Cephalophyllum spissum H.E.K. Hartmann	C	18*	6	24	8	8	2	18	2	4	0	6
Cephalophyllum staminodiosum L.Bolus	C	3	0	3	1	2	0	3	0	0	0	0
Cephalophyllum spec. 1 ('small')	C	0	1	1	0	0	0	0	0	1	0	1
Conophytum calculus (A.Berger) N.E.Br. ssp. *calculus*	C	4	0	4	1	3	0	4	0	0	0	0
Conophytum minutum var. *minutum* (Haw.) N.E.Br.	C	6*	0	6	1	4	1	6	0	0	0	0
Conophytum subfenestratum Schwantes	C	4	0	4	0	3	1	4	0	0	0	0
Dactylopsis digitata (Aiton) N.E.Br.	C	3	0	3	2	1	0	3	0	0	0	0
Delosperma crassum L.Bolus	C	1	0	1	1	0	0	1	0	0	0	0
Dicrocaulon brevifolium N.E.Br.	C	1	0	1	0	0	1	1	0	0	0	0
Dicrocaulon humile N.E.Br.	C	1	0	1	1	0	0	1	0	0	0	0
Dicrocaulon longifolium spec. Nov. Ihlenfeldt	C	2	0	2	0	0	2	2	0	0	0	0
Drosanthemum deciduum H.E.K. Hartmann & Bruckmann	C	2	9*	11	1	1	0	2	3	4	2	9

Species	Growth form type	quartz	non-quartz	total	quartz				non-quartz			
					no	moderate	high	total	no	moderate	high	total
Drosanthemum diversifolium L. Bolus	C	23*	14	37	9	6	8	23	5	4	5	14
Drosanthemum globosum L. Bolus	C	3	14*	17	1	1	1	3	3	5	6	14
Drosanthemum pulverulentum (Haw.) Schwantes	C	14	18	32	3	5	6	14	7	6	5	18
Drosanthemum ramosissimum (Haw.) Schwantes	C	1	8*	9	0	0	1	1	3	1	4	8
Drosanthemum schoenlandianum (Schltr.) L. Bolus	C	4	23*	27	1	1	2	4	7	8	8	23
Drosanthemum spec. 1 ('glossy')	C	5	14*	19	2	0	3	5	4	5	5	14
Drosanthemum spec. 2 ('ggv')	C	0	1	1	0	0	0	0	0	0	1	1
Galenia sarcophylla Fenzl	C	2	8*	10	0	1	1	2	2	1	5*	8
Lampranthus otzenianus (Dinter) Friedrich	P	1	14*	15	0	1	0	1	6	5	3	14
Leipoldtia schultzei (Schltr. & Diels) Friedrich	C	1	5	6	1	0	0	1	1	3	1	5
Malephora purpureo-crocea (Haw.) Schwantes	C	6	18*	24	1	1	4	6	5	7	6	18
Mesembryanthemum fastigiatum Thunb.	T	0	1	1	0	0	0	0	0	0	1	1
Mesembryanthemum guerichianum Pax	T	3	9*	12	3*	0	0	3	3	4	2	9
Mesembryanthemum longistylum DC.	T	10*	0	10	7*	1	2	10	0	0	0	0
Mesembryanthemum nodiflorum L.	T	11*	1	12	6	1	4	11	0	1	0	1
Monilaria chrysoleuca (Schltr.) Schwantes	C	1	0	1	0	1	0	1	0	0	0	0
Monilaria moniliformis (Thunb.) Ihlenf. & Jörg	C	5*	0	5	1	3	1	5	0	0	0	0
Monilaria pisiformis (Haw.) Schwantes	C	3	0	3	2	1	0	3	0	0	0	0
Monilaria spec.	C	0	1	1	0	0	0	0	0	0	1	1
Oophytum nanum (Schltr.) L.Bolus	C	3	0	3	3*	0	0	3	0	0	0	0
Phyllobolus nitidus (Haw.) Gerbaulet	C	1	12*	13	0	0	1	1	6	3	3	12
Phyllobolus spinuliferus (Haw.) Gerbaulet	C	0	1	1	0	0	0	0	0	0	1	1
Psilocaulon dinteri (Engl.) Schwantes	C	3	10*	13	1	0	2	3	2	3	5	10
Psilocaulon leptarthron (A.Berger) N.E.Br.	C	2	8*	10	1	0	1	2	4	1	3	8
Ruschia bolusiae Schwantes	C	10	5	15	3	5	2	10	0	4*	1	5
Ruschia burtoniae L.Bolus	C	10*	0	10	2	5	3	10	0	0	0	0
Ruschia spinosa (L.) Dehn	C	0	2	2	0	0	0	0	0	2	0	2
Ruschia subsphaerica L.Bolus	C	0	7*	7	0	0	0	0	4	3	0	7
Ruschia spec. 1 ('grünes Polster')	C	1	0	1	0	1	0	1	0	0	0	0
Ruschia spec. 2 ('knubbelfensterrand')	C	2	2	4	1	1	0	2	0	2	0	2
Tetragonia fruticosa L.	C	10	8	18	1	6*	3	10	2	4	2	8
Tetragonia microptera Fenzl	T	0	6*	6	0	0	0	0	3	2	1	6
Tetragonia verrucosa Fenzl	C	4	0	4	1	1	2	4	0	0	0	0
'Cono verzweigt'	C	0	1	1	0	0	0	0	0	1	0	1
'Mesemb'	C	7	8	15	3	2	2	7	4	1	3	8

Species	Growth form type	quartz	non-quartz	total	quartz				non-quartz			
					no	moderate	high	total	no	moderate	high	total
Apiaceae												
Apiaceae spec.		0	1	1	0	0	0	0	0	0	1	1
Apocynaceae												
Apocynaceae spec.	C	1	0	1	0	0	1	1	0	0	0	0
Asparagaceae												
Asparagus capensis L.	C	1	1	2	0	1	0	1	1	0	0	1
[1]*Asparagus rubicundus* P.J.Bergius	C	0	0	0	0	0	0	0	0	0	0	0
Asparagus spec.	C	1	0	1	0	1	0	1	0	0	0	0
Asphodelaceae												
Bulbine spec.	G	1	2	3	0	0	1	1	1	0	1	2
Trachyandra bulbinifolia (Dinter) Oberm.	G	0	1	1	0	0	0	0	0	0	1	1
Trachyandra filiformis (Aiton) Oberm.	G	0	1	1	0	0	0	0	0	0	1	1
Trachyandra tortilis (Baker) Oberm.	G	2	1	3	1	1	0	2	0	1	0	1
Trachyandra spec.	G	1	1	2	0	0	1	1	0	0	1	1
Asteraceae												
Amellus microglossus DC.	T	14	20*	34	5	4	5	14	7	6	7	20
Asteraceae spec.	T	1	2	3	1	0	0	1	2	0	0	2
Didelta carnosa (L.f.) Aiton var. *carnosa*	C	15	18	33	7	5	3	15	8	6	4	18
Felicia australis (Alston) E.Phillips	T	0	3	3	0	0	0	0	2	0	1	3
Foveolina dichotoma (Thell.) Källersjö	T	21	24*	45	9	5	7	21	8	8	8	24
Gazania lichtensteinii Less.	T	8	17*	25	2	1	5*	8	8*	4	5	17
Gazania tenuifolia Less.	T	1	2	3	0	0	1	1	1	0	1	2
Gorteria diffusa Thunb. ssp. *diffusa*	T	1	2	3	0	1	0	1	1	0	1	2
Helichrysum alsinoides DC.	T	1	6*	7	0	0	1	1	4	1	1	6
Helichrysum tinctum (Thunb.) Hilliard & B.L.Burtt	T	10	18*	28	5	2	3	10	7	7	4	18
Helichrysum spec. 1 (‘lllb’)	T	0	1	1	0	0	0	0	0	0	1	1
Helichrysum spec. 2 (‚succulent’)	T	4	6	10	2	1	1	4	1	3	2	6
Helichrysum spec.	T	0	1	1	0	0	0	0	0	0	1	1
Hirpicium alienatum (Thunb.) Druce	C	1	0	1	0	1	0	1	0	0	0	0
Hoplophyllum spinosum DC.	P	1	0	1	0	0	1	1	0	0	0	0
Leysera tenella DC.	T	0	2	2	0	0	0	0	1	0	1	2
Oncosiphon grandiflorum (Thunb.) Källersjö	T	0	2	2	0	0	0	0	1	0	1	2
Oncosiphon suffruticosum (L.) Källersjö	T	2	6	8	0	0	2	2	1	2	3	6
Osteospermum pinnatum (Thunb.) Norl.	T	4	20*	24	3	1	0	4	8	6	6	20
Othonna arbuscula (Thunb.)Sch.Bip.	C	0	2	2	0	0	0	0	1	0	1	2
Othonna intermedia Compton	G	0	1	1	0	0	0	0	1	0	0	1

Species	Growth form type	quartz	non-quartz	total	quartz				non-quartz			
					no	moderate	high	total	no	moderate	high	total
Othonna protecta Dinter	C	7	12	19	0	4	3	7	4	7*	1	12
Pteronia ciliata Thunb.	C	3	0	3	1	2	0	3	0	0	0	0
Pteronia glabrata L.f.	C	1	0	1	0	0	1	1	0	0	0	0
Pteronia heterocarpa DC.	C	1	0	1	0	0	1	1	0	0	0	0
Rhynchopsidium pumilum (L.f.) DC.	T	5	20*	25	3	0	2	5	5	7	8	20
Senecio abruptus Thunb.	T	1	10*	11	1	0	0	1	6*	3	1	10
Senecio arenarius Thunb.	T	4	16*	20	4*	0	0	4	8*	4	4	16
Senecio elegans L.	T	1	0	1	1	0	0	1	0	0	0	0
Tripteris clandestina Less.	T	5	9	14	3	0	2	5	4	2	3	9
Tripteris sinuata DC. var. *sinuata*	C	8*	0	8	1	5	2	8	0	0	0	0
Ursinia nana DC.	T	10	11	21	1	6*	3	10	3	3	5	11
Brassicaceae												
Heliophila variabilis Burch ex. DC.	T	10	16*	26	4	5	1	10	6	6	4	16
Caryophyllaceae												
Spergularia media (L.) C. Presl. ex Griseb.	C	2	0	2	0	0	2	2	0	0	0	0
Chenopodiaceae												
Atriplex spec.	C	2	1	3	0	0	2	2	0	0	1	1
Chenopodium album L.	T	0	1	1	0	0	0	0	0	0	1	1
Chenopodium murale L.	T	1	1	2	1	0	0	1	1	0	0	1
Salsola spec.	C	21	17	38	9	7	5	21	5	5	7	17
Sarcocornia xerophila (Tölken) A.J.Scott	C	4	0	4	0	0	4*	4	0	0	0	0
Crassulaceae												
Crassula barklyi N.E.Br.	C	17*	0	17	5	7	5	17	0	0	0	0
Crassula columnaris ssp. *prolifera* Friedrich	C	7*	0	7	4	1	2	7	0	0	0	0
Crassula deceptor Schönland & Baker f.	C	3	0	3	0	1	2	3	0	0	0	0
Crassula expansa Dryand ssp. *expansa*	C	0	1	1	0	0	0	0	1	0	0	1
Crassula expansa ssp. *pyrifolia* (Compton) Tölken	C	3	8	11	2	0	1	3	0	6*	2	8
Crassula muscosa var. *obtusifolia* (Harv.) G.D. Rowley	C	1	2	3	0	1	0	1	0	2	0	2
Crassula muscosa L. var. *muscosa*	C	0	1	1	0	0	0	0	1	0	0	1
Crassula subaphylla var. *virgata* (Harv.) Tölken	C	0	2	2	0	0	0	0	1	1	0	2
Tylecodon pearsonii (Schönland) Tölken	C	2	0	2	1	1	0	2	0	0	0	0
Tylecodon pygmaeus (W.F.Barker) Tölken	C	7*	0	7	4	1	2	7	0	0	0	0

Species	Growth form type	quartz	non-quartz	total	quartz: no	quartz: moderate	quartz: high	quartz: total	non-quartz: no	non-quartz: moderate	non-quartz: high	non-quartz: total
Euphorbiaceae												
Euphorbia decussata E.Mey. Ex. Boiss.	C	0	2	2	0	0	0	0	2	0	0	2
Euphorbia exilis L.C. Leach	C	0	1	1	0	0	0	0	1	0	0	1
Euphorbia hamata (Haw.) Sweet	C	2	0	2	0	0	2	2	0	0	0	0
Euphorbia muricata Thunb.	C	2	3	5	1	0	1	2	2	0	1	3
Euphorbia spec.	C	1	1	2	1	0	0	1	0	0	1	1
Fabaceae												
Crotalaria humilis Eckl. & Zeyh.	T	3	11*	14	2	0	1	3	5	2	4	11
Crotalaria meyeriana Steud.	C	4	16*	20	4*	0	0	4	8*	4	4	16
Indigofera spec.	C	1	0	1	0	0	1	1	0	0	0	0
Lessertia diffusa R.Br.	H	0	2	2	0	0	0	0	2	0	0	2
Lessertia spec. (‚long twisted fruits')	H	1	0	1	1	0	0	1	0	0	0	0
Lotononis falcata (E.Mey) Benth.	H	1	0	1	0	0	1	1	0	0	0	0
Fabaceae spec.	T	0	1	1	0	0	0	0	1	0	0	1
Geraniaceae												
Sarcocaulon crassicaule Rehm	C	2	0	2	0	0	2	2	0	0	0	0
Hyacinthaceae												
Lachenalia framesii W.F.Barker	G	1	8*	9	0	1	0	1	6*	2	0	8
Lachenalia mutabilis Sweet	G	1	0	1	0	0	1	1	0	0	0	0
Lachenalia spec.	G	0	3	3	0	0	0	0	1	0	2	3
Ornithogalum spec.	G	1	1	2	1	0	0	1	0	1	0	1
Iridaceae												
Ferraria spec.	G	0	3	3	0	0	0	0	2	0	1	3
Lapeirousia spec. (Goldblatt) Goldblatt & J.C.Manning	G	1	0	1	0	0	1	1	0	0	0	0
Lobeliaceae												
Cyphia oligotricha Schltr.	H	2	0	2	0	0	2	2	0	0	0	0
Molluginaceae												
Hypertelis salsoloides (Burch.) Adamson	C	2	3	5	0	1	1	2	1	1	1	3
Oxalidaceae												
Oxalis ambigua Jacq.	G	4	7	11	1	0	3	4	3	2	2	7
Oxalis blastorrhiza T.M.Salter	G	0	1	1	0	0	0	0	1	0	0	1
Oxalis pes-caprae L.	G	3	8	11	1	0	2	3	4	2	2	8
Oxalis spec. 1 ('comosa KV')	G	2	2	4	0	0	2	2	1	0	1	2
Oxalis spec. 2 ('erecti')	G	1	3	4	1	0	0	1	1	0	2	3
Oxalis spec. 3 ('miniblatt')	G	4	8	12	1	1	2	4	2	2	4	8

Species	Growth form type	quartz	non-quartz	total	quartz				non-quartz			
					no	moderate	high	total	no	moderate	high	total
Oxalis spec.	G	1	2	3	0	0	1	1	1	1	0	2
Plantaginaceae												
Plantago cafra Decne.	T	0	2	2	0	0	0	0	0	1	1	2
Poaceae												
Chaetobromus involucratus (Schrad) Nees ssp. *involucratus*	H	0	1	1	0	0	0	0	1	0	0	1
Karroochloa schismoides (Stapf ex Conert) Conert & Türpe	T	6	17*	23	3	1	2	6	6	5	6	17
Schismus barbatus (Loefl. ex L.) Thell.	T	0	4*	4	0	0	0	0	3	0	1	4
Schmidtia kalaharensis Stent	T	4	4	8	1	2	1	4	1	0	3	4
Tribolium utriculosum (Nees) Renvoize	T	0	1	1	0	0	0	0	0	1	0	1
Poaceae spec.	T	1	1	2	0	0	1	1	0	0	1	1
Portulacaceae												
Anacampseros spec.	C	2	1	3	1	1	0	2	1	0	0	1
Scrophulariaceae												
Zaluzianskya affinis Hilliard	T	0	1	1	0	0	0	0	1	0	0	1
Sterculiaceae												
Hermannia cuneifolia Jacq.	C	2	0	2	0	1	1	2	0	0	0	0
Zygophyllaceae												
Zygophyllum cordifolium L.f.	C	14	7	21	4	7	3	14	3	2	2	7
Zygophyllum retrofractum Thunb.	C	1	3	4	0	1	0	1	1	2	0	3
Zygophyllum spinosum L.	C	0	1	1	0	0	0	0	0	1	0	1
Zygophyllum teretifolium Schltr.	C	1	0	1	0	0	1	1	0	0	0	0
Unknown family												
'Hannahbusch'		1	0	1	0	0	1	1	0	0	0	0
'Tiny red flower'	T	1	0	1	1	0	0	1	0	0	0	0
[1] 'Little green'	T											
[1]Succulent												
Annual	T	6	13	19	3	1	2	6	6	4	3	13
Dicotyle		4	3	7	1	0	3	4	0	1	2	3
Geophyte spec.	G	11	19	30	4	3	4	11	7	6	6	19
Monocotyl		0	1	1	0	0	0	0	1	0	0	1

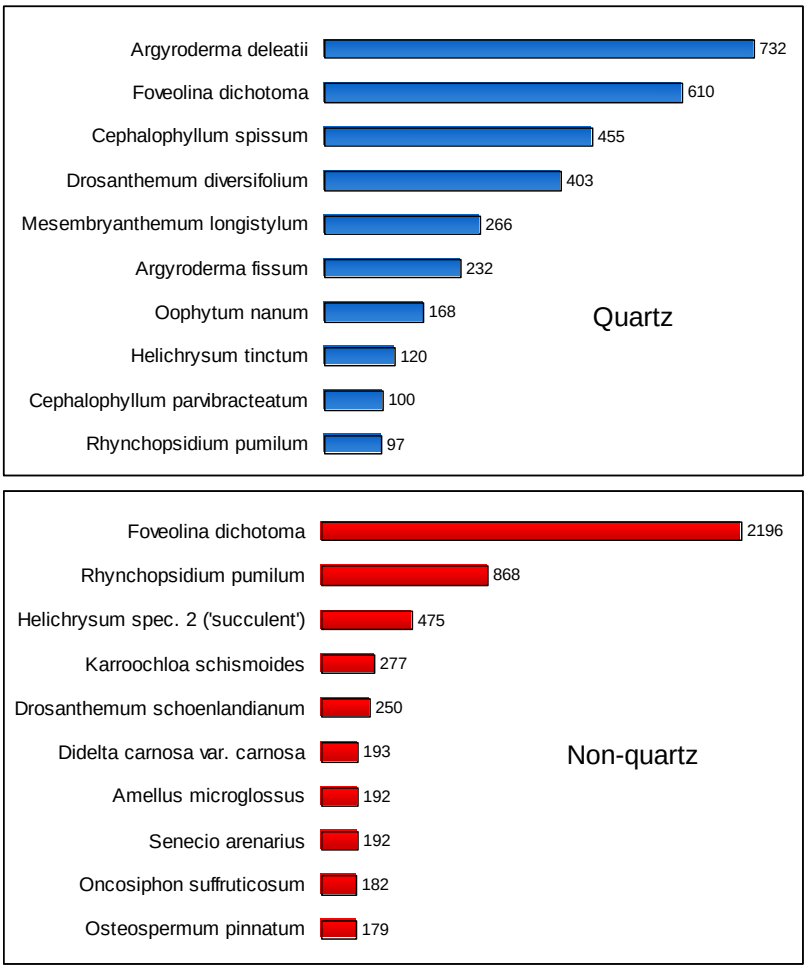
Appendix 5: List of species endemic to the Knersvlakte recorded for the plots.

Species	Family	References for distribution
Antimima excedens (L.Bolus) Klak	Aizoaceae	HARTMANN (2002)
Antimima intervallaris (L.Bolus) H.E.K. Hartmann	Aizoaceae	VAN WYK & SMITH (2001); HARTMANN (2002)
Antimima solida (L.Bolus) H.E.K. Hartmann	Aizoaceae	HARTMANN (2002)
Antimima watermeyeri (L.Bolus) H.E.K. Hartmann	Aizoaceae	HARTMANN (2002)
Argyroderma crateriforme (L.Bolus) N.E.Br.	Aizoaceae	HARTMANN (1977)
Argyroderma delaetii C.A. Maass	Aizoaceae	HARTMANN (1977)
Argyroderma fissum (Haw.) L.Bolus	Aizoaceae	HARTMANN (1977)
Argyroderma framesii L.Bolus ssp. *framesii*	Aizoaceae	HARTMANN (1977)
Argyroderma pearsonii (N.E.Br.) Schwantes	Aizoaceae	HARTMANN (1977)
Caulipsolon rapaceum (Jacq.) Klak	Aizoaceae	KLAK & LINDER (1998); VAN WYK & SMITH (2001)
Cephalophyllum caespitosum H.E.K. Hartmann	Aizoaceae	HARTMANN (1988)
Cephalophyllum framesii L. Bolus	Aizoaceae	HARTMANN (1988); VAN WYK & SMITH (2001)
Cephalophyllum parvibracteatum (L.Bolus) H.E.K. Hartmann	Aizoaceae	HARTMANN (1988)
Cephalophyllum spissum H.E.K. Hartmann	Aizoaceae	HARTMANN (1988)
Cephalophyllum staminodiosum L.Bolus	Aizoaceae	HARTMANN (1988); VAN WYK & SMITH (2001)
Conophytum calculus (A.Berger) N.E.Br. ssp. *calculus*	Aizoaceae	HAMMER (1993); SCHMIEDEL (2002)
Conophytum minutum var. Minutum (Haw.) N.E.Br.	Aizoaceae	HAMMER (1993)
Conophytum subfenestratum Schwantes	Aizoaceae	HAMMER (1993)
Cyphia oligotricha Schltr.	Lobeliaceae	LE ROUX (2005)
Dactylopsis digitata (Aiton) N.E.Br.	Aizoaceae	HARTMANN (2002)
Dicrocaulon brevifolium N.E.Br.	Aizoaceae	SCHMIEDEL (2002); HARTMANN (2002)
Dicrocaulon humile N.E.Br.	Aizoaceae	SCHMIEDEL (2002); HARTMANN (2002)
Drosanthemum deciduum H.E.K. Hartmann & Bruckmann	Aizoaceae	HARTMANN (2002)
Drosanthemum diversifolium L. Bolus	Aizoaceae	KRÄMER (2002)
Drosanthemum pulverulentum (Haw.) Schwantes	Aizoaceae	HARTMANN (2002)
Drosanthemum schoenlandianum (Schltr.) L. Bolus	Aizoaceae	HARTMANN (2002)
Euphorbia exilis L.C. Leach	Euphorbiaceae	VAN WYK & SMITH (2001)
Malephora purpureo-crocea (Haw.) Schwantes	Aizoaceae	LE ROUX (2005)
Monilaria chrysoleuca (Schltr.) Schwantes	Aizoaceae	IHLENFELDT & JÖRGENSEN (1973)
Monilaria moniliformis (Thunb.) Ihlenf. & Jörg	Aizoaceae	IHLENFELDT & JÖRGENSEN (1973)
Monilaria pisiformis (Haw.) Schwantes	Aizoaceae	IHLENFELDT & JÖRGENSEN (1973)
Oophytum nanum (Schltr.) L.Bolus	Aizoaceae	SCHMIEDEL (2002); HARTMANN (2002)
Othonna intermedia Compton	Asteraceae	SCHMIEDEL (2002); HARTMANN (2002)
Oxalis blastorrhiza T.M.Salter	Oxalidaceae	LE ROUX (2005)
Psilocaulon leptarthron (A.Berger) N.E.Br.	Aizoaceae	KLAK & LINDER (1998)
Pteronia heterocarpa DC.	Asteraceae	VAN WYK & SMITH (2001)
Ruschia bolusiae Schwantes	Aizoaceae	Ute Schmiedel, personal communication 2008
Sarcocornia xerophila (Tölken) A.J.Scott	Chenopodiaceae	LE ROUX (2005)
Tylecodon pygmaeus (W.F.Barker) Tölken	Crassulaceae	SCHMIEDEL (2002); VAN JAARSVELD & KOUTNIK (2004); LE ROUX (2005)
Zygophyllum teretifolium Schltr.	Zygophyllaceae	LE ROUX (2005)

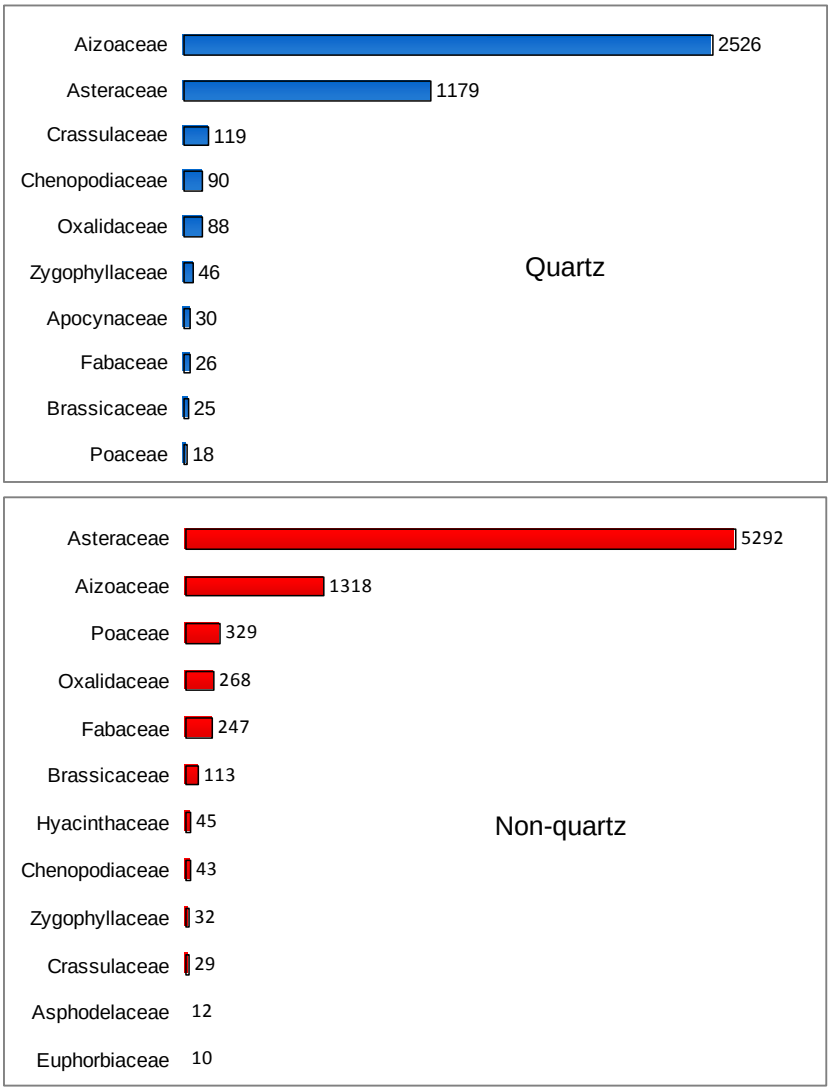
Appendix 6: Contents of the electronic appendices (CD-ROM attached at the back of this thesis).

File name	Contents	
vegsampling_haarmeyer.mdb	Raw data of vegetation sampling consisting of following tables:	
	'plots':	List of plots including respective habitat type, grazing intensity, farm, sampling date and soil parameters
	'subplots':	List of subplots, including microhabitat and microtopography
	'individuals':	List of plant individuals, including species name, age class, height, diameters and number of reproductive organs ('repro' new = fruits/flowers from 2007, 'repro old' = older fruits)
	'species':	List of species, including complete species name, family name, growth form and local endemism
	'waypoints':	GPS-coordinates of the plots (4 per plot)
germination_haarmeyer.mdb	Raw data of the germination experiment consisting of following tables:	
	'seedlings':	List of seedlings with species name, plot number and animal type
	'subsamples':	List of subsamples including respective plot number, mass of dung sample, date of germination count and number of germinated seedlings
	'species':	List of species, including complete species and family name
haarmeyer_2009.pdf	Electronic version of 'Effects of livestock on the vegetation of the Knersvlakte'	

Appendix 7: The ten most abundant species on quartz and non-quartz plots.



Appendix 8: Family abundances (for abundances > 10 individuals) on quartz and non-quartz plots.



Appendix 9: The three most abundant species of the different vegetation units and their percentage contribution to the total abundance of plant individual for the respective unit; growth forms after RAUNKIAER (1934): C=chamaephyte, T=therophyte; * endemic species.

Habitat	Grazing intensity	Species	Family	Growth form	Number of individuals	Percentage of total	Total number of Individuals per unit
Non-quartz	no	*Foveolina dichotoma*	Asteraceae	T	1396	41%	
		Didelta carnosa var. carnosa	Asteraceae	C	153	5%	
		Osteospermum pinnatum	Asteraceae	T	126	4%	
		Sum			**1675**	**49%**	**3400**
Non-quartz	moderate	*Foveolina dichotoma*	Asteraceae	T	258	19%	
		Rhynchopsidium pumilum	Asteraceae	T	104	8%	
		*Drosanthemum schoenlandianum**	Aizoaceae	C	88	6%	
		Sum			**450**	**33%**	**1368**
Non-quartz	high	*Rhynchopsidium pumilum*	Asteraceae	T	655	21%	
		Foveolina dichotoma	Asteraceae	T	542	17%	
		Helichrysum spec. 2 ('succulent')	Asteraceae	T	396	13%	
		Sum			**1593**	**51%**	**3151**
Quartz	no	*Argyroderma delaetii**	Aizoaceae	C	660	26%	
		Mesembryanthemum longistylum	Aizoaceae	T	262	10%	
		Foveolina dichotoma	Asteraceae	T	228	9%	
		Sum			**1150**	**46%**	**2515**
Quartz	moderate	*Cephalophyllum spissum**	Aizoaceae	C	228	22%	
		*Antimima watermeyeri**	Aizoaceae	C	82	8%	
		*Cephalophyllum parvibracteatum**	Aizoaceae	C	75	7%	
		Sum			**385**	**36%**	**1059**
Quartz	high	*Foveolina dichotoma*	Asteraceae	T	359	25%	
		*Drosanthemum diversifolium**	Aizoaceae	C	196	13%	
		Oncosiphon suffruticosum	Asteraceae	T	82	6%	
		Sum			**637**	**44%**	**1457**

Appendix 10: Number of species and abundances (seedlings excluded) of growth forms after RAUNKIAER (1934).

Growth form	Number of species			Number of individuals		
	Quartz	Non-quartz	Total	Quartz	Non-quartz	Total
Chamaephytes	83	57	98	3325	1710	5035
Therophytes	29	38	42	1515	5679	7194
Geophytes	15	19	21	135	428	563
Hemicryptophytes	3	2	5	23	12	35
Phanerophytes <1 m	4	3	4	6	77	83
unknown	4	4	5	27	13	40
Σ	138	123	175	5031	7919	12950

Appendix 11: List of taxa that emerged from domestic and wild animal dung; blue indicates species that exclusively emerged from domestic and orange those exclusively emerging from wild animal dung; *not found in standing vegetation of the plots (compare Appendix 4).

Species	Domestic	Wild
Aizoaceae: Mesembs		
**Antimima dualis* (N.E.Br) N.E.Br	1	
Antimima spec.	4	
Antimima watermeyeri (L.Bolus) H.E.K. Hartmann	4	
Aridaria serotina L.Bolus	5	
Caulipsolon rapaceum (Jacq.) Klak	11	
Cephalophyllum framesii L.Bolus	6	
Drosanthemum ramosissimum (Haw.) Schwantes	1	
Drosanthemum deciduum H.E.K. Hartmann & Bruckmann	4	
Drosanthemum diversifolium L. Bolus	2	
Drosanthemum globosum L. Bolus	9	
Drosanthemum spec. 1 ('glossy')	14	
Drosanthemum schoenlandianum (Schltr.) L. Bolus	137	
Drosanthemum spec.	7	
Malephora purpureo-crocea (Haw.) Schwantes	38	
Mesemb spec.	365	5
Mesembryanthemum nodiflorum L.	1	
Phyllobolus nitidus (Haw.) Gerbaulet	2	
Psilocaulon spec.	1	
Ruschia spec.	17	
Aizoaceae: Non-Mesembs		
**Galenia africana* L.	1	
**Galenia fruticosa* (L.f.) Sond.	19	
Galenia spec.	2	
Tetragonia fruticosa L.	3	
Tetragonia microptera Fenzl	11	17
Tetragonia spec.	2	
Asteraceae		
Amellus microglossus DC.	5	
Asteraceae spec.	1	
Asteraceae spec. 1 ('succulent')	1	
Foveolina dichotoma (Thell.) Källersjö	10	3
Oncosiphon suffroticosum (L.) Källersjö	3	1
Osteospermum pinnatum (Thunb.) Norl.	1	
Rhynchopsidium pumilum (L.f.) DC.	1	
Senecio spec. 1 (annua)l		2
Tripteris spec. (annual)		2
Brassicaceae		
**Lepidium desertorum* Eckl. & Zeyh.	12	
Caryophyllaceae		
Caryophyllaceae spec.	3	
Spergularia media (L.) C. Presl. ex Griseb.	1	
Chenopodiaceae		
Atriplex lindley subsp. *inflata* (F.Muell.) Paul G. Wilson	1	
Atriplex semibaccata var. *typica* Aellen	13	
Atriplex spec.	1	
Chenopodium album L.	15	21
Chenopodium spec.	48	19
Salsola spec.	1	
Fabaceae		
**Acacia* spec.		1
Fabaceae spec.	9	20
**Prosopis* spec.		2
Poaceae		
**Fingerhuthia africana* Lehm.	1	
Poaceae spec.	14	
Scrophyllariaceae		
Scrophyllariaceae spec.	1	
Solanaceae		
**Lycium* spec.	3	2
'Geophytes'		
Geophyte spec.	2	
'Non-Mesembs'		
Annual spec.	3	1
Dicotyle spec.	134	28
'Succulents'		
Succulent spec.	2	
Total number of seedlings	**953**	**124**
Mass of dung [kg]	**1.281**	**0.191**
Seedlings per kg dung	**744**	**649**

Erklärung

Ich versichere, die vorliegende Arbeit selbständig verfasst und mich keiner anderen als der angegebenen Quellen und Hilfsmittel bedient zu haben. Mit einer Veröffentlichung dieser Arbeit bin ich einverstanden.

Hamburg, den 18. Februar 2009 .....

(Daniela H. Haarmeyer)