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Cover photograph: Giraffes on the game farm Omatako Ranch (Observatory S04 Toggekry) in the Namibian Thornbush Savanna.
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# Plant functional traits and types as a tool to analyse landuse impacts on vegetation

Dirk Wesuls*, Marianne Strohbach, Anne Horn, Martijn Kos, Julia Zimmermann, John Hoffmann, Conrad Geldenhuys, Niels Dreber, Lizande Kellerman, Gretel van Rooyen & Peter Poschlod

**Summary:** Landuse, such as livestock grazing, has a major impact on the vegetation of semi-arid and arid ecosystems in southern Africa. Plant functional types and traits have proven to be useful tools in helping to understand the complexity of vegetation responses to landuse change, and to predict the impacts of landuse on the vegetation. Plant functional approaches were applied and tested in various studies of vegetation change along landuse intensity- and environmental gradients within the BIOTA project.

In the Thornbush Savanna of Namibia, a monitoring tool based on plant functional types and Landscape Function Analysis (LFA) was developed in order to characterise the state of the rangelands. In a trait based study in central Namibia, the influence of different major habitat types was found to be important for patterns of plant trait responses along grazing gradients. In studies of trait composition under different landuse intensities in the southern Kalahari, fleshy-fruited species were found to have decreased while poisonous and spiny species increased with increasing landuse intensity. Furthermore, it was observed that range condition influences plant life form composition. In the same study region, it was found that intensive sheep farming leads to an increase of animal dispersed plant species. A study of the seed bank composition in Nama Karoo rangelands of southern Namibia revealed varying patterns of seed distribution depending on seed size and microtopographical soil surface parameters. In the Succulent Karoo of South Africa, it was found that the recovery of vegetation on abandoned agricultural fields depends on landuse management practise, as indicated by the composition of plant growth forms and life history traits.

The results of all these studies contribute towards improved monitoring and management of semi-arid and arid rangelands. Further studies of plant functional types and traits could provide valuable information with regards to the restoration of degraded rangelands.

## Introduction

Landuse by humans has a major impact on the biodiversity and functioning of ecosystems worldwide. In southern Africa the main landuse is grazing by either domestic livestock or wildlife. Grazing by large wild herbivores was common before humans became sedentary, but since then grazing has been dominated by domestic livestock with grazing intensity and behaviour being completely different to that of wildlife. Today, overgrazing is one of the greatest threats to the semi-arid and arid ecosystems of southern Africa, i.e. the Karoo and Savanna ecosystems. Vegetation patterns caused by grazing have been described in many papers, summarised for the Karoo by Haarmeyer et al. (2010) and the Savanna by Skarpe (1991) and Scholes & Archer (1997). Consequences of these impacts have now focused attention on the need to understand, model, and predict the interactions between the changed environment and plant species not only due to landuse change but also climate change. Plant functional types (PFT) and/or specific functional traits (FT) are recognised as practical constructs to simplify community complexity to understand the mechanisms behind vegetation dynamics and to improve interpretation and modelling (PFT: Shugart 1997, Diaz et al. 1998, McIntyre & Lavorel 2001, Moog et al. 2005; FT: Kahmen 2004, Poschlod et al. 2005, Diaz et al. 2007, Kahmen & Poschlod 2008).

Therefore, this approach was the basis of different studies conducted by BIOTA on changes in vegetation and biodiversity along landuse intensity- and environmental gradients. Vegetation changes were analysed in both directions i.e. degradation and recovery. For the degradation processes the effects of landuse (emphasis on grazing practices and cropping) and climate change were investigated. For the recovery processes the pathways, states and possible endpoints in the natural recovery process after human-induced disturbances were investigated. The focus in both cases was on quantifying trait responses and their effects on ecosystem function and population dynamics. Traits were selected according to their relation to landuse/grazing intensity (see Table 1).

In the following paragraphs, BIOTA results regarding plant functional approaches as a tool to analyse different landuse impacts will be presented and briefly discussed.

## User-friendly rangeland monitoring with plant functional types in central Namibia

The most prominent indicators of desertification in Namibia are considered to be (a) soil erosion, (b) loss of the tree layer,

Table 1: Association of plant functional traits with plant responses to natural and anthropogenic disturbance processes (according to Cornelissen et al. 2003)

| | Natural disturbance processes | | Anthropogenous disturbance processes (land use types or practices) | | | |
|---|---|---|---|---|---|---|
| | Drought | Fire | Grazing/ browsing | Arable field use | Fertilization/ nutrient deposition | Wood cutting |
| **Whole plant traits** | | | | | | |
| Growth form | ● | ● | ● | ● | ● | ● |
| Life form | ● | ● | ● | ● | ● | ● |
| Plant height | ● | ● | ● | ● | ● | ● |
| Clonality | ● | ● | ● | ● | ● | ● |
| Spinescence | | | ● | | | ● |
| Palatability | | | ● | | ● | |
| Flammability | | ● | | | | ● |
| **Leaf traits** | | | | | | |
| Specific leaf area | ● | | ● | ● | ● | |
| Leaf size | ● | | ● | | ● | |
| Leaf dry matter content | ● | ● | ● | | ● | |
| Leaf N and P concentration | | | ● | | ● | |
| Physical strength of leaves | ● | ● | ● | | ● | |
| Leaf lifespan | ● | ● | ● | | ● | |
| Leaf phenology | ● | | ● | | ● | |
| Photosynthetic pathway | ● | | | | | |
| **Stem and belowground traits** | | | | | | |
| Stem specific density | | ● | | | ● | ● |
| Specific root length | ● | | | | ● | |
| Distribution of rooting depth | ● | | | | ● | |
| 95% rooting depth | ● | | | | ● | |
| Nutrient uptake strategy | | | | | ● | |
| **Regenerative traits** | | | | | | |
| Dispersal mode | | | ● | ● | | |
| Dispersule shape and size | | | ● | ● | | |
| Seed mass | ● | ● | ● | ● | ● | |
| Resprouting capacity | | ● | ● | ● | | |

(c) a decrease or loss of preferred grass species and shrubs, (d) bush encroachment, and (e) decreased soil fertility (de Klerk 2004). Changes of these indicators happen slowly and are thus not easily recognised over short periods of time (under 5 years). Such changes can be detected with regular monitoring practices. However, monitoring takes up time and resources and is itself not an income-generating activity, but it is an essential early-warning tool that can be used by land managers to improve their rangeland management practices. Effective monitoring tools thus need to be cost-effective or simple enough to be applied by landusers themselves, they need to address the major components and driving factors within an ecosystem, and they need to be scientifically reliable. In Namibia, where livestock production on rangelands forms a major part of the country's economy, there is a great need for such a monitoring methodology to ensure the long-term sustainable use of rangelands.

Patterns within a landscape are the result of a variety of processes that redistribute and cycle vital resources over space and time. Even at a small scale, patterns have a functional role. Highly functional landscapes are able to retain most resources within the landscape. Increased leaking of resources indicates the increasing dysfunction of a landscape.

The Landscape Function Analysis (LFA) technique (Tongway & Hindley 2000) is a rapid monitoring procedure, using field-assessed indicators to determine the functionality of landscapes at the hill slope or patch-inter-patch scale. LFA concentrates on the nature of patch- and inter-patch zones, characterising these according to various soil variables and soil-vegetation relationships that influence small-scale surface hydrology. The "traditional" LFA concentrates on soil surface properties and vegetation cover. The method was expanded to record the vegetation according to easily recognisable plant functional types to enable the landuser to monitor a change in vegetation composition as well, concentrating especially on the different types of perennial grasses. LFA surveys are conducted towards the end of the dormant
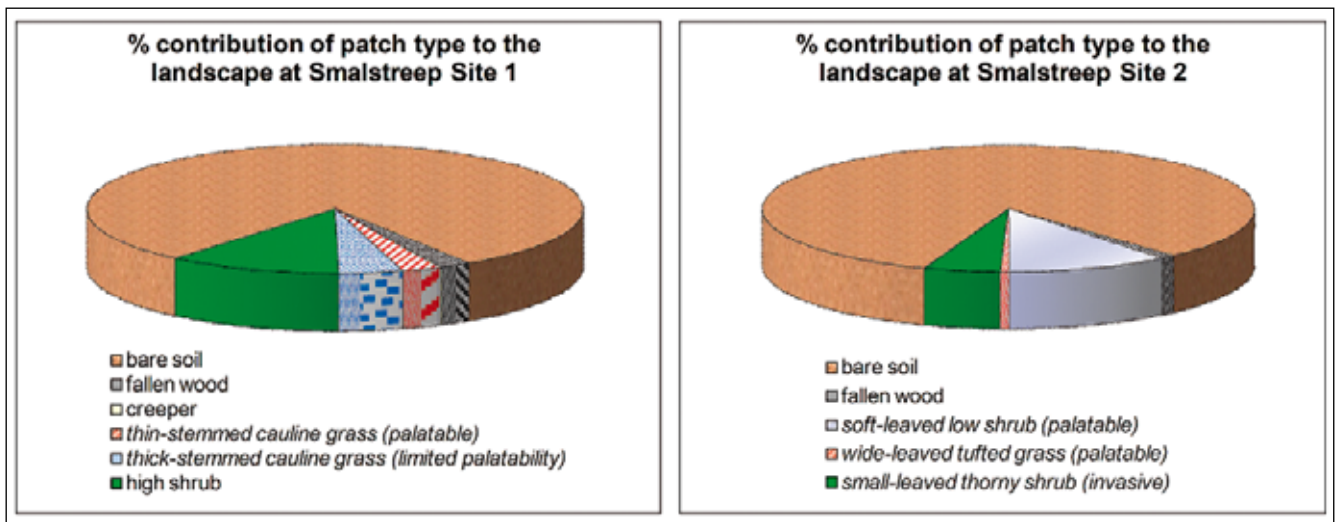
Fig. 1: Schematic representation of landscape composition in terms of the proportions of different patches—in this case, either bare soil or type of vegetation cover at Smalstreep. The high amount of bare ground and low cover of perennial palatable grasses should be of concern to rangeland managers. The corresponding indices for Site 1 and Site 2 are: Stability: 47.4 and 45.7 (78), Infiltration 24.2 and 21.3 (45), Nutrient Value 15.9 and 15.6 (33) respectively. The values in parentheses indicate what is regarded as optimal values for grasslands. Optimal values for Namibian savannas still need to be determined, but are assumed to be higher than the index values that were obtained.

season (July/August), when perennial herb cover is at its most vulnerable to overgrazing, and soils most vulnerable to erosion after rainfall impact of the first thunderstorms of the rainy season. Only when done at the time of peak landscape vulnerability, will LFA results truly show the stability of a landscape.

Collected data are entered into a spreadsheet to calculate indices for stability, infiltration and nutrient state, derived from the nature and state of the various patches encountered. Repeat measures at the same site over time show trends of either rangeland degradation or improvement. This technique was tested on the farm Smalstreep in the Etjo Erosion plains, Namibia, where the field condition was perceived to be moderate, and the results (Fig. 1) showed just how vulnerable the field actually was to erosion, judging by the low cover of stable perennial vegetation during the dormant season.

LFA is designed to derive relatively standardised indices, regardless of climate or specific vegetation type. Indices vary naturally across broad types of vegetation, e.g. savannas vs. grasslands. From the indices obtained for Smalstreep, the importance of soil surface cover for improving soil stability, water infiltration rates and nutrient accumulation became clear. However, compared to optimal grassland, the overall index values for the

sample sites appeared relatively low. The values obtained thus need to be put into context. Data need to be collected from reference or benchmark sites to be able to determine the following:
• What do the index values mean?
• What, in a specific Namibian vegetation type, is a good index value, what is "good enough" (or not degraded)?
Such data are not available for all rangelands in Namibia, thus most data will have to be collected, compiled and analysed over time. However, even without an index-reference system, the expanded LFA technique described above can, if done annually, provide a good indication of the effects of rangeland management practices. As many farmers are not always familiar with exact species names and species cannot always be identified properly during the dormant season (when the LFA is supposed to be conducted), the use of easily recognisable PFT's proves to be a suitable way of describing the vegetation, and provides the land manager with an instant overview of the composition of the veld.

## Plant trait responses to livestock grazing in central Namibia

The area around the district town of Rehoboth in central Namibia is character-

ised by commercial livestock farming with cattle, sheep and goats on privately owned farmland. Most of the farms are relatively small in size (i.e. less than 3,000 ha, Lang 2005) compared to the average size of private Namibian farms (about 4,000–5,000 ha). Overstocking of these semi-arid rangelands, which have a very low carrying capacity is a widespread problem and has often led to degradation. In order to establish indicators of overgrazing based on plant functional types, quantitative and categorical whole plant, leaf and regenerative traits were recorded along grazing gradients (so called "piosphere transects") on several farms in the Rehoboth area. The farms or farm camps differed in size, grazing management and dominant habitat parameters. With the aim of finding consistent grazing response traits, a partial direct analytical approach was used in order to remove the effect of differences in habitats, farm management and sampling in different years.

The effect of sampling in different years (2007 low rainfall and 2008 high rainfall) and in different major habitat types on plant trait composition was stronger than the effect of grazing. With the help of the partial analysis, confounding environmental effects besides grazing could be removed. The most important environmental parameters in the partial analysis were distance from water point,

cover of dung, soil pH and electrical conductivity, which are all indicators of grazing pressure (Rietkerk et al. 2000, Smet & Ward 2006). Traits with a negative grazing response, i.e. traits that decrease with increasing grazing pressure, were perennial life cycle, leaf ratio (leaf length/width), rhizomatous habit, leafy stem, entire leaf blade, anemochorous dispersal, and belowground clonality. Traits with a positive grazing response, i.e. traits that increase with increasing grazing pressure, were specific leaf area (SLA), annual life cycle, herbaceous forb growth form, prostrate-creeping habit, compound leaves, no clonality, and endo- or exozoochorous dispersal (see also Fig. 2).

One important outcome of this analysis was that some traits, which are described in the literature as responsive to grazing may also vary with environmental factors that are related to different habitat conditions. Some examples of these environmental factors are soil depth, the percentage of coarse material in the soil (skeleton content), slope, and the surface cover of gravel and stones. Some examples of important traits that are related to changes in habitat conditions are above cover density (ACD, i.e. the percentage cover of the plant canopy above a vertically projected contour of the plant), plant height and growth form. It is therefore important to consider the habitat diversity of the rangeland when using plant functional traits as indicators. Leaf ratio, SLA, life cycle, leaf blade fragmentation, dispersal mode and clonality (Fig. 2) were traits found to be responsive to grazing across habitats and different sampling years on a regional level. These results are consistent with the findings of other trait based approaches (Cingolani et al. 2005, Diaz et al. 2007, Golodets et al. 2009) and these traits can thus serve as potential indicators of rangeland condition.

## Response of vegetation patterns and plant traits to livestock grazing in the Kalahari

Vegetation pattern in the Kalahari is strongly affected by the mosaic of single trees and the matrix in-between. Subcan-opy species composition differs markedly from the matrix species composition. Mechanisms causing this pattern, as well as how this pattern is affected by different landuse intensities were studied in the Nossob river valley north of Upington. Three sites were selected: a reference site (site one) with no management since at least 1974 in South Africa; a farm (site two) with a low-intensity grazing regime by wildlife (ostriches and antelope, mostly springbok) in South Africa; and communal land (site three) heavily grazed by goats, sheep and cattle in Botswana. Studies on the vegetation patterns were performed from 2001 to 2003, and a comparative study on the effect of different landuse intensities was conducted in 2001.

Subcanopy habitats strongly supported the occurrence of many fleshy-fruited shrubs or herbs, grasses and specific annual species. The matrix was characterised by herbs, grasses and other annual species. Contrary to existing hypotheses, shading, narrower temperature fluctuations and dispersal, but not higher nutrient contents in the soil, were correlated with the specific subcanopy flora (Hoffmann 2001, Kos 2007). Plant trait responses in the subcanopy were a slower germination and root growth rate in annuals (Fig. 3; Kos & Poschlod 2010), a higher germination rate with narrower temperature fluctuations (Kos & Poschlod 2007), and a high endo-zoochorous dispersal potential revealed by faeces caught in seed traps (Kos 2007).
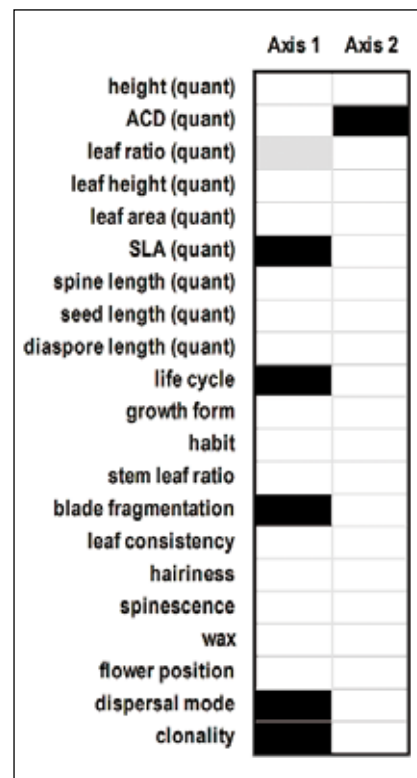


Fig. 2: Results of the fourth corner statistic with regard to quantitative (quant) and whole categorical traits (all other traits) and the first two axes of the partial RLQ analysis. The first axis represents a grazing gradient where high values indicate high grazing pressure and low values indicate low grazing pressure. The second axis represents differences in habitat conditions and farm management. Black boxes indicate a positive, and grey boxes a negative significant relationship between traits and axes. ACD = above cover density, SLA = specific leaf area.
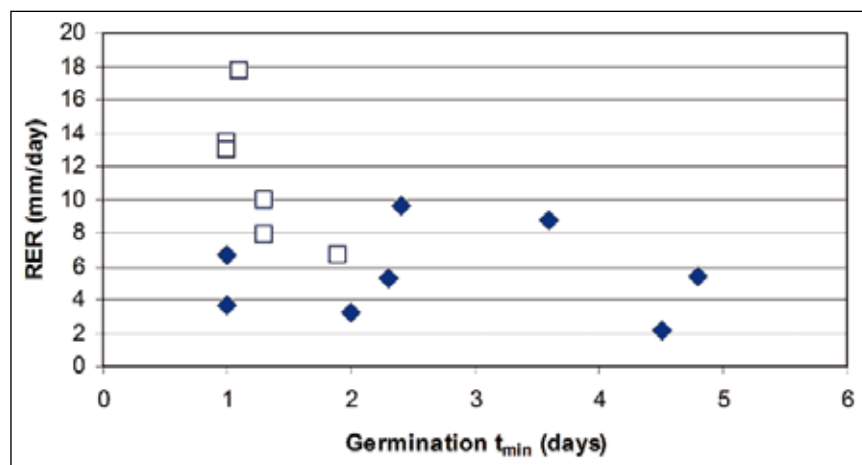


Fig. 3: Germination speed (tmin = time of germination commencement) and root elongation rate (RER) in annuals of the subcanopy (closed rhombs) and the matrix (open quadrats) in the Kalahari duneveld (according to Kos & Poschlod 2010).
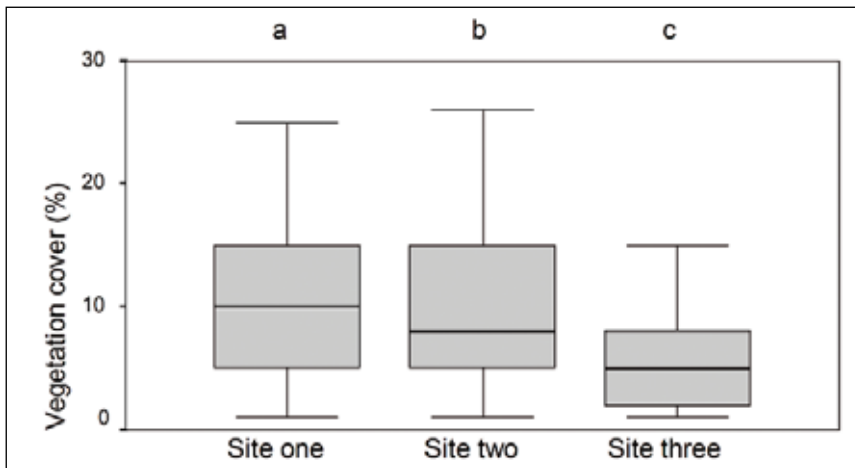
Fig. 4: Vegetation cover on a site with no management (site one), a site with low-intensity grazing (site two), and a site with high intensity grazing (site three). Sites were sampled using 280 plots in each. Significant differences between sites are indicated by letters (a, b, c).
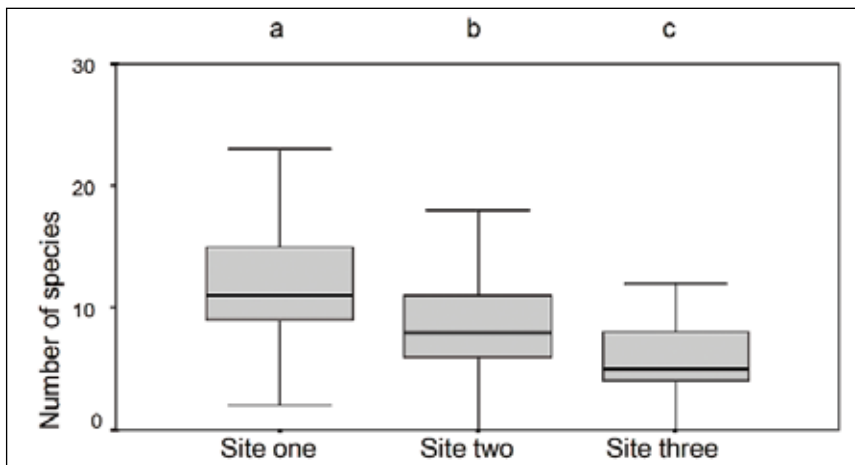


Fig. 5: Number of species on a site with no management (site one), a site with low-intensity grazing (site two), and a site with high intensity grazing (site three). Sites were sampled using 280 plots in each. Significant differences between sites are indicated by letters (a, b, c).
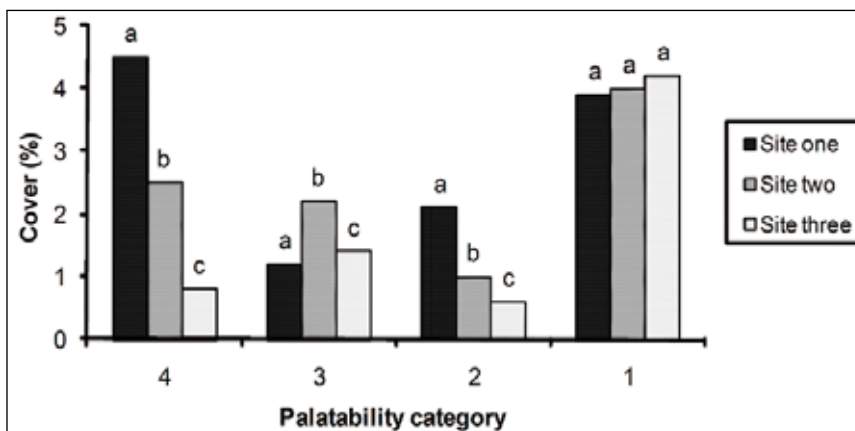


Fig. 6: The median cover values of vegetation palatability classes (4 = very good to good; 3 = medium; 2 = poor; 1 = poisonous or not grazed) on a site with no management (site one), a site with low-intensity grazing (site two), and a site with high intensity grazing (site three) (N = 280, per palatability class and per site). The letters (a, b, c) indicate significant differences in the cover for a particular palatability class between the three sites ($p \leq 0,01$; N = 560; for all significant differences).

Whereas vegetation cover and species richness was high in the subcanopy habitats of the reference site and the low-intensity grazing site, the opposite was found at the high-intensity grazing site. Vegetation cover and species richness strongly decreased along the landuse intensity gradient (see Figs. 4 & 5) as well as the cover and number of fleshy-fruited and highly palatable species (see Fig. 6). In contrast, poisonous and spiny species increased with increasing land-use intensity. The proportion of alien species was significantly higher on the communal land where grazing pressure was highest.

This shift in the proportions of functional traits is clearly related to a grazing intensity gradient. Since landusers may not possess detailed species knowledge or may not be able to measure their functional traits, easily recognisable traits may allow a clear assessment of the impacts of a certain landuse type or intensity. Cover and occurrence of fleshy-fruited species, and the presence or absence of aliens have been shown to be strongly correlated to landuse type and intensity. These species are easy to recognise and may therefore serve as suitable indicators to define suitable management interventions.

## Effect of grazing intensity on the dispersal potential of plant species in the Kalahari

Heavy grazing is known to affect the functional composition of savanna vegetation, leading to an increase of annual and small woody species, and leaving only bare ground in extreme cases (e.g. Walker et al. 1981, Skarpe 1990, Jeltsch et al. 1997). Whereas these effects are well known, the impacts on functional trait spectra have received little scientific attention. To determine the impact of landuse on plant dispersal, seeds of 57 of the most common species in the Southern Kalahari Duneveld were collected and subjected to standardised dispersal potential measuring experiments (Horn 2008, modified after Knevel et al. 2005). In the next step, dispersal potential was combined with plant cover values in 10 m
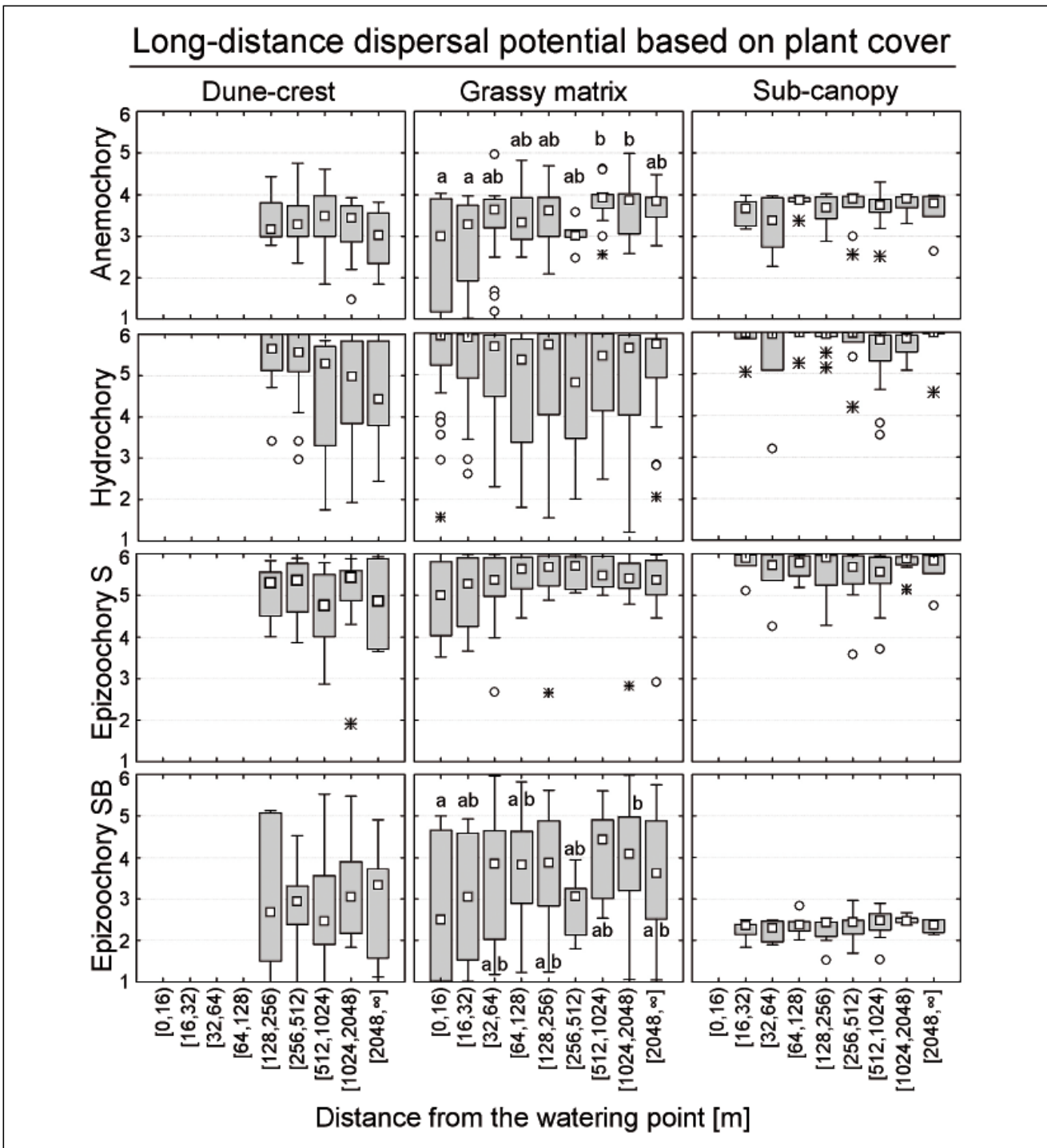
Fig. 7: Long distance dispersal potential (1 = very low to 6 = very high) of duneveld vegetation based on plant cover values in different habitats. Epizoochory S: Dispersal in sheep fur; Epizoochory SB: Dispersal in springbok fur. Significant differences are indicated by letters (Kruskal-Wallis test) (box = 25–75 % with median, brackets = non outlier max and min, o = outliers, * = extreme values).

x10 m plots placed at increasing distances from a watering point, up to a distance of over 2 km in ca. 350 ha sheep camps, to search for trends in dispersal strategies. Three habitat types were analyzed, namely the grassy matrix, the subcanopy habitat and the dune crests.

The three habitats exhibited different sensitivity to grazing and only the grassy matrix vegetation showed significant trends (Horn et al. 2008, Fig. 7). In agreement with other studies described in this article, the results showed that plant species with high wind dispersal potentials had higher cover values in areas with lower landuse intensity, i.e. greater distances from the watering point in this case. Furthermore, wind dispersal potentials were generally low as many species possessed large seeds. Plants with high dispersal potential in either sheep wool or springbok fur showed a similar pattern, which is believed to be due to a putative correlation of traits enabling either wind dispersal or external zoochory (i.e. dispersal by the seed attaching to an animal). In contrast, hydrochory potential

did not respond to landuse pressures and is likely to be of little relevance, since flowing surface water only occurs a few times every century. Seventeen of the 57 species exhibited germination percentages of over 10% after artificial chewing and digestion and most of these species could be successfully dispersed endozoochorously (Horn 2008). These species showed a slight decrease in cover with increasing distance from the watering point, but since only up to 40% of the total cover values were represented by those 17 species, this trend might be an artefact of the small dataset and is therefore not included in Fig. 7.

It is concluded that sheep farming does have an effect on the distribution of dispersal traits in the landscape and could lead to an increase of animal-dispersed species in heavily used areas. As seedbanks of perennial grasses are often depleted in degraded areas (O'Connor & Pickett 1992) and most grasses showed only low to moderate wind dispersal potential, re-seeding or introduction of soil from intact areas need to be considered as options for restoration in these environments. Although dispersal potential in sheep wool was generally high, the proportion of seeds transported in sheep wool that would actually fall off and are thus able to germinate and establish needs to be studied in further detail before sheep can be considered as effective dispersal vectors for externally dispersed seeds.

The facilitation of spread of animal-dispersed species could be a serious problem in heavily grazed areas, such as in the case of the internally dispersed shrub *Grewia flava* (Tews et al. 2004), but a more important issue is probably the long-term sensitivity of the palatable perennial grasses to heavy grazing, because of depleted seedbanks and low abiotic dispersal potentials. Because of this, successful restoration is likely to be a laborious and costly process that needs to be studied further to identify the most effective strategies. It is important to remind landusers that an abundance of forage can be deceptive, and forage is virtually irreplaceable if used unsustainably.

# Functional analysis of vegetation response to landuse intensity in the Kalahari

Environmental factors act as filters that select for those plant traits that promote species establishment, persistence and reproduction (Woodward & Diament 1991, Diaz et al. 1998). Landuse is an important filter that determines plant species assemblages and their associated plant traits in an area. The southwestern Kalahari is characterised by duneveld with relatively homogenous soils of aeolian origin, and is ideally suited for comparative analyses of the influence of landuse practices on vegetation structure and plant functional attributes. The influence of historic grazing intensity was investigated by comparing plant life forms, species richness and the Shannon-Wiener index of diversity and selected plant trait attribute scores across a range condition gradient. Range condition was determined for ten commercial livestock farms and one communal farm using line transect surveys in the dune street, dune slope and dune crest habitats of each farm. A selection of 112 dominant plant species was investigated for 46 vegetative and reproductive plant traits.

Principal coordinate analyses of plants species revealed that prominent growth forms constituting trees, shrubs, perennial, and annual grasses, as well as perennial and annual herbs could be further subdivided into various plant trait group permutations. Major life forms were linked with range condition over the study gradient. In the dune street habitat, perennial grass cover decreased and annual grass cover and shrub cover increased with decreasing range condition (Fig. 8a). In the dune crest habitat, perennial grass cover decreased and bare surface area increased with decreasing range condition (Fig. 8b). Plant species richness was positively correlated with increasing range condition in the dune street and dune crest habitats, and the Shannon-Wiener index was positively correlated with increasing range condition in the dune street and dune slope habitats.

Bush encroachment as an indicator of range condition deterioration due to sus-tained intensive grazing (Kalikawe 1990, Skarpe 1990, Skarpe et al. 2007) was supported by this study. In addition to increases in shrub cover by species such as black thorn (*Acacia mellifera*) and driedoring (*Rhigozum trichotomum*), other indicators of range condition can also be employed. Bare surface area in the dune crest habitat and annual grass cover (predominantly Kalahari sour grass *Schmidtia kalahariensis*) in the dune street habitat are also good indicators. Improved management of land should lead to greater species diversity and species richness, although higher species numbers may be encountered during the transition phase from good to poor range condition due to the simultaneous presence of late successional and pioneer species.

# Interaction between diaspore size, microsites and livestock pressure in the Nama Karoo

It is well known that seed traits interact with microsite characteristics, which determine where a ground-drifting seed comes to rest (Chambers 2000). This interaction contributes to the spatial variation in seed abundance and specific seed distribution patterns at both community- and population levels. In a rangeland context, the degree of disturbance by grazing (i.e. the condition of the biophysical environment) selects for diaspore attributes that are linked to successful incorporation into the soil seed bank (Navie & Rogers 1997). This issue was investigated at the adjacent BIOTA Observatories Gellap Ost (S10) and Nabaos (S11) using data on seed densities in different microsites and diaspore mass as a proxy of seed size (N. Dreber, University of Hamburg, submitted).

In arid south-central Namibia, rangeland productivity is low due to a mean annual rainfall of 150 mm, high spatio-temporal variability of this rainfall, and frequent droughts. The vegetation is therefore sensitive to overgrazing and rangelands deteriorate easily. At the communal rangelands of Nabaos, situated near the town of Keetmanshoop in Namibia, long-term overstocking has con-

tributed to a transformation of formerly grassy shrublands into open shrublands with perennial grasses replaced by annual, grazing resistant species. This degradation is expected to have altered the seed bank composition, and thus species related traits. In this regard, the response of mean diaspore size of seed bank species to the grazing regime, and the role of the grazing regime in the spatial patterning of the soil seed bank was analysed.

Seed densities were assessed at Nabaos (hereafter referred to as DEG for 'degraded') using the seedling emergence method, and compared with seed densities from the adjacent non-degraded Gellap Ost as a reference (REF). Sampling took place in January 2007 and 2008 just before summer rains and the onset of germination events. In order to account for small-scale spatial heterogeneity, seed banks were sampled in distinct microsites: (1) under shrubs (termed 'CAN' for canopy), (2) small physical barriers in the inter-shrub matrix (termed 'OBS' for obstacle), and (3) bare ground ('BG'). OBS included grass tussocks, surface rocks, deadwood and soil depressions, which were all regarded to be able to trap ground-drifting seeds. In 2009, mature diaspores of the most common species previously found in the seed bank ($N = 35$) were collected in the standing vegetation, and the mean dry-mass (including appendages and enclosing structures, $N = 90–100$ diaspores species[-1]) used as a measure of diaspore size. Diaspores were classified into four size categories: tiny = < 0.3 mg, small = 0.3–0.9 mg, medium = 1–5 mg, and large = > 5 mg.

The mean diaspore size of seed bank species for both years combined did not differ significantly between REF (mean 2.0 mg) and DEG (mean 2.7 mg). However, abundances of diaspores according to size varied with grazing intensity (Fig. 9). Overall seed densities were significantly higher in the degraded rangeland, which was particularly pronounced in 2008. While small diaspores constituted a dominant fraction of the seed bank at both REF and DEG, high grazing pressure clearly favoured the abundance of species with tiny diaspores (the most dominant being *Trianthema parvifolia*), which were considerably
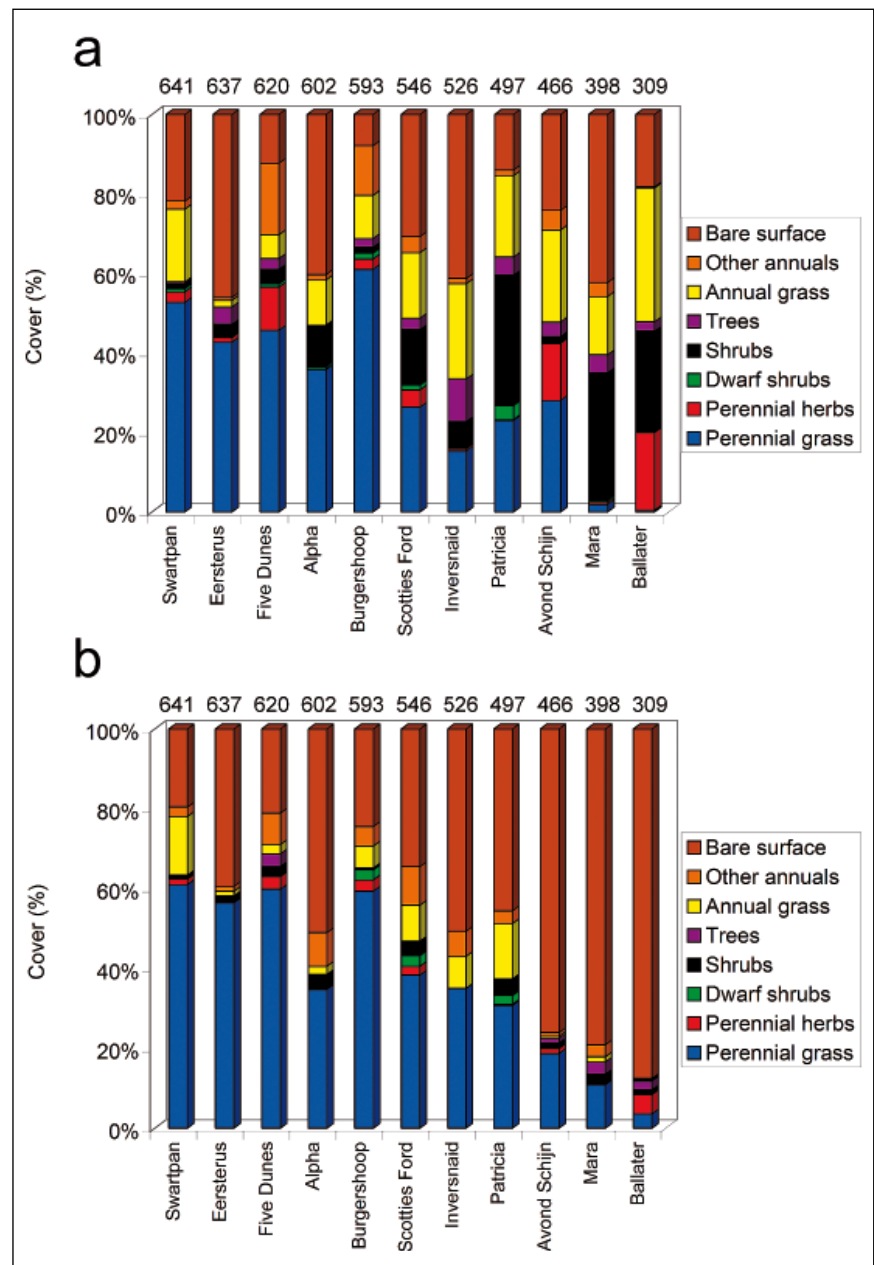


Fig. 8: The contributions of different life forms to vegetation cover (as percentage of total cumulative cover) across a previously identified range condition gradient in (a) the dune street habitat and (b) the dune slope habitat of the southwestern Kalahari. The farms are arranged from those representing good range condition on the left to those representing poor range condition on the right, with range condition scores (indicated as a score out of 1,000) on top of the bars.

less abundant in the seed bank of REF. In contrast, medium-sized diaspores were more common under low grazing pressure (the most dominant being *Dicoma capensis* and *Stipagrostis hochstetteriana*). Most large-sized diaspores were detected in samples collected on DEG (Fig. 9).

Diaspore size also interacted with microsite, but patterns varied with sampling year due to the availability of readily germinable seeds in the seed bank (Fig. 9).

There was an overall trend of decreasing seed densities in the order of CAN, OBS, BG, particularly in 2008. However, this pattern was less pronounced for tiny-sized and small-sized diaspores in the seed bank of DEG, where obstacles in the inter-shrub matrix trapped a similar amount of diaspores as shrubs. Large diaspores were clearly associated with CAN, which was obvious in 2008 when more readily germinable diaspores of this size were present in the seed bank. Most
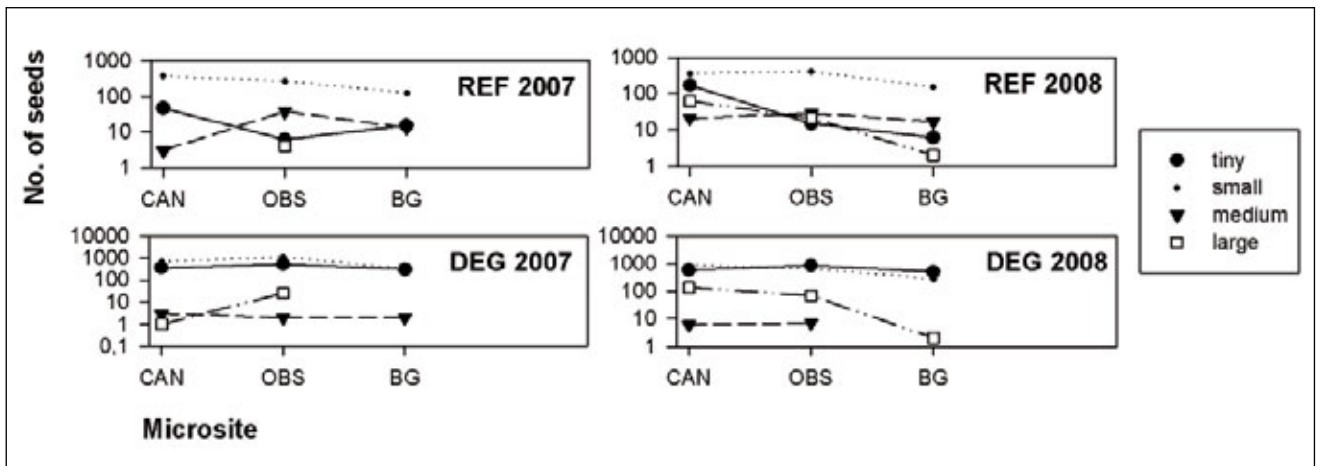
Fig. 9: Spatial distribution of diaspores by size among the sampled microsites according to their abundance in the germinable seed bank. REF = Gellap Ost (reference), DEG = Nabaos (degraded), CAN = canopy, OBS = obstacle, BG = bare ground.

diaspores of this size category belonged to the shrubs *Calicorema capitata*, *Phaeoptilum spinosum*, and *Rhigozum trichotomum*. Their high abundance under shrub canopies indicates either short distance dispersal and/or the harvesting activity of rodents, which have their burrows underneath shrubs. The seed bank in 2007 comprised less large diaspores, and those found belonged to the open-matrix forbs *Tephrosia dregeana* and *Tribulus terrestris*, with the former being very common in the standing vegetation of both REF and DEG. This is a possible reason why this size category was only abundant in OBS-microsites of the open-matrix. At REF, tiny diaspores (the most dominant being *Mollugo cerviana* and *Setaria verticillata*) were more common than expected by chance in CAN, as were medium-sized diaspores in OBS. Overall, bare ground was only able to retain mainly tiny or small diaspores, which might be due to its smooth and crusted soil surface. The high abundance of this seed size category on DEG and the fact that bare ground is more prominent at DEG (Petersen 2008) indicates a selection for species adapted to bare environments, under high grazing pressure.

The results show shifting patterns of diaspore distribution in response to spatial heterogeneity and grazing. Besides differences in the ability to trap and accumulate diaspores (e.g. large physical barriers such as shrubs are most effective in doing so), the type of microsite acts as a filter to some degree for certain

diaspores. Most obvious was a tradeoff between the number of diaspores and their size, which was characteristic for DEG. Smaller seeds are more likely to get incorporated into the soil seed bank, even when the soil surface is smooth. This interaction is important as it shows, for example, that for bare land restoration in arid Nama Karoo ecosystems, loosening crusted soil surfaces has to be considered in order to promote accumulation of a variety of different sized diaspores. However, detailed investigation is needed to provide clarification on the interactions between soil surface structures and morphological diaspore traits at the patch-scale.

## Plant functional types as indicators of landuse impacts in the Succulent Karoo

The Kamiesberg region has been the home of colonising farmers and indigenous herders for many centuries (Adamson 1938, Archer et al. 1989, Hoffman et al. 2007). However, unpalatable forage, a paucity of grasses and the lack of water limit livestock grazing and related agricultural practices not only on commercial farms, but also on the communal lands in this area. Most of the region is currently still utilised for extensive grazing by domestic livestock such as goats and sheep, resulting in overgrazing being a major environmental problem, which influences

people's daily livelihoods (Baker & Hoffman 2006, Anderson & Hoffman 2007). While stocking rates on privately owned or commercial farmland have generally adhered to those recommended by the government, adjacent communal areas in the region have been stocked at approximately twice this rate over a period of decades (Hahn et al. 2005). Destructive agricultural practices, specifically large-scale cultivation and small-scale crop farming, have resulted in severe disturbance of the natural vegetation leaving patches of degraded land struggling to recover via natural successional processes. Many fallow or abandoned agricultural fields in the region, which were ploughed for cropping in previous years, are now only grazed by livestock (Kellerman & van Rooyen 2009).

Plant functional types were used as a tool to analyse and/or describe the effect of overgrazing and rotational crop farming in order to assess landuse impacts on the vegetation of abandoned agricultural fields (old fields) on communal and commercial farmland. Plant functional traits, which were recorded, measured, and analysed for selected plant species dominating old fields of different ages included the following: (a) growth form, (b) plant height, (c) canopy diameter, (d) percentage plant cover, (e) leaf surface area, (f) fresh and dry leaf mass, (g) leaf length and width, (h) specific leaf area, (i) percentage leaf water content, (j) dispersal mode, (k) diaspore morphology, and (l) seed mass (Cornelissen et al. 2003).

In 2005 and 2006, 44 plots of 50 x 20 m were surveyed on selected old fields throughout the Kamiesberg region (Shmida 1984, Stohlgren et al. 1995). Fifteen of these plots were representative of communal farmland and 29 of privately owned land, all at varying altitudes. Within each plot, all plant species were recorded and the cover of each species was visually estimated. Each species was assigned to one of ten plant functional types based on growth form and life history, and included the following categories: (a) annuals/ephemerals, (b) annual grasses, (c) geophytes, (d) perennial forbs, (e) perennial grasses, (f) dwarf succulents, (g) dwarf succulent shrubs, (h) succulent shrubs, (i) dwarf woody shrub, and (j) woody shrub.

Preliminary findings indicated that the practice of sustained heavy grazing on communal farmland in the Kamiesberg region leads to a decrease in palatable perennial woody and succulent shrubs and a shift towards annuals and geophytes. The sustained heavy grazing retarded vegetation recovery on the old fields. Rotational grazing on commercial farms promoted the recovery of the disturbed vegetation and led to an increased occurrence of palatable woody and succulent shrubs on old fields of commercial farms, with a general reduction in cover of ephemeral plants and geophytes.

## Conclusions and identified research needs

A variety of plant functional approaches regarding the impact of different landuse regimes or landuse changes were applied in various regions and on different spatial scales within the BIOTA Southern Africa framework. Common features of all the different study areas were the semi-arid to arid climate and the pastoral landuse, either on communal or privately owned rangeland. Differences in plant functional trait patterns and plant functional type composition were studied along grazing gradients under different land tenure systems taking habitat and microsite variability into account.

One common goal of the trait based approaches within BIOTA was to iden-tify indicators of rangeland states in response to grazing history and present grazing intensity. In this context, the use of plant traits instead of species enables the identification of general patterns in vegetation response to livestock disturbance across taxonomic levels. Another reason for using traits as surrogates for species is that not all landusers are familiar with species names and proper species identification. The use of traits could thus facilitate regular monitoring activities for land managers—a crucial requirement in these variable semi-arid/arid environments, which are expected to face additional future problems caused by climate change. A simple, yet effective monitoring tool is the adapted Landscape Function Analysis (LFA, Tongway & Hindley 2000). This tool, coupled with the use of plant traits to indicate a pioneer or a late successional state of the vegetation, could be a promising way to support landusers in their management decisions. Detailed growth form features, which have been proven to decrease or increase with increasing grazing pressure (e.g. in the Namaqualand region of South Africa) can easily be incorporated into rangeland monitoring tools such as LFA. However, the task still remains to adapt monitoring tools based on plant functional types to the different biomes or to broad vegetation types. Furthermore, even at the landscape scale, major changes in habitats require indicator traits that respond consistently to grazing across different soil types or other environmental parameters related to these habitats. Traits that fulfilled this criterion in a study in central Namibia were specific leaf area (SLA), life cycle, leaf blade fragmentation, clonality and dispersal mode. Seed traits, such as the dispersal ability, are highly indicative of landuse changes and were found to be influenced by grazing in the southern Kalahari. Here, animal dispersed species were more likely to occur in areas that were heavily utilised by livestock. Furthermore, it was shown that the cover and occurrence of fleshy-fruited plant species was strongly correlated to landuse type and intensity. These species are easy to recognise and may therefore serve as suitable indicators to define suitable management strategies and grazing intensities. Other seed traits, such as diaspore size and morphology, interact with the physical environment during dispersal which, in combination with a certain grazing intensity, significantly influences the spatial distribution and composition of seed banks as shown in the Nama Karoo. The seed bank in turn is a crucial factor with respect to the restoration of degraded rangelands. Further studies of the distribution of dispersal traits and factors influencing the seed bank composition under different landuse intensities will help to make future restoration efforts more cost effective and successful.

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