The suitability of the degradation gradient method in arid Namibia

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Abstract

The Degradation Gradient Method (DGM) is a sophisticated technique for the assessment of range condition. It applies multivariate analyses of herbaceous species data to detect subtle degrees of overgrazing. The suitability of this multivariate method was tested in the central Highland Savanna of Namibia by comparing its results against a univariate analysis of herbaceous data in a simple but robust Range-Unit Model. Despite aridity and topographical heterogeneity, the DGM performed unexpectedly well under these conditions. The relative instability of this dry savanna system favoured the applicability of the DGM by promoting a clear grazing gradient. Using species density data only resulted in an incorrect outcome of the multivariate analysis. The sensitivity of the DGM could be improved by combining density and cover data.

Key words: aridity, cover and density data, grazing gradient, ordinations, species response curves, topographical heterogeneity

Résumé

La méthode du gradient en dégradation (DGM) s'avère une technique sophistiquée dans l'évaluation de la condition des habitats. Elle applique des analyses multivariées aux données sur les espèces herbacées afin de déceler même une mesure subtile de surpturage. L'appropriation de cette méthode multivariée fut expérimentée dans la savane des montagnes centrales de la Namibie à travers une comparaison des résultats avec une analyse univariée des données sur les espèces herbacées dans un modèle Habitat-Unité simple mais robuste. Malgré l'aridité et l'hétérogénéité topographique, le DGM a fonctionné étonnamment bien. L'instabilité relative de ce système de savane sèche a favorisé l'applicabilité du DGM à travers la promotion d'un gradient de pâturage distinct. L'utilisation des données sur la densité d'espèces n'a résulté que dans un aboutissement erroné des analyses multivariées. La sensibilité du DGM pourrait être améliorée en combinant les données de densité et couverture.

Introduction

Land degradation is an undesirable result of overgrazing in many regions of Sub-Saharan Africa. Degradation is characterized by a loss in plant cover and top soil, a decline of palatable climax grasses and an increase in less palatable, annual grass species (Cook, 1983; Dodd, 1994). In southern Africa, the Degradation Gradient Method (DGM) is currently the most objective and sensitive technique used for detecting and quantifying various stages of veld retrogression (Hurt & Bosch, 1991; Jordaan, Biel & du Plessis, 1997). It uses multivariate ordination techniques to reduce multidimensional data sets (sample plots with relative species frequency data) to two dimensions, where the first one explains the greatest variability in the data. Hence, the first dimension (axis 1) may visualize a dominating gradient in grazing-induced degradation.

The major statistical tool of the advanced DGM version (Bosch & Gauch, 1991; Bosch & Kellner, 1991) is Principal Component Analysis (PCA), an ordination technique based on a linear model. Although PCA is entirely satisfactory if the multidimensional data set is linear, it may give misleading results if the data set is nonlinear (Pielou, 1984). Therefore, the application of PCA is seriously weakened by its linear structure and should be limited only to sample sets of relatively high homogeneity (Orloci, 1973). Thus, PCA works only effectively and without distortion if an investigated grazing gradient (usually along increasing distances from a water point) is not much influenced by between-habitat or beta-diversity

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of a heterogeneous landscape (Whittaker & Gauch, 1973).

The DGM has been applied and tested quite extensively in the semiarid to subhumid 600–800 mm rainfall zone of southern African savannas (Bosch, 1989; Bosch & Gauch, 1991; Bosch & Kellner, 1991; Dörgeloh, 1999). However, no true test has been undertaken to examine its suitability for the more arid 300–400 mm rainfall zone of Namibia, especially under conditions of high topographical heterogeneity.

The hilly topography in central Namibia could complicate the establishment of a grazing gradient as hill crests, different slope positions or drainage channels may cause an increase in between-habitat diversity and thus decrease the effectiveness of PCA ordinations (Fynn & O'Connor, 2000). For example, in a study done in the South African Lowveld, Venter *et al.* (1989) found that differences in topography, rather than differences in land-use practice explained the greater variability in the data.

In addition, aridity may influence the applicability of the DGM in a negative manner. In many of the more arid regions, rainfall has a greater effect on grass composition than grazing (Sullivan, 1996; Ward *et al.*, 1998; Van Oudtshoorn, 1999). Bothma (1996), for example, states that in arid regions the terms 'increasers' and 'decreasers' are not applicable, because the relative abundance of grass species would not 'linearly' increase or decrease with grazing pressure but rather be masked by the influence of stochastic rainfall.

While the academic emphasis on much phytosociology and gradient analysis is understandable, equally, there must be a greater role for vegetation description and analysis using multivariate methods, within biological conservation and environmental management (Kent & Ballard, 1988). Generally the application of formal methods of ordination does not automatically ensure validity or objectivity. The truncated data commonly presented after ordination may well mask a high degree of subjectivity in the treatment of raw data, the choice of methods of ordination, or the interpretation of the results (Barnes *et al.*, 1984). Some studies (e.g. Du Plessis, Bredenkamp & Trollope, 1998) have applied the DGM, but only with a Detrended Correspondence Analysis (DCA), which is more appropriate to distinguish different habitat types than to distinguish grazing-induced, subtle changes in within-habitat or alpha diversity (Gauch, 1982; Pielou, 1984; Bosch & Gauch, 1991; Van Rooyen *et al.*, 1994).

This study aimed at testing the performance and potential of the full DGM method for arid Namibia. In order to do so, the multivariate DGM was compared against results of a simple univariate Range-Unit Model that is similar to the Benchmark method proposed by Foran, Tainton & Booysen (1978). In this robust and easily interpretable standard model, degradation indicators of each range unit (RU) were analysed as single entities and their increasing or decreasing proportions compared with a benchmark, which has been rested from grazing for many years (Wilson & Tupper, 1982). Differing degradation stages were obtained by selecting RUs with different distances to a watering point. The primary aim of this study is not to show that this selection of RUs represents an optimal degradation transect in the landscape, but to show how well the DGM discriminates between the differing degradation stages of the RUs. Quantification of the different degrees of degradation was made with the overall objective univariate Range-Unit Model and thereafter, the outcome of the multivariate DGM was compared with this standard model.

Materials and methods

Study area

The research was conducted in the Highland Savanna of central Namibia, within the Daan Viljoen Game Park and along the western park fence on farmland (Fig. 1). Undulating hills and mountains with numerous drainage channels range in altitude from around 1600–1800 m. The underlying geology is that of the Kuiseb Formation of the Damarasystem (Kellner, 1986), consisting of erodible mica schist and hard, unweathered quartz variations. Soils are shallow metamorphic lithosols, too stony for cultivation. Most of the rain falls between January and April with a mean of 350 mm per annum, supporting a predominating *Acacia hereroensis* Engl. – *Eragrostis nindensis* Ficalho & Hiern alliance (Kellner, 1986).

Data collection

A grazing gradient was established in April 1999 by sampling five RUs with partly known grazing history at different distances to a watering place. Although some of these RUs were relatively close to a fence (*c.* 100 m), their different distances to the watering place was assumed to be the primary variable in causing different degrees of grazing

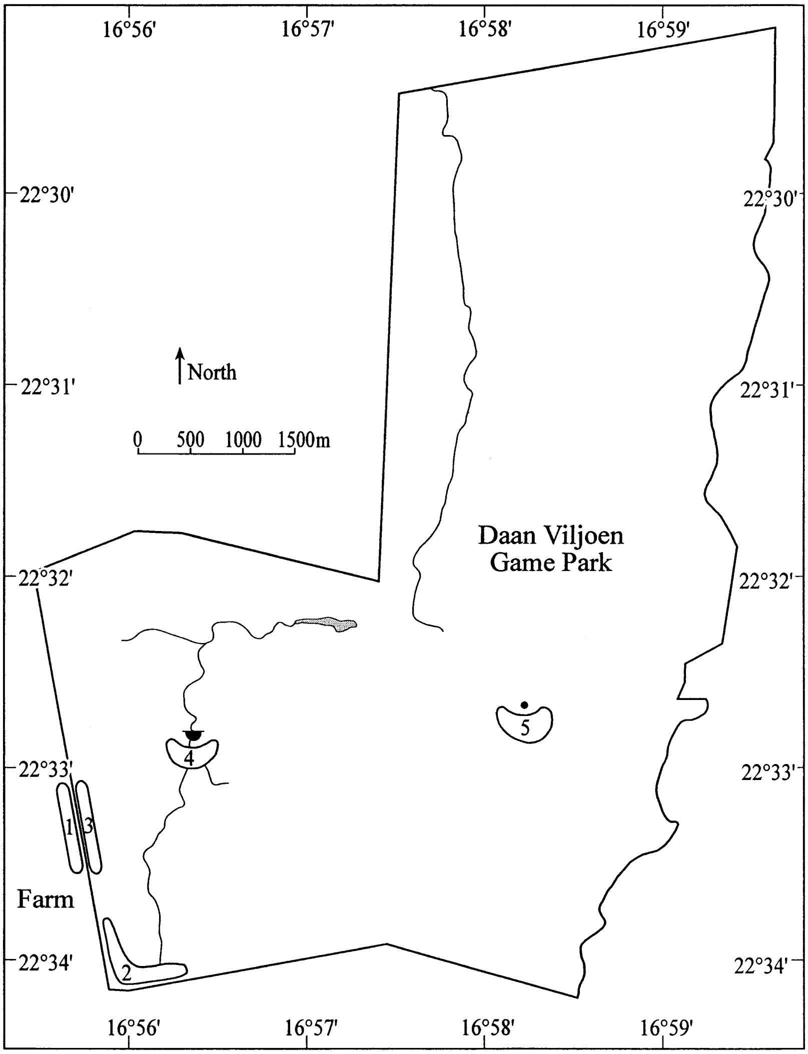

Fig 1 The distribution of the five range units (RUs) in the study area. RU5 was expected to be most degraded and RU1 to be least degraded

impact. RU1 on farmland served as benchmark for veld in lightly utilized condition. Except for very few roaming game no cattle had grazed on that RU for 5 years previous to this study (H. Stegmann, pers. comm.).

With distance classes of 2050–1450 m for RU2, of 1010–930 m for RU3, and 670–340 m for RU4 these RUs were located at decreasing distances from a dam inside the game park. RU3 was directly across from RU1. These two RUs served as a fence-line comparison (Fig. 1). RU5, with 540–260 m close to an artificial waterhole in the east of the park, was known to be severely degraded because of extreme overgrazing prior to building the game park (Kellner, 1986). This RU served as a second but contrasting reference site, being furthest away from the benchmark on the degradation gradient.

Within the RUs three to five morphologically similar hills were chosen for a relatively homogeneous sampling basis. Only hills with clear north, south, east or west facing slopes were selected. Hills were subdivided into drainage channels, footslopes, midslopes and crests. As the mountainous landscape of this Highland Savanna has only very few lowland areas, these four topographical positions on the catena represent the major potential grazing area. Transect belts of 20 m length and 0.5 m width were horizontally placed onto the topographical positions. On average, each RU provided around twenty transects that were subdivided into these four topographical positions. For each of the 26 encountered grass species absolute abundances were recorded by counting individuals in the transects. These numbers were converted into relative species frequencies and expressed as percentage (%). In 101 transect belts on eighteen hills a total of over 17,000 individual grass records were collected. Forbs were not considered in this study because of identification problems. Additionally, crown cover was visually estimated as total projected herbaceous plant cover for each transect.

Data analysis

The Range-Unit Model (univariate). In order to judge the relative strength of influence from grazing and topography on grass species compositions, an index of similarity (Si) was calculated as follows: $\text{Si} = 2C/(A + B)$, where $A =$ number of species in sample A; $B =$ number of species in sample B; and $C =$ number of species common to both samples (Table 1). Due to the high Si-value, only samples from midslopes and footslopes were used for assessing range condition, as these topographical positions demonstrated more homogeneity in species composition.

Based on the fence-line comparison between RU1 and RU3, seven degradation indicators with significant positive or negative response to grazing (significance tests not shown) were chosen for use in the Range-Unit Model. All sampled mid- and footslopes contributed to the univariate indicator results of each RU, making this basic model a highly objective standard for quantifying the different stages of degradation and for defining the degradation gradient.

The DGM (multivariate). The advanced and refined version of the DGM (Bosch & Gauch, 1991) was chosen for a suitability test. This version applies at first a DCA ordination which is suitable for data sets with relatively long gradients (Hill & Gauch, 1980; Gauch, 1982). Thus, DCA is used to identify relatively homogeneous habitat types (Van Rooyen *et al.*, 1994) or relatively homogeneous grazing areas (RHGA) (Dörgeloh, 1999). Thereafter, the DGM applies three subsequent centred PCA ordinations, as this ordination method is best suited for short vegetation gradients to detect the grazing-induced change in species composition. This tested DGM version (Bosch & Gauch, 1991) strictly prescribes three subsequent PCA ordinations because only a consecutive removal of those outliers which do not fit a degradation gradient will finally lead to an optimal condition assessment of this method.

The DGM was applied as follows: at first all 101 sample plots from all four topographical positions were ordinated by means of DCA. Midslopes and footslopes were then ordinated using PCA ordinations. The position of sample plots along the first axis represents a degradation gradient whereas the position along the residual axis 2 indicates a gradient in model fit. Thus, all sample plots with residuals larger than an arbitrary 50% of the Euclidean length of axis 1 were regarded as an unreliable basis for the condition assessment of these particular samples and were therefore discarded from the data matrix (Bosch & Gauch, 1991). PCA ordination was then repeated and outliers removed as before. In order to identify key species – those indicator species which respond to grazing impact – sample scores on the first ordination axis (degradation gradient) were used as independent variable and species abundances as dependent variable for regressions. Polynomial regression techniques of higher order were considered as adequate, because most species responses appear to be skewed (Austin & Smith, 1989; Brits, Van Rooyen & Van Rooyen, 2000) and Gaussian species response surfaces may be

Table 1 The index of similarity (Si) for fence-line transects and different positions on the catena

Si on fence line (RU1/RU3)	Si of crest/midslope comparison	Si of mid-/ footslope comparison	Si of footslope/ drainage comparison
Crest: 0.73	RU1 0.51	0.69	0.63
Midslope: **0.62**	RU2 0.48	0.75	0.76
Footslope: **0.62**	RU3 0.68	0.70	0.58
Drainage: 0.56	RU4 0.67	0.75	0.63
	RU5 0.71	0.70	0.47
	Mean = 0.61	Mean = **0.72**	Mean = 0.61

Bold numbers show that midslopes and footslopes were most similar to each other (0.72), and related to the fact that grazing differences on the same topographical position had a stronger influence on species compositions (0.62) than topography itself.

modified by competition (Gauch, 1982). Species with low correlations were regarded as unresponsive to a degradation gradient and discarded from the data matrix. PCA ordination using key species only was then repeated once more. All ordinations were done using the CANOCO-Program by Ter Braak (1988).

This DGM procedure was strictly followed in order to test its outcome against the defined degradation gradient (order of RUs), as quantified by the Range-Unit Model. In those cases where there was no agreement of the DGM with the defined degradation gradient, modifications of the DGM were tested to improve its performance.

Results

The Range-Unit Model

Midslopes and footslopes were the most homogeneous habitat types with a mean index of similarity of 0.72 and lowest variation within the index (Table 1). Only these topographical positions were used to compare degradation indicators between the RUs. Grass species proportions on these topographical positions are shown for each RU in Table 2. Because RU1 and RU5 were expected to be least and most degraded, respectively, an ideal indicator of veld

Table 2 Absolute abundances of grass species were recorded in each transect and converted into relative species frequencies, expressed as percentage

	Relative species frequencies (%)				
Grass species	RU1	RU2	RU3	RU4	RU5
Antephora pubescens Nees	3.5	0.8	0.5	0.8	1.1
Aristida adscensionis L.	2.3	7.0	18.7	19.4	17.9
Aristida meridionalis Henrard	1.1	2.0	1.1	3.3	1.4
Brachiaria nigropedata (Ficalho & Hiern) Stapf	2.3	5.5	4.9	1.0	0.2
Cenchrus ciliaris L.	1.0	0.4	2.0	1.0	0.2
Chloris virgata Sw.				0.1	
Digitaria eriantha Steudel	1.3				
Enneapogon cenchroides (Roemer & Schultes) C.E. Hubb.	0.9	2.0	0.3	2.5	2.8
Eragrostis echinochloidea Stapf					
Eragrostis nindensis Ficalho & Hiern	70.6	53.2	29.7	45.0	33.2
Eragrostis porosa Nees					0.2
Eragrostis rigidior Pilger				0.3	
Eragrostis superba Peyr.	0.1				
Eragrostis trichophora Cosson & Durand	0.4		0.1	0.1	0.1
Fingerhuthia africana Lehm.	0.7				
Heteropogon contortus (L.) Roemer & Schultes	0.4				
Melinis repens (Willd.) Zizka subsp. *grandiflora* (Hochst.) Zizka	10.9	11.6	30.5	13.8	28.1
Microchloa caffra Nees	1.9	15.0	8.8	8.7	3.7
Monolytrum luederitzianum Hackel	0.9	0.1	1.2	0.7	2.1
Pogonarthria fleckii (Hackel) Hackel		0.6			0.8
Schmidtia pappophoroides Steudel	0.6	0.1	0.1	0.1	0.3
Sporobolus fimbriatus (Trin.) Nees	0.1				
Stipagrostis uniplumis (Lichtenst. ex Roemer & Schultes) De Winter var. *uniplumis*	0.7	0.8	0.3	1.7	5.6
Tragus berteronianus Schultes		0.2	1.3	1.4	2.3
Triraphis ramosissima Hackel	0.1				
Urochloa bolbodes (Steudel) Stapf		0.5	0.4	0.1	0.1

Based on transects from midslopes and footslopes, the average of these relative species frequencies is shown for each range unit. *Eragrostis echinochloidea* has no data here as it was not found on midslopes or footslopes.

retrogression should show linear response to this degradation gradient.

Suitable indicators to define the gradient were the ratio of annuals to perennials, the relative frequencies of the grass species *E. nindensis* Ficalho & Hiern and *Melines repens* (Willd.) Zizka subsp. *grandiflora* (Hochst.) Zizka (Fig. 2), crown cover, and the decline in succession status along the gradient (Fig. 3), classified according to Müller (1984).

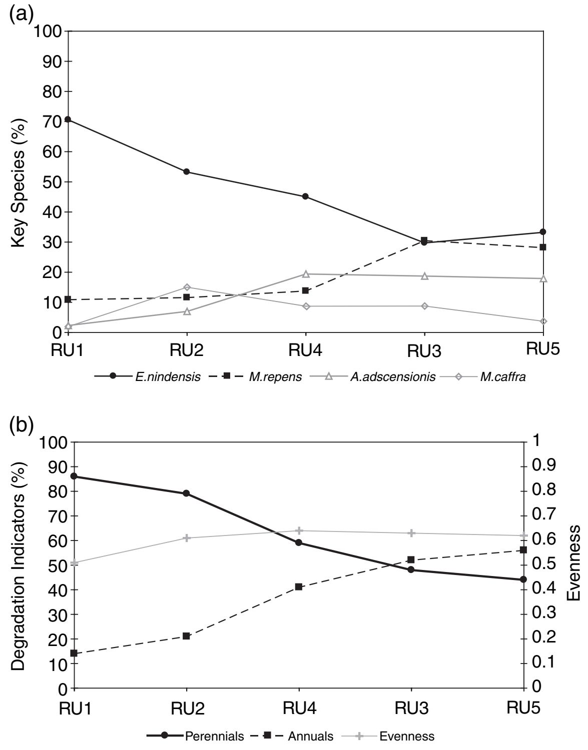

Fig 2 Based on all sample plots of midslopes and footslopes, relative frequencies (%) of key species (a) and other degradation indicators (b) are shown for each range unit in increasing degradation order from left to right

Less suitable indicators were the grass species *Aristida adscensionis* L., *Microchloa caffra* Nees, and Shannon-evenness as these indicators did not show a linear response to degradation (Fig. 2). They were only used for supplementary explanation.

Defining a degradation gradient

Based on these suitable grazing indicators identified by the Range-Unit Model, a degradation gradient was defined by this objective model in the following increasing order.

RU1 – The suitability as benchmark for being least degraded was confirmed by the high proportion of climax grasses (81%), perennials (86%), *E. nindensis* (71%) and an average crown cover of 63%, indicating a high successional status and thus, veld in 'well-managed' condition.

RU2 – According to the same indicators as in RU1, RU2 turned out to second least degraded.

RU4 – Unexpectedly, this RU was less degraded than RU3, despite being closer to the dam. A markedly higher climax proportion probably resulted from more soil water around the dam's catchment area and thus, from a greater recovery potential of the site. However, the lower crown cover (37%) on RU3 indicates that grazing pressure on RU4 was, as *a priorily* assumed, very high. Being less degraded RU3 does not affect the test of the DGM because

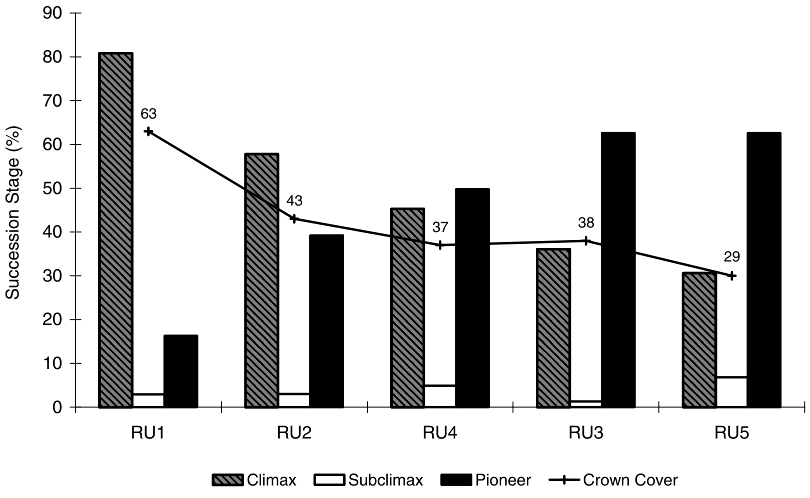

Fig 3 Veld retrogression of the range units. Grass species were classified as climax, subclimax and pioneer species following Müller (1984), and shown as relative frequencies (%) for each range unit. Additionally, percentage data are given for the decline in crown cover

the primary interest of this study is whether or not the DGM will detect such subtle differences between the RUs.

RU3 – Veld retrogression of this RU was much more similar to RU5 than to RU4, making this RU second most degraded.

RU5 – This reference site close to the artificial waterhole showed greatest signs of degradation. The low proportion of climax grasses (31%), and perennials (44%), and the poor crown cover (29%) made RU5 most degraded.

The performance of the DGM

In the first analytical step of the DGM, DCA ordination identified midslopes and footslopes as RHGA (Fig. 4). This agrees with the findings of the Range-Unit Model (Table 1).

Thus, only midslope and footslope samples were ordinated by means of centred PCA. Just four grass species showed distinct species scores in the species–environment biplot of the PCA (Fig. 5b) and were used as key species in the third and final PCA. Of these, *E. nindensis* and *Melinis repens* subsp. *grandiflora* were the grass species showing least deviation in *y*-axis direction. These grass species also had highest correlations to the degradation gradient (Fig. 6). The two other grass species *Microchloa caffra* and *A. adscensionis* had only low correlations to the degradation gradient. Their greater spread in *y*-axis direction in the species–environment biplot indicates that the relative frequency of these two latter grass species was also strongly influenced by factors other than grazing. These results are in agreement with the Range-Unit Model: *E.nindensis* and *M. repens* were suitable and *M. caffra* and *A. adscensionis* were less suitable degradation indicators.

The final ordination using the four key species only is shown in Fig. 5a. The high eigenvalue of axis 1 (0.774) indicates the high importance of the *x*-axis as a degradation gradient. The low eigenvalue of axis 2 (0.140) shows that the DGM has effectively minimized data noise by removing outliers from the ordinations. The DGM has removed most data noise as samples from RU1, probably due to the markedly different grazing history on the cattle farm, when compared with the continuous grazing impact inside the game park (Fig. 5a).

In Fig. 5b the degradation order of the RUs is illustrated in a species–environment biplot where the closeness of RU3 and RU5 confirm the correctness of the obtained degradation gradient. Therefore, the results of the DGM agree with the Range-Unit Model.

However, this correct outcome of the DGM was only achieved when the relative frequency of *E. nindensis* was downweighted with the total projected herbaceous plant cover (crown cover) in each transect. Without this adaptation for data of *E. nindensis*, the DGM showed RU3 to be more degraded than RU5, which is in disagreement with the range condition assessment of the Range-Unit Model. As *E. nindensis* was the only perennial climax grass whose crown cover decreased considerably with degradation and because its proportion was similar on RU3 and RU5 (Fig. 2a), it was crucial for the DGM's discriminating ability to transform the percentage value of this co-dominant species. This was done by multiplying (downweighting) the relative frequency (%) of *E. nindensis* in each transect with

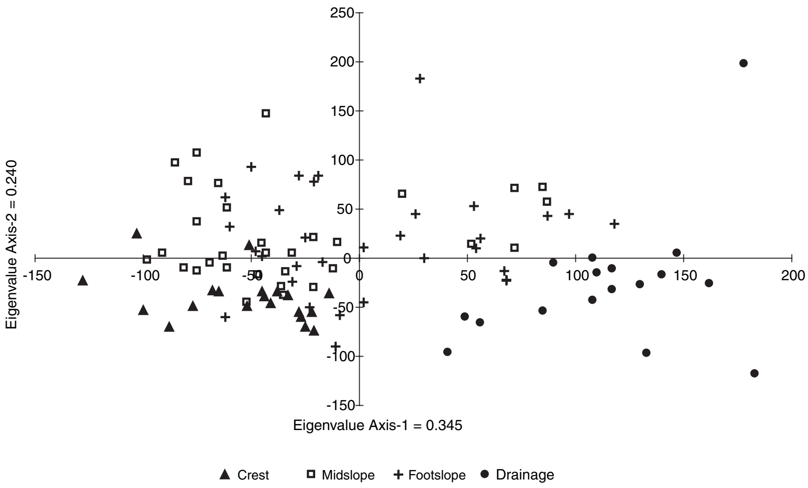

Fig 4 Detrended correspondence analysis of the habitat types. The clear separation of crests and drainage channels indicates their extreme positions on the catena, whereas midslopes and footslopes cannot be separated

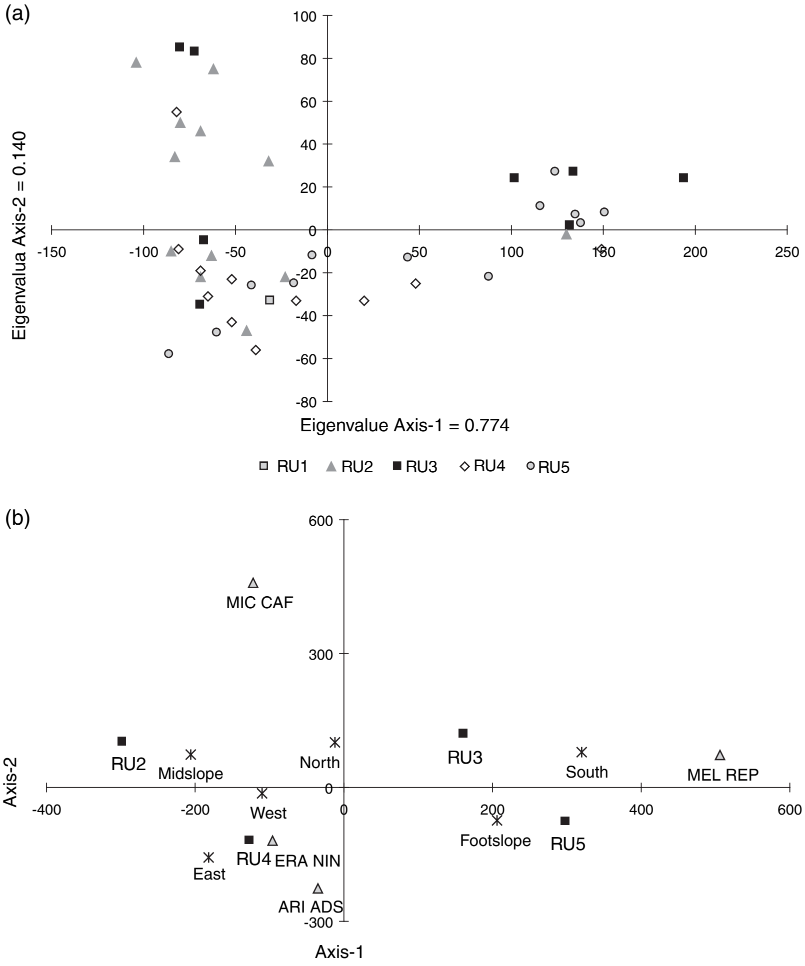

Fig 5 Principal component analysis (PCA) (a) shows the position of each sample plot along the increasing degradation gradient (axis 1) from left to right. Note, the DGM has removed all but one sample from the farm benchmark and even the whole category RU1 in the species–environment biplot (b). Only the range units and no other variable were significantly correlated to the axes in the biplot. Four key species were identified by PCA: *Microchloa caffra* (MIC CAF), *Eragrostis nindensis* (ERA NIN), *Aristida adscensionis* (ARI ADS) and, *Melinis repens* (MEL REP)

the total crown cover of the transect. The proportion of *E.nindensis* on RU3 was multiplied with 0.38 and the proportion on RU5 with 0.29 (Fig. 3). Downweighting *E.nindensis* with the total crown cover of the sample transect had no influence on other species proportions because percentage data were not readjusted afterwards.

Discussion

Methodological problems and alternatives

As shown by the Range-Unit Model, the degradation order from slightly utilized to severely degraded was RU1, RU2, RU4, RU3, RU5. Initially, the DGM has given incorrect results when *E. nindensis* proportions were not downweighted with crown cover. RUs were arranged in the following increasing degradation order: RU1, RU2, RU4, RU5, RU3. The relatively high similarity of RU3 and RU5 in degradation status could not be discriminated adequately by the DGM when just relative frequency data (%) were used. If plants are larger in more productive environments and the quadrat size is fixed, fewer individuals will be recorded (Marañón & García, 1997). Hence, along a successional gradient the use of density data would overestimate dominance in early stages of succession but underestimate it in later stages. Ideally, multiple species variables, notably density, cover, biomass, and energy utilization should be used to identify the similarities and differences among ecological communities (Guo & Rundel, 1997). Therefore, an applied synthesis of density and cover values, as done in this study, may improve the performance of the DGM.

It must also be stressed that the correct degradation order of the RUs was only achieved by the DGM when

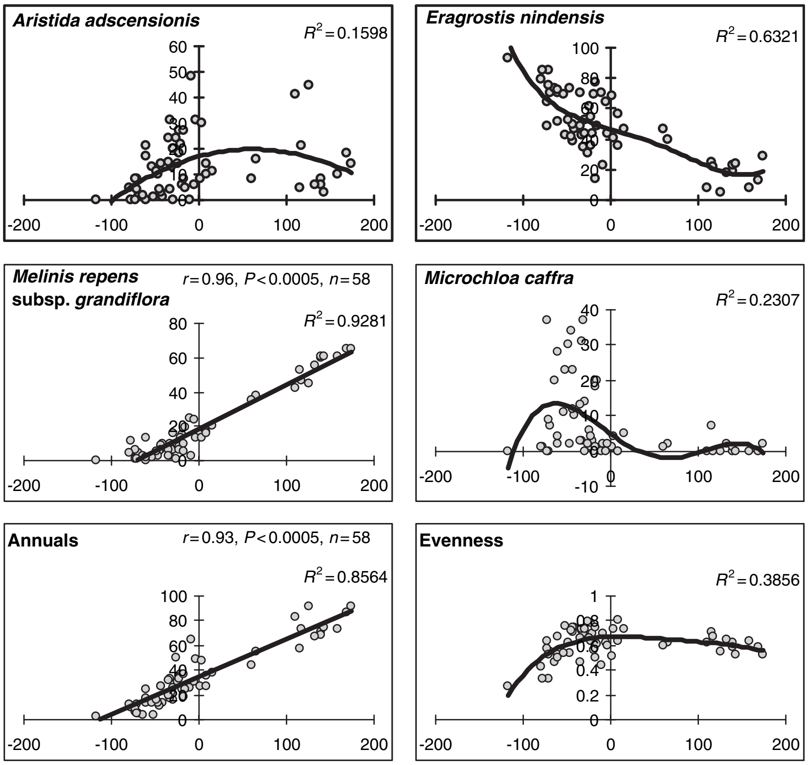

Fig 6 Relative frequency data (%) of grazing indicators were used as dependent variable (y-axis) and their sample scores on the degradation gradient (axis 1 from PCA) as independent variable. Degradation increases from left to right. Where a linear regression showed clear results, it was preferred to polynomial regression techniques

three subsequent PCA ordinations were applied and outliers removed as prescribed by Bosch & Gauch (1991). This is important to emphasize because data noise not accounting for a grazing gradient did negatively influence the performance of the DGM when only one or two PCAs were applied.

Topographical heterogeneity and the DGM

Because of analysis by DCA ordination, the selection for midslopes and footslopes resulted in a clear grazing gradient that dominated the change in grass species composition. This also became evident in the species–environment biplot (Fig. 5b) where only the RUs with their differing average distances to the water point, but no other abiotic variables (slope position, aspect) were significantly correlated with the primary gradient of the ordination (axis 1). Thus, the changes in species compositions were mainly induced by differences in grazing intensity rather than by spatial heterogeneity.

The results from the DGM agree with the initial fence-line comparison between RU1 and RU3. Table 1 shows an index of similarity (Si) of 0.62 for midslopes and footslopes, when the same (opposing) topographical positions were compared with each other on the fence line. But, when midslopes and footslopes were directly compared with each other on every RU, the Si-values had an average of 0.72. Hence, a difference in grazing pressure caused a greater change in species composition (lower Si) on the same topographical positions, than a difference in the position on the catena under equal grazing conditions. Such a relationship was also true for the drainage/drainage comparison on the fence line (Si = 0.56) and the footslope/drainage comparison for each RU (Ø Si = 0.61). However, it was not true for the crest/crest comparison (Si = 0.73) and the crest/midslope comparison (Ø Si = 0.61). The reverse case for crests probably indicates that the observed low biomass and grass proportion on hilltops (due to water run-off) is little consumed by herbivores. Therefore, the diminished magnitude of difference in grazing pressure affects species compositions much less on either side of the fence.

These findings are contrary to a study by Venter *et al.* (1989), carried out in a 600–650 mm rainfall zone of South Africa. There, differences in topography explained the greater variability in the data instead of differences in land-use practice, indicating more stability of this semiarid savanna.

Aridity and the DGM

Arid range systems are generally not very resistant to grazing disturbance and a typical effect of grazing impact is an abrupt change from climax to pioneer veld (Sullivan, 1996; Van Oudtshoorn, 1999). This effect was also visible in this study. Figure 3 illustrates a continuous decline of climax grasses and a simultaneous increase of pioneer species with progressing degradation. Although numbers of climax (nine), subclimax (eight), and pioneer species (nine) were almost evenly distributed over the 26 grass species encountered in the study area, a subclimax stage did hardly exist. This abrupt retrogression of range land demonstrates the vulnerability of arid grasslands to increasing grazing pressure and thus, the delicate balance between veld in 'well-managed' and veld in 'badly managed' condition.

The almost untransitional change from climax to a dominating pioneer veld had rather positive consequences for the DGM and its applicability to arid savanna. A clear result of this abrupt grazing-induced transition was the dominance of just four key species. The reduction to only a few key species was of advantage to the DGM in that it made the ordinations clearer and better understandable. These findings still need to be further investigated by sampling vegetation over several rain seasons. Yearly rainfall variation in this arid savanna type may have noteworthy effects on species compositions.

Presumably, another advantage favouring the application of PCA ordinations in the DGM was the fact that few dominant grass species of prevailing pioneer veld showed greater linearity along the degradation gradient (*E. nindensis* and *M. repens*). Probably, average niche breadths of grass species increase with veld retrogression. According to Glenn-Lewin, Peet & Veblen (1992), early in succession when competitive pressures are low, species should be widely distributed along environmental gradients. In contrast, late in succession when competitive pressures are high average niche breadths should decrease. The decline in competitive pressure between grass species may also be inferred from the decline in Shannon evenness under veld retrogression (Fig. 6). With ongoing degradation fewer grass species may tolerate the increasingly harsh conditions hence, inter-specific competition is probably reduced.

In summary, the DGM performed very well under these arid climate conditions as long as *E. nindensis* was downweighted with crown cover. The low annual rainfall (average = 350 mm) in central Namibia did not hamper or mask the establishment of a grazing gradient. In fact, the opposite seems to be true: aridity in this particular rainfall zone leads to a strongly reduced resistance to grazing that is well detected by the DGM via multivariate analysis of changing species compositions. The dominance of the grazing gradient was underlined in the PCA by the high eigenvalue (0.774) of axis 1. Sample plots whose species composition did not fit the degradation model were effectively excluded from the ordination, mainly as outliers from RU1. Thus, the DGM detected systematically most prominent data noise in differential past grazing history on the farm benchmark, to the extent, that only a single sample plot from the farm remained in the diagram. This emphasizes the strong effects of grazing on grass species composition. Generally, these results are in contrast to degradation dynamics under more arid climate conditions (200–230 mm annual rainfall) of the Kalahari, where grass species compositions were not correlated with decreasing grazing intensities away from watering points, but were masked by abiotic factors like soil water (Van Rooyen *et al.*, 1994). Similar results were found for desert savanna in western Namibia (165 mm annual rainfall) where stochastic rainfall events had greater influence on species compositions than varying grazing intensities (Ward *et al.*, 1998). Hence, the grazing-related classification of grass species into 'increasers' and 'decreasers' were not applicable to these extremely dry savannas.

Conclusion

Despite the importance of rainfall stochasticity in arid savannas, the DGM performed unexpectedly well in central Namibia. The arid Highland Savanna of Namibia may be seen as a transition between both extremes, where the relative resistance of semiarid savanna may be indicated by topography dominating grass species compositions over grazing (Venter *et al.*, 1989) and where rainfall and abiotic factors dominate over grazing in nonequilibrial, desert-like savannas (Van Rooyen *et al.*, 1994; Ward *et al.*, 1998). For this 300–400 mm rainfall zone it is proposed, that the influence of rain is low enough to cause a grazing gradient largely dominating topographical heterogeneity, but it is high enough to allow grazing to override the influence of rain. The applicability of the DGM to this savanna type was thereby favoured by a strong grazing gradient, as indicated by the high eigenvalue of axis 1. However, two points need to be emphasized:

1 An undesirable effect of the strong grazing impact on the performance of the DGM was the removal of all but one benchmark samples of the farm and thus, a qualitative loss in guiding the interpretation of the ordination. It is therefore suggested to choose benchmark samples rather in similarly utilized areas than in those with differential past grazing history.

2 Without the presented combination of density and cover data for the weighty perennial key species *E. nindensis*, no correct outcome of the DGM would have been obtained. The incorporation of both variables into the multivariate analysis appears ideal for this range condition assessment technique under arid conditions.

As this study was done in and along a game park with sites of extreme difference in degradation status, it is difficult to judge in how far topographical heterogeneity would disturb the DGM under less pronounced grazing differences. Yet, from a technical point of view it must be concluded that the DGM is a suitable and very sensitive method to analyse degradation dynamics under these particular climate conditions in arid Namibia. Though, these findings need to be further supported by sampling herbaceous community data over several rain seasons.

Acknowledgements

I am grateful to Dr Fergus Molloy from the University of Namibia, to Dr Joh Henschel from the Desert Research Foundation of Namibia, and to Dr Hugh G. Gauch, Jr from Cornell University for making valuable comments on the script. Thanks also to Ben Strohbach from the National Botanical Research Institute, to Bessie Bester from the Ministry of Agriculture, Water and Rural Development and to Dave Joubert from the Polytechnic of Namibia for discussing various grass species. Finally, thanks to Dr Kerstin Wiegand and Katrin Meyer from the University of Jena for some last comments on the manuscript.

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(Manuscript accepted 21 July 2005)