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Grazing gradients in the Highland Savanna vegetation of Namibia

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Abstract

A grazing gradient for the south to east facing slopes of the Highland Savanna was established. A significant negative correlation between slope angle and grazing intensity suggests that steeper slopes are less accessible to grazers, especially cattle. Steep slopes were vegetated with mainly perennial Decreaser species, and this may also be partially due to the protection against erosion and evaporation which is afforded to the steep slopes, by the associated high percentage stoniness. The responses of certain grass species was investigated, and the three Gaussian curve parameters were found to describe the species' responses with some accuracy. Species were categorized as broad range, medium range or narrow range Decreasers / Increasers II, III and IV, according to the narrowness of the curve and the position of their optimum response (maximum abundance) on the axis, respectively. Some species were found to be not responsive. Some species responded differently to what previous literature suggests. It is suggested that some species may respond differently to different grazers, and that this may have a significant influence on species composition under different range utilization (game reserves and farmlands). Grazing was found to reduce basal cover significantly. Three woody species appeared to respond in very different ways to grazing pressure, as suggested by fitting their densities to Gaussian curves along the grazing gradient. It is suggested that some of the hypotheses generated in this study need to be tested.

Introduction

Range management philosophy holds that grazing has a significant influence on grass species composition (for example, Tainton, 1981), and that palatable perennial grasses are often replaced by less palatable perennials, and annual grasses when grazing pressure is increased. Recent studies, in the grasslands regions of South Africa in particular, make use of ordination techniques to determine "grazing" or "de-

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gradation" gradients (changes in species composition with increasing grazing pressure), and to determine the "ecological status" of species (the response of different species to grazing pressure of different intensities) (Bosch & Janse van Rensburg, 1987; Bosch, 1989; Janse van Rensburg & Bosch, 1990; Bosch & Gauch, 1991; Bosch & Kellner, 1991). In a recent comparison with other range condition assessment techniques currently used in South Africa, the degradation gradient method was considered to be the most sensitive and objective (Hurt & Bosch, 1991). Apart from the apparently successful use of ordination techniques in the Northern Kalahari region (Strohbach, 1992), the method has not been tested in the various Namibian savanna types. The woody component in savannas adds a dimension whose influence has also not been tested with this technique. This study tests the suitability of ordination techniques to establish a grazing gradient for south to east slopes in the Highland Savanna vegetation of the Khomas Hochland region west of Windhoek. The influence of slope and stoniness on the grazing gradient is discussed. Further, the responses of certain important grass species to grazing intensity are examined and discussed. The value of the three parameters in the Gaussian curve equation (Gauch, 1982) in describing a species response to grazing are particularly emphasized. The influence of grazing intensity on grass basal cover, the density of 3 woody *Acacia* species of different height classes, and tree canopy cover percentage is investigated. This study does not attempt to suggest "veld condition" scores or management practices for the region. It is felt that the complex topography and resultant patchiness of the vegetation of the region, and the recent uncertainty about the appropriateness of existing theories of rangeland management (which have largely evolved in studies of rangelands at equilibrium in the United States), in studying rangelands not at equilibrium, in erratic and variable rainfall areas of Africa (Behnke & Scoones, 1991), warrant much more research and thought in this area, before any bold statements in this regard can be made. This study should rather be seen as a preliminary testing of the usefulness of ordination techniques in investigating grazing influences on species composition, and the "ecological status" of grass species.

In a following paper, the value of this method in generating hypotheses regarding the responses of three *Acacia* species to grazing pressure will be discussed.

Methods

Study area

The samples were obtained from the Highland Savanna vegetation region (Giess, 1971), in the Khomas Hochland region, west of Windhoek. Plots were situated in the Daan Viljoen Game Reserve, and on four neighbouring farms (22°33'S, 16°57'E) at an altitude ranging from 1550m to 1730m. The soils are described as shallow, stony metamorphic lithosols of no agricultural value (van der Merwe, 1983) and are situated on the Kuiseb Formation of the Damara System. The Kuiseb Formation consists mainly of micaceous and quartzitic schists (Kellner, 1986). The study area consisted predominantly of steep hills. An average rainfall of 300-400mm falls mainly between October and March. Rainfall variability is high (van der Merwe, 1983). The vegetation of the area has been classified as an *Acacia hereroensis - Eragrostis nindensis* alliance by Kellner (1986).

Data collection

35 plots of 30m x 30m were studied on south, south-east and east facing slopes. The plots were subjectively selected, with the aid of farmers, to represent vegetation in different stages of "degradation" due to grazing. The methods of Bosch (1989) were attempted, but "fence-line" effects on south to east facing slopes were rare, and vegetation changes were not well correlated with differing distances from watering points.

The wheel-point apparatus (Tidmarsh & Havenga, 1955) was used to make nearest plant recordings at 200 points in each plot, in order to estimate the species composition of grasses and herbs (herbaceous layer). Slope angle within the plot was measured with an Abney level. Percentage stoniness was visually estimated for each plot. Aspect was measured with a compass. The relation of the plot to its surroundings was also recorded in order to determine possible effects of the surroundings on grazing and species composition. Basal strikes were used to provide a rough estimate of percentage basal cover for each plot.

Nearest plant recordings in the "shade" of trees, simply estimated as the area under the canopy, were noted for each species, in order to estimate the influence of tree cover on the abundance of each species. The percentage of points in the shade of trees was also used as a measure of the percentage tree cover for each plot. These and other measurements related to the tree component will be used in a separate paper to be published.

Data analysis

The establishment of a grazing gradient

Species composition data for the herbaceous layer were ordinated for each sample using detrended correspondence analysis (DCA) (Gauch, 1982). Because many variables were eliminated or reduced, the first ordination axis was expected to largely represent a grazing gradient.

The influence of environmental factors (slope angle and percentage stoniness) on the first ordination axis

The possible influence of environmental factors (slope angle, percentage stoniness) on the first ordination axis was tested, using linear regression techniques.

The influence of grazing on basal cover

The influence of grazing intensity (first ordination axis) on basal cover was tested using linear regression techniques.

The ecological status of grass species

Species abundance curves were fitted on the first ordination axis, for each species, in order to determine the response of species to different grazing intensities (the ecological status of species). This was done with polynomial regression techniques using the Statgraphics statistical computer programme (version 6). In each case, the data were fitted to the normal distribution curve, or Gaussian curve, as it was felt that this should best describe the response of a species to any environmental gradient (Gauch, 1982). The Gaussian model of community structure suggests that the abundances of each species along an environmental gradient (in this case a grazing gradient) approximately follows the normal or Gaussian distribution (Gauch, 1982). However, Hardy & Hurt (1989) suggest that some species do not respond strongly to grazing pressure.

The Gaussian curve is calculated as follows:

$$y = a\,exp^{-k(x-b)^2}$$

where:

a represents the maximum abundance a species achieves along the grazing gradient, indicating the optimum conditions for this species on the grazing gradient.

k represents the narrowness of the species range along the grazing gradient, the higher the k value, the narrower the range.

b represents the position along the gradient at which the species achieves maximum abundance. A species with a high b-value increases with increasing grazing pressure.

A low r^2 value suggests that a species does not respond strongly to grazing pressure. Figure 6a - 6m shows the shape and position of the Gaussian curves for each species along the grazing gradient. The species which were significantly responsive to grazing pressure were placed into the Increaser/Decreaser categories (Janse van Rensburg & Bosch, 1990) in the following way: **Decreasers Species** which achieve their maximum relative abundance in lightly utilized veld, and decrease with increasing utilization. **Increasers II Species** which achieve their maximum relative abundance in moderately utilized veld, and whose relative abundance decreases with heavy grazing, and with light grazing. **Increasers III Species** which achieve their maximum abundance with heavy utilization, and which decrease with very heavy utilization, and moderate to light utilization. **Increasers IV Species** which achieve their maximum relative abundance with very heavy utilization, and decline progressively with decreasing grazing pressure. Typically, the position on the first ordination axis of their maximum abundance lies beyond the extreme right of the constructed grazing gradient. The categorization has been further refined by determining whether the species has a narrow, medium or broad range along the grazing gradient.

A significant correlation suggested that a species abundance was significantly influenced by grazing pressure. If a species abundance curve was not significantly correlated, other factors were considered in order to explain the poor fit.

In all of the above regression tests, a t-test was performed, and a significance level of 5% or less was considered significant.

Results and Discussion

The grazing gradient

All samples subjectively selected, to represent heavily utilized areas (near waterholes and in easily accessible places), are found towards the right side of the first ordination axis (high DCA scores), whereas samples selected to represent low intensity

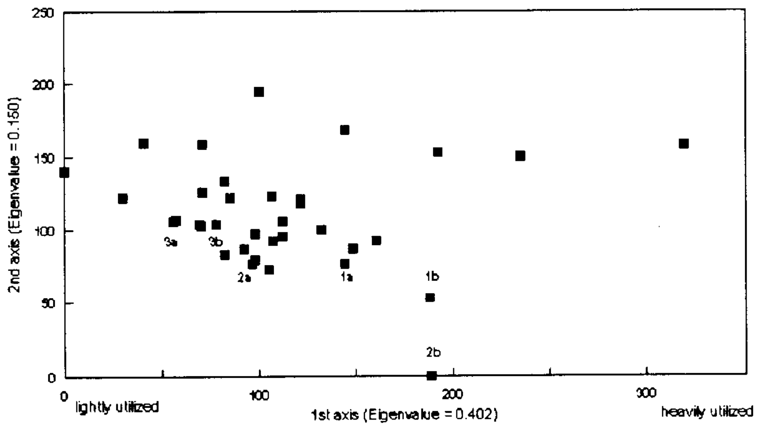

Figure 1: The distribution of sample plots on the first and second axes of the DCA-ordination. The first axis represents a grazing gradient. Numbers 1, 2 and 3 represent slopes which were sampled twice, a representing the sample on the steeper part of the slope, and b representing the less steep part of the slope. 1a is a midslope sample (slope angle = 10°) in a paddock with a history of heavy utilization and 1b (slope angle = 5°) is at the foot of the same slope. 2a is a midslope sample (slope angle = 19°) from a fairly heavily utilized paddock, and 2b (slope angle = 8°) is at the foot of the same slope. 3a is a midslope sample (slope angle = 12°) in a lightly utilized area in the Daan Viljoen Game Reserve, and 3b (slope angle = 9°) is at the crest of the same slope.

grazing (for example, less accessible areas, and areas such as the entrance to the game reserve where the continuous movement of a large number of people deters animals) are found towards the left side of the first ordination axis (low DCA scores) (Figure 1). No quantitative data on long-term grazing pressure were available and thus the gradient is qualitatively described as varying from lightly utilized to heavily utilized. The DCA 1st and 2nd axes accounted for the majority of the variation in the data set (Eigenvalues for axes 1, 2, 3, and 4 were 0.402, 0.150, 0.087, and 0.053 respectively). Although variation in 2nd axis values (195) was more than 50% of the variation in 1st axis values (319), no samples were regarded as outliers, since 50% is only an arbitrary cut-off value (Bosch & Gauch, 1991). Also, no sample was considered to be far enough away from any other sample to be an outlier. Variation in rainfall within the region, both in amount and seasonal distribution may also have accounted for some of the first axis ordination variability. Low rainfall and overgrazing both have an adverse effect on soil moisture, which provides a competitive edge for "pioneer" species over the more mesophytic "climax" species. Sample plots have been marked and some of them will be resampled in further studies. The ordination results can be compared, and if rainfall data are collected, the influence of rainfall on the ordination may be better understood. In further studies the "trajectories" (Hurt *et al.*, 1993), or movements of ordinated plots on the axes, may provide more insight into grazing influences, particularly if quantitative data on grazing pressure are made available. Heavily grazed areas were undersampled.

The influence of slope angle and percentage stoniness on the grazing gradient

Three slopes in the study were sampled at different topographical positions. They are denoted 1a and 1b; 2a and 2b; and 3a and 3b (see Figure 1). a denotes steep

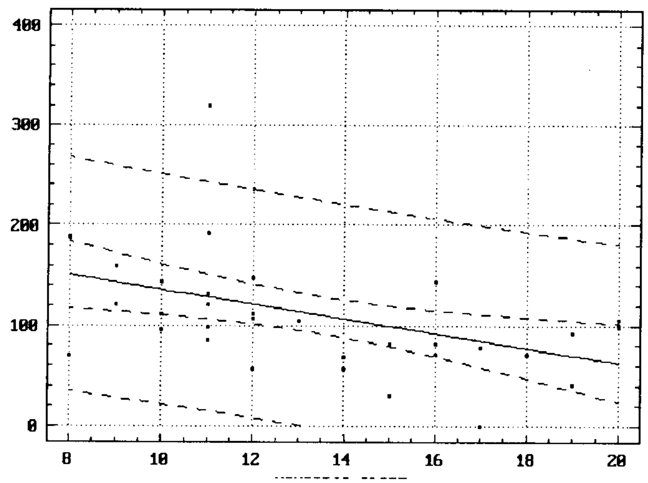

Figure 2: The linear regression relationship showing the effect of slope angle on the first ordination axis values (grazing gradient).($P< 0.05$; $r = -0.5$).

midslope, whilst b denotes a less steep footslope (or crest in the case of slope 3). In all instances, besides having smaller slope angles, the footslopes (and the crest on slope 3) (see Figure 1), were closer to flat areas (large flat, dry drainage channels and valleys in the case of 1 and 2, and extensive plateau-like hilltop in the case of 3). In all three instances, the steeper slopes, were more lightly utilized than the flatter slopes, as is indicated by their position along the grazing gradient (Figure 1). Linear regression analysis shows a significant negative correlation ($r = -0.45$; $P < 0.05$) between slope (independent variable) and sample x-ordination value (dependent variable) (Figure 2). That is, the steeper the slope the less the grazing pressure. The positions of samples 1, 2, and 3, on the ordination axes (Figure 1), and the negative correlation between slope and the grazing gradient (Figure 2), suggest that there is a relationship between the grazing pressure on a specific area of grazing on a slope, on the one hand; and the steepness of the slope and the distance from the area to a flat, easily accessible area where grazers are likely to concentrate, on the other hand. It may be that the extra energy expenditure, and the discomfort endured by grazing on these steeper slopes discourages grazers, and this affords some measure of protection from overgrazing to these areas. Linear regression analysis also showed a significant negative correlation ($r = -0.63$; P) between % stoniness (independent variable) and sample x-ordination values (dependent variable) (Figure 3). This also suggests that a high percentage of stones (in many cases between 90-100%) protects areas from grazing pressure, perhaps by causing discomfort to the hooves of herbivores such as cattle.

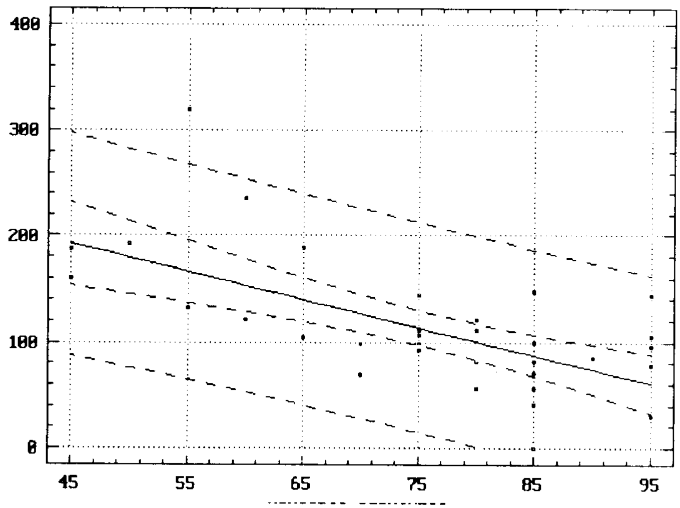

Figure 3: The linear regression relationship showing the effect of stoniness on the x-ordination axis values (grazing gradient). Although significant ($P < 0.05$; $r = -0.63$), the fact that percentage stoniness was causally related to slope angle suggests that this relationship is less significant than it appears.

However, percentage stoniness (dependent variable) was also correlated with slope angle (independent variable) (P< 0.05), in what is considered to be a causal relationship (Figure 4).

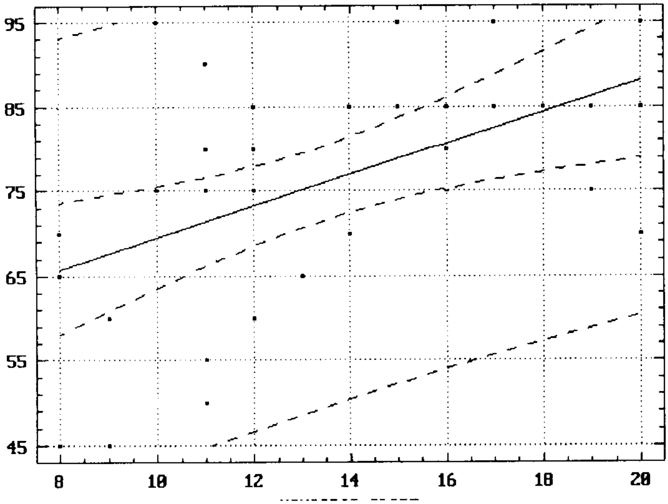

Figure 4: The linear regression relationship showing the influence of slope angle on percentage stoniness (P< 0.05; r = 0.48). It is likely that this reflects more the influence of slope position on percentage stoniness.

It is difficult to discern between the increased moisture status of the soil as a result of increased stoniness or decreased grazing pressure, and this warrants further study. Although steep slopes are potentially more prone to erosion, and would thus be expected to be dominated by species associated with "degraded" conditions, the converse is true, partially, it is suggested, due to the protection afforded against excessive grazing, but also partially because steeper slopes are protected from erosive processes, by their generally high percentage stoniness. The significant positive relationship between slope angle and percentage stoniness (Figure 4), reflects a relationship between upper slopes and footslopes, as well as slope angle, as smaller sand particles would be more prone to erosion movement than heavier stones (Morgan, 1980) and would thus tend to "settle" and accumulate on the more gradual footslopes, as water velocity decreases. This would account for the relationship, but paradoxically, also accounts for the protection of slopes from excessive soil erosion. The high percentage of stone acts, in much the same way as vegetation or mulch cover, as a buffer between the rain and the soil, and also reduces evaporation from the soil, thus affording a more favourable water balance in the soil. The stoniness probably also protects the loosening of soil by the hooves of herbivores. More rigorous testing of a hypothesis that slope influences grazing pressure, the degree of which depends on the breed of cattle, and the species of game, should provide enlightening and useful information which may influence rangeland management options. Particularly interesting is the implication that a variety of more mobile and agile herbivores such as oryx, may result in a significantly different plant species composition and spatial vegetation pattern than more sedentary and less agile cattle breeds which concentrate on less stony lower slopes.

The influence of grazing on basal cover

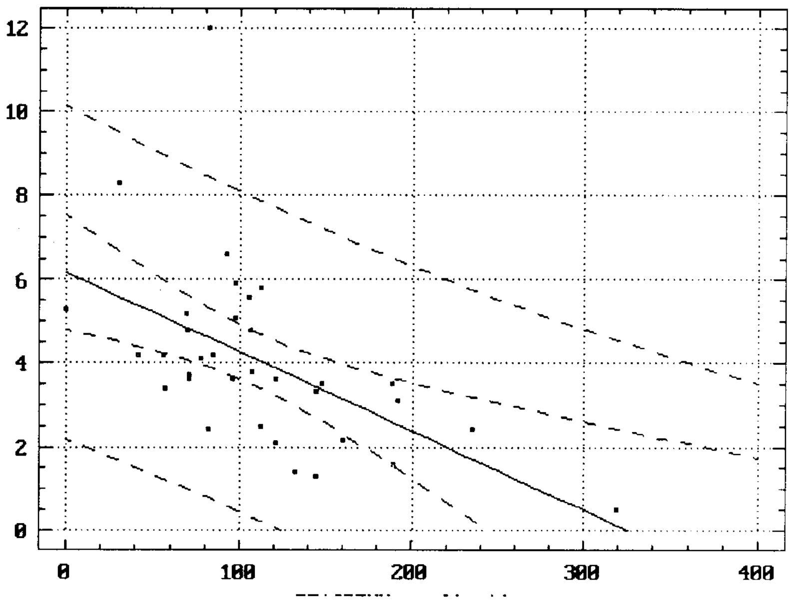

Figure 5: The linear regression relationship ($P < 0.05$; $r = -0.54$), showing the effect of grazing (x-ordination values) on grass basal cover.

Linear regression analysis showed a significant negative correlation ($r = -0.54$; $P < 0.05$) between the x-ordination values (independent variable) and the percentage basal cover of grasses (dependent variable) (Figure 5). As grazing pressure increases, perennial species with large basal tuft diameters are selected for by grazers, and annuals with negligible basal tufts increase in numbers and significance. A reduction in basal cover has a significant effect on soil crusting and soil erosion, as rain drops of high velocity are not intercepted by vegetation, and, consequently, rainsplash impact is greater (Morgan, 1980).

The ecological status of grass species in relation to the grazing gradient

Table 1: The grass species recorded, their r^2-values, the significance of fit (S = significant; NS is non-significant at P< 0.05) to a normal distribution curve using polynomial regression techniques, and their a, -k and b values (see Methods for explanation), in ascending order of b values.

	Species	r^2	S/NS	a	-k	b	Ecological category
a	*Anthephora pubescens*	0.097	NS	5.86	0.0002	0	Decreaser? Not responsive
b	*Brachiaria nigropedata*	0.775	S	24.2	0.00045	20.3	Decreaser Responsive
c	*Heteropogon contortus*	0.457	S	4.94	0.00079	35.9	Decreaser Responsive
d	*Eragrostis nindensis*	0.613	S	56.1	0.00008	66.7	Decreaser/ IncreaserII? Responsive
e	*Aristida meridionalis*	0.025	NS	2.74	0.00014	98.3	IncreaserII? Not responsive
f	*Melinis repens* subsp. *grandiflora*	0.024	NS	3.92	0.00008	99.6	IncreaserII? Not responsive
g	*Fingerhuthia africana*	0.128	S	0.42	0.00062	150	IncreaserII/III? Responsive
h	*Monelytrum luederitzianum*	0.103	NS	1.25	0.00022	151	IncreaserII/III? Not responsive
i	*Michrochloa caffra*	0.295	S	23	0.00009	156	IncreaserII/III Responsive
j	*Eragrostis porosa*	0.492	S	9.75	0.00016	195	IncreaserIII/IV Responsive
k	*Enneapogon cenchroides*	0.90	S	33.8	0.00019	267	IncreaserIV? Responsive
l	*Pogonarthria flecki*	0.889	S	45.4	0.00003	480	IncreaserIV Responsive
m	*Stipagrostis uniplumis*	0.837	S	***	0.00002	611	Increaser IV? responsive

**** denotes an impossible value (above 100%)*

Table 1 shows the various values (r^2, a, -k and b) for each species fitted to a normal ditribution curve using polynomial regression techniques. Each value, and its relevance is explained in the methods section. Figure 6a - 6m shows the shape and position of the Gaussian curves for each species along the grazing gradient, and is obtained from the values in Table 1. Each species will be discussed in ascending order of b value:

a. *Anthephora pubescens* Nees (b = 0). Because of the poor fit to the Gaussian curve, *Anthephora pubescens* appears to be fairly unresponsive to grazing pressure (Table 1). According to Müller (1984), this very valuable, palatable grass can withstand reasonably heavy grazing. This may be responsible for the low -k value (Table 1). Most of the individuals recorded in samples on the right side of the grazing gradient were small tufted, and this may have been a sign of "veld recovery" of some of the samples.

b. *Brachiaria nigropedata* (Fical. & Hiern) Stapf (b = 20. 3) appears very responsive to grazing pressure, as indicated by the high r^2 value (Table 1). The high -k value reflects the narrowness of its ecological range on the grazing gradient (see Table 1 and Figure 6b). On most farmland sampled, *B. nigropedata* was either absent or very rare. According to Müller (1984), it is one of the first species to disappear with selective grazing. Interestingly, it was relatively abundant in samples in the Daan Viljoen Game Reserve, which were toward the middle of the grazing gradient on the 1st axis (fairly heavily grazed) (Figure 1). The possibility that *Anthephora pubescens* and *B. nigropedata* (and other species) respond differently to different grazing regimes urgently needs testing, and may reveal important insights into the dynamics of the grass layer in relation to different grazing behaviour. *B. nigropedata* can be termed a "narrow- range" Decreaser.

c. *Heteropogon contortus* (L.) Roem. & Schult. (b = 35. 9) was only found on lightly utilized sites, to the left of 100 on the grazing gradient (Figure 6c). It has a high -k value, and can thus also be regarded as a "narrow-range" Decreaser, although Müller (1984) refers to it as a "sub-climax" grass, which provides only reasonably good grazing until it flowers and becomes hard and thus differs from the findings of this study.

d. *Eragrostis nindensis* Fical. & Hiern (b = 66. 7) was the most abundant species in most of the plots. Its low -k value suggests that it has a broad response to grazing. It nevertheless drops markedly towards the far right of the grazing gradient (Figure 6d). It's apparent resistance to drought (Müller, 1984), makes its presence very useful, and its absence in heavily utilized areas is cause for concern. It can be regarded as a "broad-range" Decreaser/Increaser II species.

e. *Aristida meridionalis* Henr. (b = 98. 3). The low r^2 value for this species suggests that it is responding more significantly to other environmental variables than grazing pressure, such as soil moisture. It is regarded as a "moisture-loving" grass (Müller, 1984).

f. *Melinis repens* (Willd.) Zizka subsp. *grandiflora* (Hochst.) Zizka (b = 99. 6) is usually an annual. It also appears to be relatively unresponsive to grazing pressure as evidenced by the low r^2 value (Table 1). *M. repens* subsp. *grandiflora* was commonly found in the shade of the larger trees (2m) in the samples. This implies that this species could be significantly associated with shade, or high soil-moisture. Müller (1984) describes it as a "pioneer" species, but it is rare in very heavily utilized samples (Figure 6f), reaffirming the suggestion that it is relatively unresponsive to grazing pressure.

g. *Fingerhuthia africana* Lehm. (b = 150) could be regarded, from the relatively large -k value, as a narrow-range Increaser 3 species. This is in contrast to Müller's (1984) description of it as "a climax species in the dry regions". However, it was not abundant in any samples (maximum relative abundance - 1. 4%), and its value as an indicator species is, for this reason, limited.

h. *Monelytrum luederitzianum* Hack. (b = 151) appears unresponsive to grazing pressure ($P < 0.05$). Müller (1984) describes it as a pioneer grass, but the results of this study do not corroborate this opinion.

i. *Michrochloa caffra* Nees (b = 156) occurs as the second most abundant species generally, and usually occurs with *Eragrostis nindensis* as the most dominant species in the moderately to heavily grazed samples, but it achieves its maximum abundance in more heavily grazed areas, apparently gradually replacing *E. nindensis*, as the dominant species. It also has a fairly broad ecological distribution (small -k value) along the grazing gradient and can be regarded as a broad-range Increaser II/III species. Müller (1984) describes it as a pioneer that is never abundant. Figure 6i shows that it is abundant and that its status as a pioneer is dubious. Figure 6i shows some scatter towards the top left-center of the graph, away from the fitted curve. This suggests a fairly noticeable response to another environmental factor, or perhaps, as for *A. pubescens* and *B. nigropedata*, different responses to different grazers.

j. *Eragrostis porosa* Nees (b = 195). This study supports Müller's (1984) view of *E. porosa* as a pioneer grass. The high r^2 value suggests that it is strongly responsive to grazing pressure. It can be regarded as a medium-range Increaser III/IV species (-k value is fairly high).

k. *Enneapogon cenchroides* (Roem. & Schult.) C.E. Hubb. (b = 267) appears to respond much like *E. porosa* to grazing pressure, but achieves maximum abundance in more heavily grazed areas (see b value). It can be regarded as a medium-range Increaser IV species. In very heavily grazed areas, it occurs in dense stands of up to 30% relative abundance. This supports Müller's (1984) view that it is a valuable pioneer species "which quickly covers bare ground and thus counteracts erosion".

l. *Pogonarthria flecki* (Hack.) Hack. (b = 480) is common in unshaded areas. It is often almost the only grass growing in and next to game-paths, which suggests that the trampling effect is also important in its establishment. It can be considered to be a broad-range Increaser IV species (low -k value), which is associated with open, unshaded areas. If the curve is extrapolated, its maximum occurs beyond the constructed grazing gradient, implying that it's optimal conditions are in severely disturbed veld.

m. *Stipagrostis uniplumis* (Licht.) De Winter (b = 611). The results are totally in contrast with what has been previously suggested. Müller (1984) describes *S. uniplumis* as a sub-climax species whereas the results of this study suggest that *S. uniplumis* is an Increaser IV species. There are some reasons suggested for the rather surprising fitted curve: 1. Large tufted *S. uniplumis* individuals were found to the left of the grazing gradient in what could be described as moderately-utilized samples. Visually, these sites appeared almost to be dominated by *S. uniplumis*, but with the wheel-point sampling, their relative abundance was found to be only a few percent (up to 8 %). 2. The very high relative abundance of the species (34 %) in the sample to the extreme right of the grazing gradient, consisted of very small tufts of an almost annual habit. An annual form *S. uniplumis* var. *intermedia* is found in the Namib Desert. It is hypothesized that this ecotype may be an invader from more xeric regions, establishing itself in areas of low soil moisture, induced by excessive overgrazing and trampling resulting in unfavourable soil-moisture conditions for Decreaser species. The sample scatter on Figure 6m, suggest that a bimodal curve could be fitted to the data set. Some species have been found to have bimodal and even trimodal responses

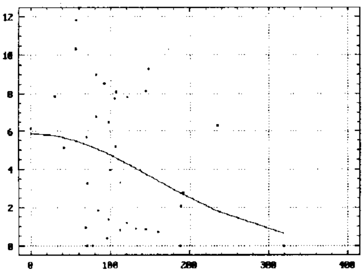

Figure 6 a: *Anthephora pubescens*

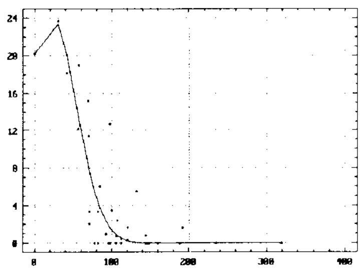

Figure 6 b: *Brachiaria nigropedata*

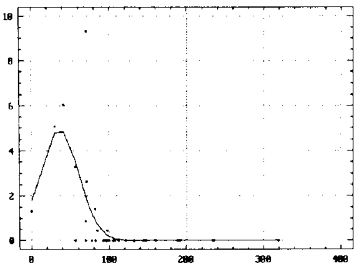

Figure 6 c: *Heteropogon contortus*

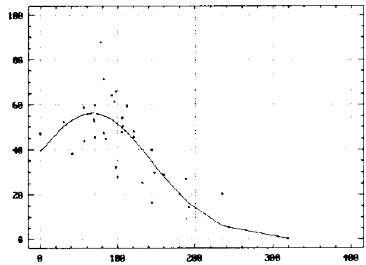

Figure 6 d: *Eragrostis nindensis*

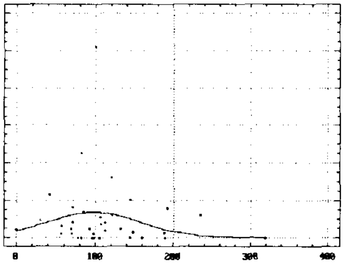

Figure 6 e: *Aristida meridionalis*

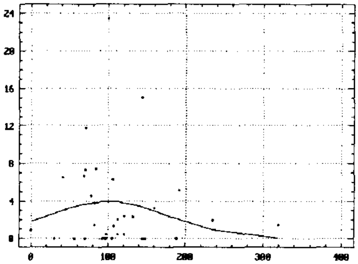

Figure 6 f: *Melinis repens* subsp. *grandiflora*

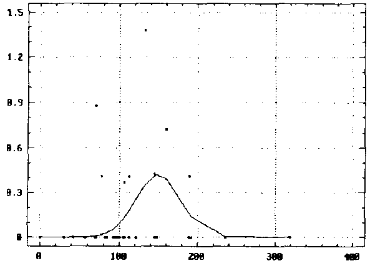

Figure 6g: *Fingerhuthia africana*

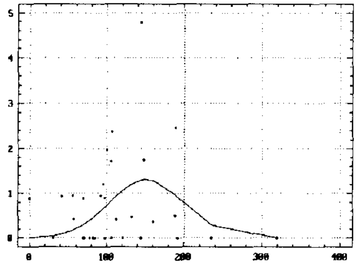

Figure 6h: *Monelytrum luederitzianum*

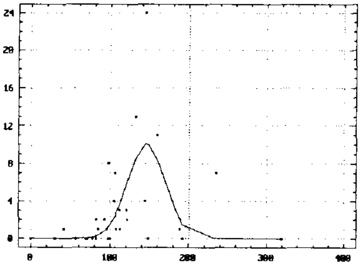

Figure 6 i: *Microchloa caffra*

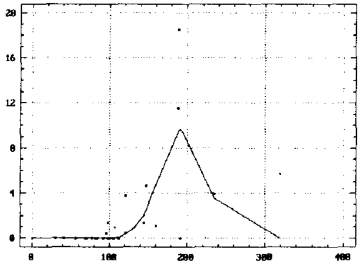

Figure 6 j: *Eragrostis porosa*

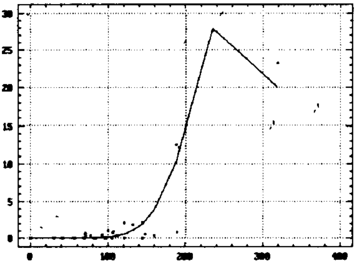

Figure 6 k: *Enneapogon cenchroides*

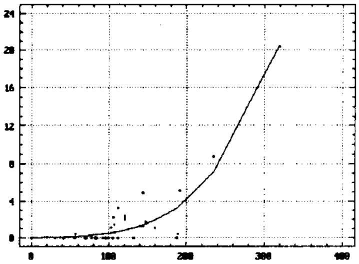

Figure 6 l: *Pogonarthria flecki*

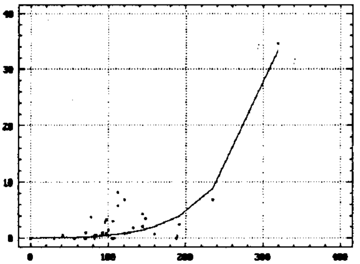

Figure 6 m: *Stipagrostis uniplumis*

Figure 6 a - m: The responses of 13 grass species to grazing pressure. The x-axis is the first ordination axis (partially a grazing gradient), and the y-axis is the percentage relative abundance in each case. The Gaussian curve was fitted in each case, using polynomial regression techniques. See Table 1 for r^2, a, -k and b values.

to environmental gradients (Gauch, 1982), and this may indicate different ecotypes with different environmental responses. If the sample on the extreme right was ommitted, the response of *S. uniplumis* could be interpreted as an Increaser II species or a "sub-climax" species.

Autecological and ecophysiological studies on grass species in the Highland savanna region would be valuable to substantiate or repudiate the tentative suggestions put forward here, not least for species such as *Anthephora pubescens*, *Heteropogon contortus, Melinis repens,* subsp. *grandiflora* and *Stipagrostis uniplumis* whose results here suggest different responses to what was previously thought. Many species seem to be responding to other environmental variables, such as shade (or lack of shade), or soil moisture (which is partially a function of grazing pressure). Others appear to respond differently to different grazing behaviour. The same species in different habitats may respond differently to grazing pressure. Janse van Rensburg & Bosch (1990) found, for example, that *Eragrostis racemosa* responded as a Decreaser on midslopes, and an Increaser I on footslopes in the Highland Sourveld of the Orange Free State. Müller

(1984) divides the grass species of Namibia into 3 broad successional groups: pioneers; sub-climax species; climaxs pecies. It is hoped that the results of this study, and further studies in this field will assist in refining these groups, as has been attempted here. It is suggested that this technique, in particular the analysis of the Guassian curve parameters, could be useful in this regard.

Conclusion

This study has shown that it is possible to construct a grazing gradient for the Highland Savannas. The grazing gradient may only be partially explained by grazing, and soil-moisture may play an important role as well. Future studies need to resample some of the same plots, as well as new ones, to determine the "ecological" trajectories of the samples, with time, and with different conditions. Samples from long-term grazing trials would be important to include as markers on the ordination axis. This is the first time that a grazing gradient has been constructed for the Highland Savanna. With the above suggestions, it can be refined, tested and extended, by sampling slopes on all aspects. The relationship between slope and grazing needs further investigation, and the monitoring of the movements and feeding behaviour of different breeds of cattle, and different wild ungulates should shed more light on a relatively untouched area of study. The apparent protection afforded by slopes, and the apparent protection that stones afford against erosion and evaporation, may be key factors as to why steeper slopes appear to be less heavily utilized. The inference of the ecological status of grass species in relation to grazing in this study, may provide new insights. More data is needed, however. As mentioned, the responses of species may vary according to the aspect of the slope upon which it is situated. Direct comparisons of Daan Viljoen Game Reserve with surrounding farms, with more long and short term history available (not an objective of this study) are also essential, in order to determine whether there is any difference attributable to different grazing behaviour. The hypothesis that some species respond differentially, according to the species of grazer, should be tested, and the influence of shade or the presence of trees, on different grass species should be examined. It should not be an objective of rangeland management to achieve uniform left hand side x-ordination values, a situation unlikely in the heterogenous vegetation of the Highland Savannas. Instead, more research effort should be put into understanding the system, and its components. The possible depletion of seed banks of important pioneer species, as a result of the elimination of "degrading" disturbances, cannot be disregarded, until further studies prove otherwise.

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