

THE DIET SELECTED BY FREE-RANGING BEEF CATTLE AND ITS EFFECT ON THE CONDITION OF A SEMI-ARID SAVANNA IN NAMIBIA

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SUMMARY

A long-term systems trial set up in 1984 to determine the optimal stocking rate of beef cattle in the camelthorn savanna of east-central Namibia was used to determine diet selection of free-ranging cattle, and its effects on animal performance and rangeland condition during three hot-wet, two cold-dry and one hot-dry season from 2001 to 2003.

Two cattle frame sizes (CFS), the small-framed purebred Sanga and the large-framed Afrikaner x Simmental crossbreed, and four systematically increasing stocking rates (SR), from low (15 kg cow mass/ha) to high (45 kg cow mass/ha), were combined in a 2 x 4 factorial design. Diet selection of cows was observed directly by bite-counting, replicated for cow, time of day, day and season. Dietary abundance of forage species was calculated from bites taken, and principal forages were identified. Rangeland condition was determined by measuring canopy cover of the soil, botanical composition, total herbaceous yield and the tuft vitality of six indicator grasses in every treatment plot before grazing commenced.

The dietary preference of the cattle was calculated for every forage species by comparing its dietary to its botanical abundance. The nutrient content and digestibility of herbaceous forage was determined from randomly collected samples, and compared to samples collected from each forage species individually by hand-plucking in a manner imitating the selectivity of cattle. Assumed dietary nutrient content was calculated from the dietary abundance and nutritive value of each forage species, and related to animal productivity. During statistical analysis using GLM procedures, data was pooled for CFS, SR and season.

Of all treatments, SR had the greatest effect on the diet selected by cattle and the condition of the rangeland. It was mostly season that affected the former, while CFS had little effect on either. The principal forage species were the perennial grasses *Schmidtia pappophoroides*, *Antheophora pubescens* and *Eragrostis lehmanniana*. Together, they contributed 59 %, on average, to cattle diet, but as much as 74 % at the lowest SR. These grass species were also highly preferred forages but their utilisation depended on SR ($P < 0,01$). The utilization of forbs and woody plants increased at higher SR ($P < 0,01$) and during drier seasons ($P < 0,01$). Small-framed cattle were less dependent on the highly preferred grass species than were large-framed cattle

($P < 0,01$) and were better able to exploit the available forage resource. This may have contributed to their higher fertility ($P < 0,05$) and systems productivity ($P < 0,01$) compared to large-framed cattle.

The botanical abundance and tuft vitality of the preferred grass species declined with increasing SR, while that of the less-preferred grass species increased ($P < 0,01$). Preferred grass species differed in their tolerance of grazing ($P < 0,01$) and only *S. pappophoroides* was able to maintain a sizeable presence in the sward even at the highest SR. The botanical abundance of woody plants was highest at the highest SR ($P < 0,05$), especially that of the known invasive species ($P < 0,01$). The effects of season and CFS on rangeland condition were much smaller.

The nutritive value of imitated forage samples was much higher ($P < 0,01$) than that of random herbaceous samples, especially in crude protein content, indicating that cattle were able to select a more nutritious diet than the average of the vegetation on offer. This ability decreased at higher SR ($P < 0,05$) and during drier seasons ($P < 0,01$), whereas CFS had little effect. The assumed dietary nutrient concentration appeared adequate, especially for small-framed cattle, except that the completely inadequate forage phosphorus content and grossly imbalanced dietary calcium:phosphorus ratio required supplementation.

In conclusion, cattle could pursue their dietary preferences at low SR only, and were forced to select previously less-preferred forage species at high SR. This resulted in a less nutritious diet and reduced animal performance; this was more pronounced during drier seasons and in large-framed cattle. From an SR of 25 kg cow mass/ha, changes in the diet selected by cattle induced changes in the species composition of the grass sward, reduced the vitality of the indicator grasses and reduced the productivity of individual animals. The threshold towards bush-encroachment was approached at an SR of 45 kg cow mass/ha, and this SR should thus not be exceeded, even though the productivity of the beef system continued to increase across all SR.

The perennial grass *S. pappophoroides* was a good indicator of the change in rangeland condition brought about by foraging cattle in the camelthorn savanna of Namibia. It is recommended that stockbreeders pursuing optimum individual animal production should limit their stocking rate to 25 kg cow mass/ha, whereas this can be increased to

45 kg cow mass/ha if the aim is to optimise beef production on the ranch while maintaining an acceptable rangeland condition.

INTRODUCTION

Namibia is one of the driest and most sparsely populated countries in southern Africa, and very dependent on the lucrative export of range-fed beef to the European Union. However, the number of ranches and beef cattle in Namibia has declined by 50 % since the 1960s (Rawlinson, 1994), as a result of degradation of its semi-arid savannas into a bush-encroached state. Bush encroachment occurs when a few, but usually only one of the indigenous woody species opportunistically exploits conditions, such as the weakening of the grass layer, that are favourable to it and so enable it to develop gradually into very dense stands that dominate the remaining vegetation (Smit, Richter and Aucamp, 1999). This encroachment has reduced the grass-based carrying capacity of Namibian savannas by 20 to 90 % (Adams and Werner, 1990; Bester, 1998). While the symptoms and treatment of rangeland degradation have been researched intensively, many of the underlying ecological processes, such as the interaction between free-ranging domestic ruminants and the vegetation, are not properly understood (Rothauge, 2000; Ward, 2005).

Diet selection of domestic ruminants is at the nexus of the plant – animal interface (Forbes, 1995). It refers to the ability of an animal to select from all the foods on offer those that it needs to satisfy its bodily requirement of nutrients. The composition of the diet depends on factors relating to the foraging animal and to the forage resource (Forbes, 1995). The ability of a free-ranging herbivore to select adequate food from the variety of plants on offer is crucial to its well-being (Rogers and Blundell, 1991), determines its level of production and reflects its habits and habitat (Milne, 1991).

At the landscape level, the choice of where to forage is a spatial one, whereas at the microsite level, the choice is between different forage species and even different parts of the same plant (Stuth, Lyons and Kreuter, 1993). In the semi-arid savannas of Namibia, free-ranging beef cattle face a huge choice of potential forage species: more than 4 200 taxa of plants are found on the range (Craven, 1999), including 391 different species of grass (Klaassen and Craven, 2003).

Foraging animals select preferred and principal foods. Preferred foods are those that an animal consumes first if given a choice. They are proportionally more abundant in the diet than in the feeding area (Petrides, 1975). Principal foods are those that contribute most to the total diet of an animal (Grunow, 1980) and may not necessarily be preferred (Petrides, 1975). The dietary preference ratio (DPR) is the ratio between the abundance of a plant species in the diet and its abundance in the herbage (Petrides, 1975; Senft, 1989), and enables us to rank forage species according to their preference. Forage species that are proportionally used more frequently than they occur in the feeding area

(DPR > 1) are preferred; those taken less frequently than they occur (DPR < 1) are not preferred or are avoided, while those taken in roughly the same proportion as they occur (DPR ~ 1) reflect a neutral appetite on the part of the animal.

The manner in which plants are defoliated by animals, the feeding habits of animals and the diet they select exert a shaping influence on the characteristics of savanna vegetation (Owen-Smith, 1999). African savannas co-evolved with herbivory (Skarpe, 1991) and although grazing is not the only parameter that shapes vegetation (O'Connor, 1994), it is a major factor in vegetation dynamics (Clements, 1928; Westoby, Walker and Noy-Meir, 1989). The condition of a rangeland, relating to some functional characteristic of the range, such as its productivity or botanical composition (Tainton, 1999), also reflects the effect of herbivory on vegetation.

Trends in rangeland condition are commonly used to determine whether animals have a positive or negative effect on the vegetation. As diet selection represents the interface between animal production and vegetative processes that react to defoliation (Emmans, 1991; Prache, Gordon and Rook, 1998), it is influenced by the stocking rate of animals, which determines the intensity of defoliation of plants as well as the competition between foraging animals (Jones and Sandland, 1974; Skarpe, 1991).

In Namibia, an existing systems trial of 20 years, which sought to determine the optimum stocking rate of different types of beef cattle for beef production to be sustainable in a semi-arid savanna (Kruger, 1998), offered an ideal opportunity to investigate the plant – animal interface in greater detail. This trial served to elucidate the diet selected by cattle and its effect on rangeland condition. The objective of the diet-selection trial between 2001 and 2003 was to quantify the diet of free-ranging beef cattle and its nutritive value, as well as the reaction of the vegetation to grazing and how these parameters were affected by grazing pressure, difference in cattle type and season of the year.

MATERIALS AND METHODS

Trial site

The long-term systems trial was initiated in 1984 on 5 516 ha of the Sandveld Research Station (22°00,237'S and 19°09,226'E at an altitude of 1 523 m above sea level) and was terminated in 2004. The station is situated in the central Kalahari camelthorn tree savanna, which is the most important commercial beef-producing region of Namibia (Rawlinson, 1994). It had received 392 ± 182,4 mm rain p.a. since 1984. Typically, rainfall is highly variable in time and space. The climate is characterised by a short hot-wet (HW) season with a vegetative growing period of only 48 days from January onwards, followed by a cold-dry (CD) season with frost occurring until August, and a hot-dry (HD) season of variable length from September onwards until the advent of the summer rains.

Experimental treatments

The long-term systems trial was a 2 x 4 factorial experiment of two cattle frame sizes (CFS) and four stocking rates (SR), resulting in eight individual treatments. The two CFSs were the small-framed, purebred Sanga (S) and the relatively large-framed Afrikaner x Simmental rotational crossbreed (L), weighing $381 \pm 41,6$ kg and $506 \pm 67,0$ kg, respectively ($P < 0,01$). The SR treatments were based on cow mass/ha and started at a low (L) rate, increasing systematically to a low-medium (LM), medium-high (MH) and high (H) SR (Table 1). The targeted SR was achieved by fixing the number of cows in a treatment herd at the outset of the trial in 1984, and the actual SR thus fluctuated around the target.

Table 1. Targeted and actual stocking rates (in kg cow mass/ha and ha/LSU) of the eight treatments, achieved by fixing the number of cows in a treatment herd

Treatment (CFS–SR)	Targeted stocking rate		Herd size (number of cows)	Actual stocking rate	
	(kg/ha)	(ha/LSU)		(kg/ha)	(ha/LSU)
L-L	15	30,0	18	17,7±0,65	25,4
L-ML	25	18,0	28	27,6±0,67	16,3
L-MH	35	12,9	40	35,8±0,12	12,6
L-H	45	10,0	52	44,1±0,16	10,2
S-L	15	30,0	25	17,2±0,32	26,2
S-ML	25	18,0	42	29,1±1,11	15,5
S-MH	35	12,9	60	40,5±0,10	11,1
S-H	45	10,0	78	49,8±0,09	9,0

Animal management and the preventive health routine were identical among treatments, as was the breeding and culling policy. Cows were weighed monthly after overnight fasting, while the body condition score (BCS) was determined on a 5-point scale at four critical stages of a cow's production cycle, viz. before the mating season started (December) and again at its end (April), when calves were weaned (July) and when cows started to calve (October). Weaners were raised outside the grazing area of a treatment, but at an SR similar to that of their treatment-of-birth. Pregnant replacement heifers were returned to their treatment-of-birth shortly before calving. Treatment effects thus accumulated over the generations of cattle.

Rangeland management was also identical among the different treatments, save for the SR. Each of the eight individual treatments was allocated a grazing area of $690 \pm 4,4$ ha, subdivided into six camps (paddocks) distributed randomly over the ranch. Cattle were rotated through these six camps on a set cycle of 7 days' occupation followed by 35 days' rest during the HW season and 14 days' occupation followed by 70 days' rest during the dry seasons. Drinking water was freely available at all times, as was a mineral lick during the HW and a protein, energy and mineral lick during the dry seasons. Fire and arboricides were excluded completely as rangeland management tools.

At the outset of the long-term systems trial, cows were blocked for age and parity, and camps for condition and

productivity, so that all treatments started from the same base. Beef-production parameters, such as calving and weaning rates and weaned-mass production per area, were recorded routinely for every individual animal and every treatment.

Duration of the diet-selection trial

The diet-selection trial was conducted during the last stage of the long-term systems trial and consisted of six seasonal experiments, viz. in the HW seasons of 2001, 2002 and 2003, the CD seasons of 2001 and 2002 and the HD season of 2002. Initially, the diet-selection trial had been scheduled for the HW and CD seasons only, but when it was realised that the nadir of grazing conditions was reached in the HD season only, one of the CD seasons was scrapped belatedly in favour of a single HD experiment.

In the HW season, experiments were conducted in March, when the vegetation had developed maximally as most of the rains had already fallen. Cows at this stage were suckling calves and were joined by the bulls. Experimentation during the CD season was timed to coincide with the coldest time of the year, June – July, shortly after the calves had been weaned off their pregnant dams, while experimentation occurred in October during the HD season, when cows were in late pregnancy. To minimise intra-seasonal variation, every one of the six seasonal experiments was completed within a period of four weeks.

Treatment plots

Only one camp of the six allocated to each treatment was selected to serve as the treatment plot in which the diet-selection experiment was carried out. To eliminate inter-camp variation, the same camp was used every time. The eight treatment plots averaged $142 \pm 28,9$ ha. They were selected on the basis of their soil and vegetation type as well as their proximity to each other. Treatment plots were dominated by red, sandy Hutton soils, which are more fertile and thus support a larger botanical diversity and herbaceous production than the alternative, the white-grey soils of the central Kalahari (Scholes, Dowty, Caylor, Parsons, Frost and Shugart, 2002).

Treatment plots were rectangular, with a watering point in one corner. A line transect was fixed by GPS coordinates from the watering point to the diagonally opposite corner of the camp. The eight diagonal line transects averaged $1\,535 \pm 251,8$ m in length and were used during botanical surveys before and after grazing of the treatment plots.

Methodology of diet-selection observations

Diet selection of cows in the treatment plots was observed on four consecutive days per treatment, twice during the morning and twice during the afternoon, when cattle, which are crepuscular feeders, are most active (Albright and Arave, 1997). Each time, six cows were selected at random from a treatment and observed at close quarters (< 5 m) for

a continuous period of 10 minutes per cow. Observed cows were identified for retrospective coupling to their production data and life history. All observations were performed within the first half of the period of plot occupation, because the plot at this early stage of occupation still offered animals the maximum choice of forage. Also, forage plants had not yet been defoliated to an extent that would limit their identification.

During observation, all bites taken by the cow were counted and all plants utilised were identified, as were the plant parts utilised, by following the bite-counting method developed by Narjisse (1991) for goats but found by Ortega, Bryant and Drawe (1995) to be applicable to cattle too. The dietary abundance of every forage species was calculated as a percentage based on the frequency of its occurrence in the diet. The DPR of every forage species was calculated from its abundance in the diet and vegetation respectively. During bite counting, the height at which forage was utilised was determined as being either above or below 120 cm, which corresponds roughly with the head-height of cattle. The habitat of the utilised grasses was also determined, i.e. whether they were utilised from the open or from underneath the canopy of a leguminous or a non-leguminous woody plant, in recognition of the importance of the association between savanna trees and grasses (Smit and Swart, 1994).

Methodology of the botanical surveys

A botanical survey was conducted in every treatment plot the day before cattle entered it. The survey was conducted along the diagonal line transect, and consisted of determining the botanical composition, canopy cover of the soil and herbaceous productivity. The botanical composition was determined by systematic point sampling (Tothill, 1987), using a free-falling, 3 m-long rod of steel to indicate accurately the point of impact. The plant whose canopy covered the point of impact was identified or, if a plant canopy did not cover the point, the nearest plant was identified.

The botanical abundance of plants was calculated as a percentage based on the frequency of occurrence in the point surveys. Multiple readings at one point were possible if a small plant at that point occurred under the canopy of a larger plant. In this manner, grasses were classified according to their sub-canopy habitat, occurring either in the open habitat or under the canopy of a leguminous or non-leguminous woody plant. The height of woody plants was also recorded as being either above or below 120 cm.

The proportion of points of impact that fell on bare soil or on soil covered by a plant canopy was used to calculate the canopy cover of the soil. Herbaceous productivity was determined by clipping 40 quadrats of 1 m² spaced regularly along the diagonal transect. All rooted herbaceous plants within the quadrats were clipped at ground level (Bester, 1988) and the material sorted immediately into ten fractions:

- the separate yields of six perennial grass species that had been chosen to indicate rangeland condition, viz. *Antheophora pubescens*, *Aristida stipitata*, *Brachiaria nigropedata*, *Eragrostis rigidior*, *Schmidtia pappophoroides* and *Stipagrostis uniplumis*,
- the yield of all other perennial grasses,
- the yield of all annual grasses,
- the yield of all dicotyledonous herbs and forbs and
- all moribund herbaceous matter.

Total herbaceous yield was obtained from the sum of the ten yield fractions. During clipping, the numbers of tufts of each of the six indicator grass species occurring inside the quadrats were counted, to calculate the tuft density and tuft yield of the indicator grasses, which indicated the vigour of these grasses. The yield fractions were weighed as was, sampled and the sample dried to constant mass in a forced-draught oven at 65 °C to determine its dry matter (DM) content. The six samples of the indicator grasses were retained for laboratory analysis.

The same clipping and tuft counting procedure was repeated in every treatment plot immediately after cattle had completed their period of occupation of the plot. The difference between the before- and-after grazing measurements was presumed to be due to the grazing. Rangeland condition was deduced from the botanical composition of the treatment plots, the canopy cover of the soil, herbaceous DM yield and the vigour of the indicator grasses.

Forage sampling and analysis

Dried samples were obtained from the six indicator grass species from every treatment plot before grazing commenced, as explained above. In addition, a seventh sample, representing the herbaceous bouquet on offer in the treatment plots, was collected from the yield fractions obtained during clipping, by reconstituting a composite sample proportional to the mass of the fractions, excluding only the moribund herbaceous matter. All dried samples were ground through a 1 mm sieve and subjected to standard laboratory analysis of their nutrient content and digestibility (Menke, Raab, Salewski, Steingass, Fritz and Schneider, 1979; Robertson and Van Soest, 1981; AOAC, 1995). Since these samples were collected by harvesting at ground level, they represented the total nutrients on offer in the herbaceous layer of the savanna and were termed 'random' samples.

After every seasonal bite-counting observation, the six indicator grass species and the six principal forage species in every treatment were sampled by hand-plucking in a manner imitating the selectivity displayed by cattle and in a manner representing the sub-canopy habitats – open sub-canopy (O), sub-canopy under a leguminous tree or bush (L) and sub-canopy under a non-leguminous tree or bush (NL) – from which they were selected by the cattle. In addition, every other forage species that had been utilised but had not yet been sampled was sampled once, from any

treatment, in a manner imitating the selectivity displayed by cattle. All imitated samples were collected in the morning to prevent diurnal variation in their nutrient content, and were immediately sealed in plastic bags to obtain their true field moisture content. They were then subjected to the same laboratory analyses as the random samples, and represented the nutrients selected by the cattle from the herbaceous bouquet on offer.

Statistical analysis of the data

All data entries were pooled for the three main treatments of CFS, SR and season of the year. All percentage frequency data was first transformed by arcsine, as recommended by Zar (1999) to eliminate bias due to a large number of small and a small number of large percentages, before being subjected to analysis of variance (anova) procedures of the general linear model (GLM) using the Statistical Procedures for Social Scientists (SPSS) package, version 10 (Bryman and Cramer, 1997). The alpha value was set at 0,05 and confidence limits at 95 %. Tukey's multiple range test was used to evaluate differences between specific means further, while partial eta-square (ζ^2) was used to estimate the size of a particular effect.

RESULTS AND DISCUSSION

Diet selection of cattle

The cows were observed to have taken 436 953 bites, or 37,9 bites per cow per minute during the six seasonal experiments. The vast majority of bites were from the grasses (Table 2), confirming that cattle are grazers (Forbes, 1995). In fact, they are specialist grazers, because over all treatments, three grass species, *Schmidtia pappophoroides*, *Antheplora pubescens* and *Eragrostis lehmanniana* constituted 59,2 % of the diet.

Table 2 The diet selected by free-ranging beef cattle in a semi-arid savanna of Namibia (arranged in descending order of importance)

Forage group and species	Abundance in diet (%)
Grasses:	83,9±11,72
<i>Schmidtia pappophoroides</i>	33,7±18,23
<i>Antheplora pubescens</i>	14,5±19,65
<i>Eragrostis lehmanniana</i> / <i>E. trichophora</i> *	11,0±10,50
<i>Stipagrostis uniplumis</i>	7,5±9,54
<i>Melinis repens repens</i>	5,8±5,11
<i>Eragrostis rigidior</i>	5,0±6,75
All other grasses (18 species)	6,4
Woody plants:	9,8±10,65
<i>Grewia flava</i> / <i>G. flavescens</i> **	2,6±4,34
<i>Tarchoanthus camphoratus</i>	2,6±4,17
All other woody species (9)	4,6
Dicotyledonous herbs and forbs:	6,3±7,46
<i>Nidorella resedifolia</i>	2,8±5,89
All other dicots (20 species)	3,5
Total diet (56 species)	100,0

**E. lehmanniana* can easily be distinguished in-hand from *E. trichophora*, but it was impossible to distinguish them at the distance and speed required during diet selection.

These species are the principal diet components of free-ranging beef cattle in the camelthorn savanna of east-central Namibia. In other arid southern African savannas, *S. pappophoroides* has also been reported to be a principal component of cattle diets (Mphinyane, 2001). Cattle utilised 24 of the 27 grass species occurring in the treatment plots, 12 of the 13 woody species and 21 of the 25 dicots.

Reliance on the three principal forage grasses increased to 74,3 % when cows were stocked at a low rate (Figure 1), indicating that these principal forage grasses were also highly preferred. Even at the highest SR treatment, these grasses still contributed 41,6 % of the diet ($P < 0,05$). Cattle thus relied greatly on a small number of highly preferred grass species under optimum grazing conditions, as has also been reported from Kenya (Odadi, Young and Okeyo-Owuor, 2003) and had to adjust their diet drastically to less favourable grazing conditions brought about by an increase in the SR. At the highest SR, the woody plants' contribution to the diet had doubled to $12,8 \pm 11,88$ % compared to the lowest SR ($P < 0,05$), but that of the dicots remained relatively constant across all SR treatments ($P > 0,05$).

The season of the year had as similarly a large effect on the composition of the diet as SR had, whereas the effect of CFS was small, affecting mainly the dietary abundance of the bulky grasses *Eragrostis rigidior* and *Stipagrostis uniplumis*, which were utilised better by small- than by large-framed cattle ($P < 0,05$ and $P < 0,01$ respectively). Cattle responded to increasing seasonal aridity by utilising more browsed forage at the expense of the grasses ($P < 0,01$) (Figure 2). In particular, the shed leaves of *Acacia mellifera* increased from 0 % in the HW diet to $4,4 \pm 6,06$ % in the CD diet ($P < 0,01$). Changes in the dietary abundance of individual forage species were magnified by a large number of significant two- and three-way interactions between treatments, indicating that the composition of cattle diets is sensitive to factors under managerial control, such as the stocking rate of cattle and to natural factors, such as the seasonality of climate.

Rangeland condition

The botanical composition of treatment plots was based on 477 ± 68,2 survey points per plot, safely exceeding the minimum number required for scientific monitoring (Hardy and Walker, 1991). More than 64 species of plants were recorded in the treatment plots, but some of the dicotyledonous herbs could be identified at the genus level only, e.g. the *Indigofera* spp. The rangeland was dominated by grasses (Table 3), of which nearly 99 % were perennial. The principal forage grasses of cattle, *S. pappophoroides*, *A. pubescens* and *E. lehmanniana*, made up 30,7 % of all rangeland plants across all treatments.

The SR of cattle ($P < 0,01$; $r^2 = 0,95$) and the season of the year ($P < 0,05$; $r^2 = 0,92$) had the greatest effect on the botanical composition of treatment plots, whereas the effect of CFS was negligible ($P = 0,34$; $r^2 = 0,91$). The botanical abundance of the three principal forage grasses decreased from 43,7 % at the lowest to 20,0 % at the highest SR

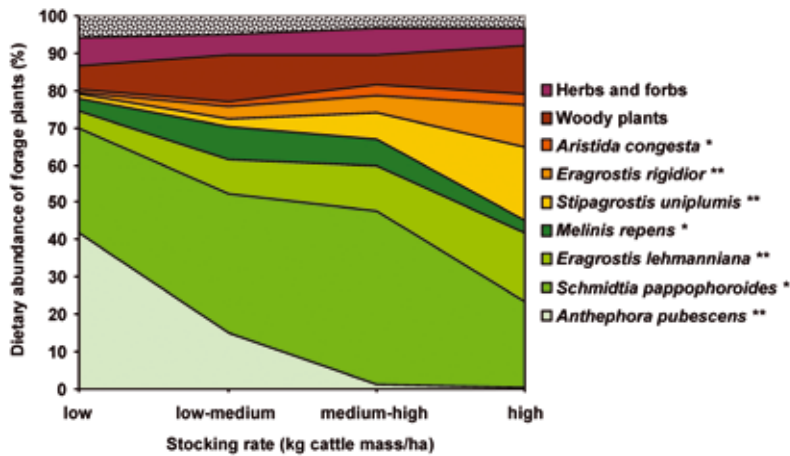


Figure 1. The abundance (%) of forage plants in the diet of free-ranging beef cattle as affected by the stocking rate of cattle (*: $P < 0,05$; **: $P < 0,01$).

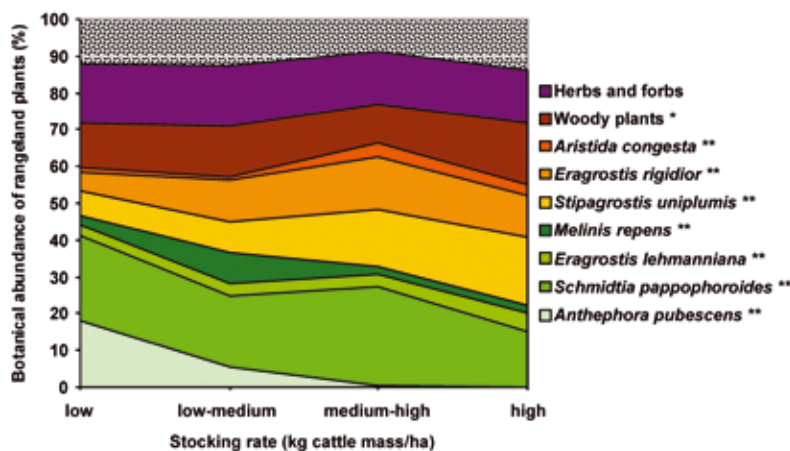


Figure 2. The abundance (%) of forage plants in the diet of free-ranging beef cattle as affected by the season of the year (*: $P < 0,05$; **: $P < 0,01$).

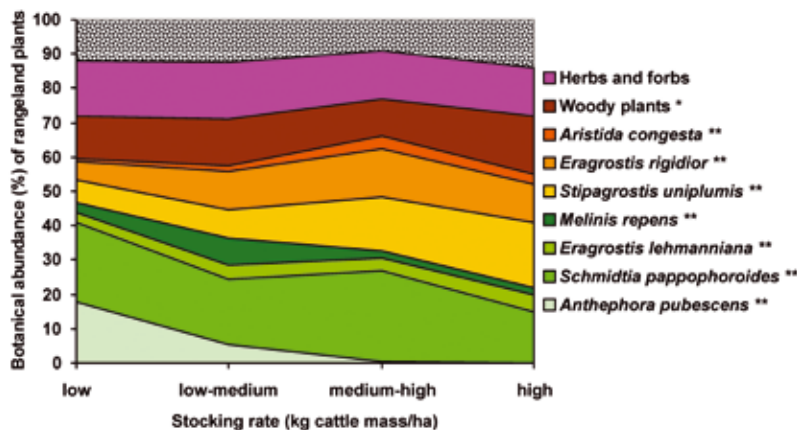


Figure 3. Botanical composition (%) of the rangeland as affected by the stocking rate of cattle (*: $P < 0,05$; **: $P < 0,01$).

Table 3. Botanical composition of a semi-arid rangeland in Namibia (arranged in descending order of importance)

Plant group and species	Botanical abundance (%)
Grasses:	71,4±5,19
<i>Schmidtia pappophoroides</i>	21,0±5,33
<i>Stipagrostis uniplumis</i>	12,5±5,68
<i>Eragrostis rigidior</i>	10,4±4,39
<i>Anthephora pubescens</i>	5,9±7,30
<i>Aristida stipitata</i>	5,2±3,32
<i>Eragrostis lehmanniana/ E. trichophora</i> *	3,8±1,73
<i>Melinis repens repens</i>	3,6±2,94
<i>Aristida congesta</i>	2,2±1,81
All other grasses (19 species)	6,8
Woody plants:	13,4±3,21
<i>Acacia erioloba</i>	3,9±1,38
<i>Dichrostachys cinerea</i>	2,0±1,01
All other woody plants (10 species)	7,5
Dicotyledonous herbs and forbs:	15,3±5,44
<i>Tylosema esculentum</i>	5,6±2,43
<i>Nidorella resedifolia</i>	2,7±2,21
All other dicots (23 species)	7,0
Total (64 species)	100,0

*These two grasses were grouped together because of difficulties distinguishing them during diet selection observations. However, 95 % were *E. lehmanniana* and only 5 % were *E. trichophora*.

($P < 0,01$), with only *E. lehmanniana* able to increase in abundance ($P < 0,01$) despite the increased grazing pressure (Figure 3). In contrast, the botanical abundance of the less preferred, bulky grasses *S. uniplumis* and *E. rigidior* increased from 12,0 % at the lowest to 30,1 % ($P < 0,01$) at the highest SR. Different responses by individual grass species to grazing had caused a transformation of the grass sward over the years, by weakening the more preferred species to the advantage of the less preferred species.

The implication is that rangeland managers cannot simply evaluate the abundance of 'grass' to estimate rangeland condition, but have to use individual grass species to obtain a good indication of the effect of grazing on the grass sward. *Schmidtia pappophoroides* appears to be very suited to this purpose, as it is a principle and a preferred forage species of cattle and is abundant in pristine and under-utilised rangeland, yet still able to maintain a sizeable presence at stocking rates that appear to be viable in ranching practice.

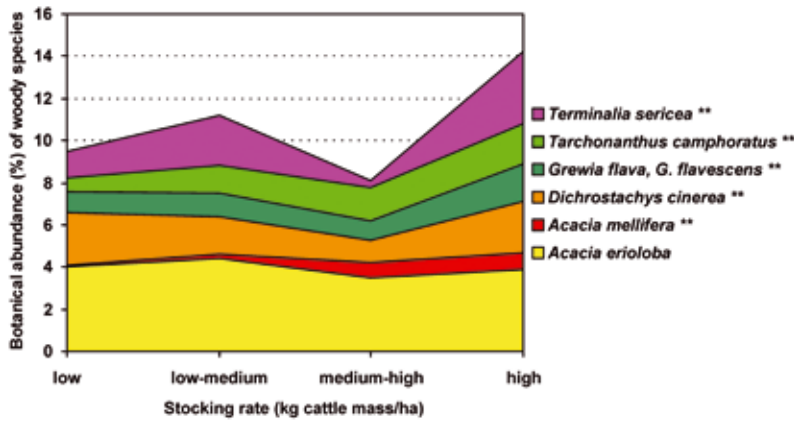


Figure 4. The botanical abundance (%) of woody species as affected by the stocking rate of cattle (**: $P < 0,01$).

Increasing the SR initially had little effect on the botanical abundance of woody plants, but in plots stocked at the highest rate, the abundance of woody plants increased significantly ($P < 0,05$) to 16,8 %, compared to 12,1 % at the lowest SR. The abundance of known invasive species such as *A. mellifera* and *Dichrostachys cinerea* increased by 89 % at the highest compared to the lowest SR (Figure 4). It thus appeared that the ecological threshold towards densification of woody plants as a result of grazing pressure had been reached at the highest SR applied in this trial, although the woody component still consisted of a mix of micro- and macrophyllous, evergreen and deciduous species. Increased grazing pressure is well known to change the balance between herbaceous and woody components of a savanna (Smit *et al.*, 1999).

The major effect of increasing seasonal aridity was to decrease the botanical abundance of herbs and forbs ($P < 0,01$), although most were perennial, and to increase the relative abundance of *E. lehmanniana* ($P < 0,01$). The canopy cover of the soil was affected by the SR of cattle ($P < 0,05$), decreasing from 81,1 % to 73,6 %, but not by season of the year or CFS ($P > 0,05$).

The mean herbaceous DM yield before grazing was $172,1 \pm 39,51$ g/m² over the six seasonal experiments. It was reduced by 8 % to $158,8 \pm 36,52$ g/m² after grazing. Herbaceous yield before grazing was not affected by CFS and season of the year ($P > 0,05$), but SR reduced it by 21 %, from $185,5 \pm 31,81$ g DM/m² to $153,5 \pm 40,89$ g DM/m² ($P < 0,05$).

The fractional yields of the principal grasses *A. pubescens* and *S. pappophoroides* declined sharply due to an increase in SR (by 99,5 % and 25,5 % respectively; $P < 0,01$), while that of the bulky grasses *Aristida stipitata*, *E. rigidior* and *S. uniplumis* increased just as noticeably (by 83 %, 247 % and 233 % respectively; $P < 0,01$). In addition, the density and tuft yield of the principal forage grasses declined dramatically with an increase in the SR ($P < 0,01$), whereas the density and tuft yield of the bulky grasses increased ($P < 0,01$) (Figure 5). Therefore, even though the vigour of preferred forage grasses declined over the years as grazing pressure increased, as was also recorded by Kirkman and Moore (1995), it was partly compensated for by an increase in the vigour of the less preferred, bulky grasses.

Although this compensatory effect may have partly obscured the weakening of the grass sward generally, it was still apparent that increasing the SR of cattle reduced the productivity and condition of the rangeland. Due to significant two- and three-way interactions between

treatment effects on various grass species, the degradation of the range appeared to be worse in plots frequented by large-framed cattle and during the drier seasons of the year. If, therefore, a grass such as *S. pappophoroides* is to be used as an indicator of rangeland condition, not only should its abundance be monitored, but also the yield and density of its tufts.

Moribund herbaceous matter comprised 24,3 % of the total herbaceous yield over all treatments (Figure 6). Its proportional contribution to total yield was not affected by treatment ($P > 0,05$), but the absolute yield of moribund matter, in g/m², declined with SR ($P < 0,05$) and increased during the HD season ($P < 0,01$), emulating the yield of living herbaceous matter. The large amount of moribund matter produced by the herbaceous layer of this semi-arid savanna did not appear to increase the organic matter content of the upper soil layer (Rothauge, Smit and Abate, 2003), possibly because it was oxidised above the soil surface before its nutrients could be recycled into the soil.

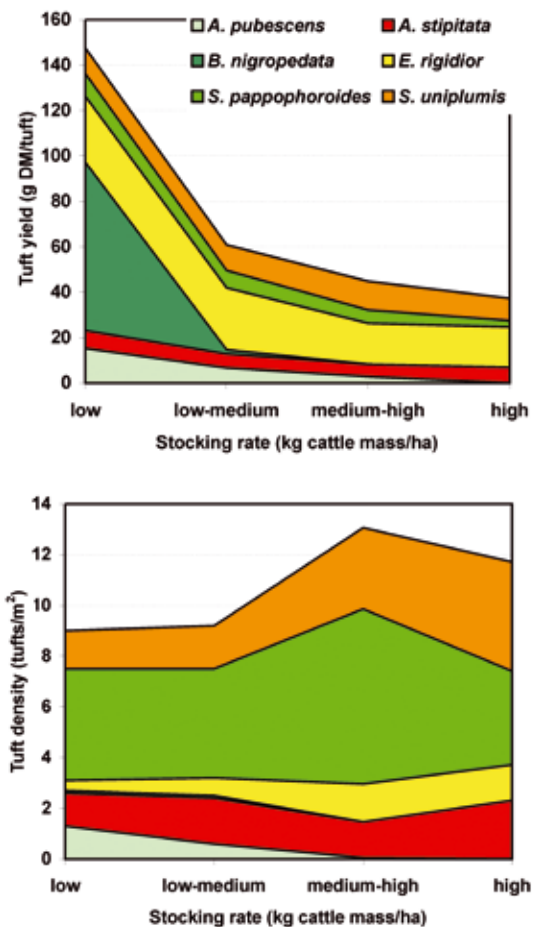


Figure 5. The effect of stocking rate of cattle on the vigour of six grass species, as represented by the yield of DM per tuft (top) and the density of tufts (bottom).

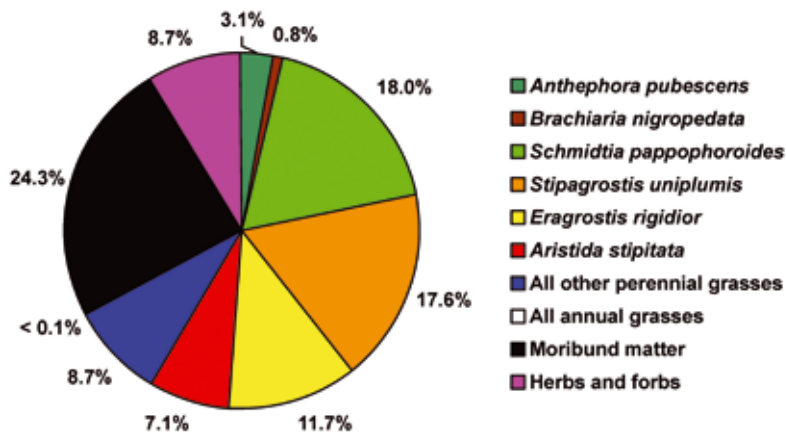


Figure 6. Proportional composition (%) of the total herbaceous DM yield before grazing of the treatment plots

Preference for forage species

The principal forage grass species *A. pubescens*, *E. lehmanniana* and *S. pappophoroides* were highly preferred by cattle irrespective of treatment, with an average DPR of 2,5, 2,9 and 1,6 respectively. Their palatability resulted in cattle utilising these grasses uniformly to a residual stubble height that became lower with increasing SR.

The bulky grass species *E. rigidior* and *S. uniplumis* were not preferred at any treatment, and their DPR varied from virtually zero at the lowest to close to 1,0 at the highest SR. As soon as the more-preferred grass species were eaten out of the sward at the higher SR, the bulky grasses became more prominent in the diet of cattle; not because they were intrinsically palatable but merely because more-preferred grasses were no longer freely available in the transformed grass sward. The bulky grasses were utilised by cattle extremely selectively: large tufts were ignored whereas smaller tufts and those utilised before were utilised preferentially (inter-tuft selection), and stems and leaves were utilised only once all inflorescences had been utilised (intra-tuft or organ selection). The third category of grass species was not utilised much at any treatment and thus remained unpreferred, with a DPR close to zero, e.g. *A. stipitata* and *Eragrostis pallens*.

The dietary preference of cattle for the grasses was influenced by season of the year, with grasses being considerably more preferred during the HW season, when they were green; and CFS, with large-framed cattle displaying a slightly more pronounced preference for grasses than that displayed by small-framed cattle. Approximately 84 % of the grasses occurred in the open, but as the SR of cattle increased, grasses from the canopied habitats, and especially from underneath leguminous trees and bushes, constituted 20 % and more of the diet of cattle ($P < 0,01$; $r^2 = 0,89$). However, this effect was dependent on the particular grass species, as not all species occurred in the canopied habitats.

Increasing aridity of the season further enhanced the utilisation of grasses occurring in the canopied habitats

($P < 0,01$; $r^2 = 0,80$). In turn, a highly preferred grass such as *A. pubescens* increasingly found refuge in the canopied habitats at higher SR, when up to 63,7 % were in canopied habitats compared to only 10,7% at the lowest SR ($P < 0,01$), indicating that woody canopies offered highly preferred grasses some protection against intensive utilisation. Some of the most highly preferred forage species were woody plants, but in most instances they represented niche forages that contributed to diet only occasionally.

The most preferred of all forages was *A. mellifera*, with an average DPR of 4,0, but only its fallen leaves were utilised late in the CD season. It was a seasonally limited resource enriched by imported matter such as bird droppings, spider webs and soil, and was soon exhausted. *Grewia flava* was one of the few woody plants that was utilised at all

seasons of the year: its green leaves were eaten in the HW season, the shed, dry leaves in the CD season and the buds in the HD season and, accordingly, it had a high average DPR of 2,2. The height at which cattle browsed was influenced by season of the year only. The evergreen, broad-leaved woody plant *Tarchonanthus camphoratus* for example, was utilised mainly at a height less than 120 cm above ground in the HW season, but as seasonal aridity increased, cattle utilised it progressively higher up ($P < 0,01$) until it was completely stripped during the HD season.

The nutritive value of forage

Altogether 1 012 forage samples were collected over the six seasonal experiments; of these roughly one-quarter were collected randomly and three-quarters in a manner imitating the foraging selectivity of cattle. Imitated forage samples had a much higher nutritive value than random samples (Table 4, next page), indicating that cattle were able to select a more nutritious diet from the vegetation than the average that was on offer. The difference between random and imitated samples extended to the individual forage species too.

The nutritive value of the randomly sampled herbaceous bouquet on offer was severely affected by the season of the year, as the protein ($P < 0,01$), energy ($P < 0,01$), mineral content ($P < 0,05$) and digestibility ($P < 0,01$) of herbage declined during the dry seasons, while the fibre content increased ($P < 0,01$ for NDF; $P < 0,05$ for CF). Even though the effect of SR was not significant, it tended to consistently decrease the nutritive value of the herbaceous bouquet on offer. The effect of CFS was negligible.

The effect of season on the nutritive value of imitated forage samples was profound, and only the CF and ADF content were not affected ($P > 0,05$) by season. However, the effect depended on the individual forage species. In general, the nutritive value of imitated forage samples declined from the HW to the CD season but recovered again slightly during the HD season, especially that of the principal forage grasses. This was a result of renewed availability of fresh

Table 4. Nutrient content and digestibility of all random and imitated forage samples

	Random samples	Imitated samples	Difference
Number of samples	280	732	–
Field dry matter (DM, %)	76,8±15,09	65,2±22,61	$P < 0,01$
Crude protein (CP, %)	4,5±1,63	7,7±3,74	$P < 0,01$
Calcium (Ca, %)	0,37±0,238	0,70±0,779	$P < 0,01$
Phosphorus (P, %)	0,03±0,018	0,05±0,032	$P < 0,01$
Crude fibre (CF, %)	37,9±3,21	33,6±7,43	$P < 0,01$
Acid detergent fibre (ADF, %)	45,1±3,74	40,7±6,24	$P < 0,01$
Neutral detergent fibre (NDF, %)	72,7±5,50	63,9±13,64	$P < 0,01$
Fat (%)	1,4±0,37	2,1±1,28	$P < 0,01$
Ash (%)	8,2±2,41	9,3±5,89	$P < 0,01$
Digestibility (DOM, %)	44,9±8,49	50,4±9,27	$P < 0,01$
Metabolizable energy (ME, MJ/kg)	6,2±1,03	7,2±1,18	$P < 0,01$

regrowth when the increase in temperature and daylight length caused perennial grasses to break their dormancy. Since the sprouting is driven by stored reserves within the grass, it is unsustainable until the rainy season starts (Wolfson and Tainton, 1999).

In contrast to its effect on random samples, SR significantly affected the nutritive value of the imitated forage samples (Table 5). Imitated samples collected in plots stocked at the lowest SR contained 27 % more Ca ($P < 0,01$), 6 % less CF ($P < 0,05$), 6 % less NDF ($P < 0,05$), 26 % more fat ($P < 0,01$) and 6 % more ME ($P < 0,01$), and were 4 % more digestible ($P < 0,05$) than samples collected in plots stocked at the highest SR. Thus, cattle stocked at a low SR were better able to exploit the nutritional resource on offer in the vegetation than were cattle stocked at a higher SR. This was due mainly to the effect of SR on grasses, whose P ($P < 0,05$; $r^2 = 0,02$), ADF ($P < 0,01$; $r^2 = 0,03$) and ash content ($P < 0,01$; $r^2 = 0,03$) reacted significantly to SR, as did the above nutrients. Even the CP content of imitated grass samples tended to decrease with an increase in the SR, but increased again at the highest SR ($P > 0,05$), indicating that at the highest SR treatment grasses were grazed right down into the reproductive tillering part at the base of the tuft. This was also recorded when severe grazing was applied by Mufandaedza (1977), and it is highly detrimental to continued productivity and survival of the perennial grass tuft.

In contrast, SR had a small effect on the nutritive value of woody plants, affecting only their ADF ($P < 0,05$; $r^2 = 0,14$), NDF ($P < 0,05$; $r^2 = 0,12$) and ash content ($P < 0,05$; $r^2 =$

0,13), and had no effect on dicots. Imitated samples from woody plants and dicots were also unaffected by treatment interactions, as was the case for many grass species, indicating that it was the combination of treatments that put pressure on grasses.

Grasses from canopied habitats were utilised more frequently by cattle that were under stress from a high SR and/or the aridity of the season than they were utilised by cattle that did not experience such stress. Grasses occurring in the canopied habitats had a significantly higher nutritive value than those occurring in the open, even if they were of the same species. Grasses from the leguminous habitat, for example, contained 22 % more CP ($P < 0,01$), 12 % more fat ($P < 0,01$), 2 % less CF ($P < 0,05$) and 3 % less NDF ($P < 0,01$) than grasses from the open, indicating clearly that the grass – tree association so common of semi-arid savannas extended nutritional benefits to foraging cattle (Rothauge *et al.*, 2003).

Animal production

When the changes in the composition of the diet of cattle were combined with changing nutritive value of the utilised forage, it was obvious that cattle stocked at a high rate experienced a worse nutritional status than cattle stocked at a lower rate, and that this effect was aggravated by the increasing aridity of the season. In addition, cattle stocked at a high rate had less herbage at their disposal in the treatment plots than cattle stocked at a lower rate, although this trial did not attempt to quantify the amount of forage actually ingested by cattle. A drop in animal production was thus expected at the higher SR treatments, especially since the nutritional nadir coincided with the weaning of calves in the CD season and renewed calving in the HD season.

Over the three years of the diet-selection trial and in accordance with results obtained by Els (2002) over the much longer period of the systems trial, the increase in SR resulted in deteriorating performance of individual cows (Figure 7). As SR increased from lowest to highest, cows became 11 % lighter ($P < 0,01$), 13 % lower in BCS ($P < 0,01$), 3 % less fertile in terms of their calving rate ($P < 0,01$) and inter-calving period (ICP, $P < 0,01$), while the average age of the cow herd was reduced by 9 % ($P > 0,05$).

Since the culling policy was the same for all treatments, the reduction in cow age at the higher SR treatments implied a shorter lifetime in the treatment herd because of the need to replace the individual sooner. The response curves for body mass and ICP have exactly the same shape as those predicted by Jones and Sandland (1974).

Productivity of the beef system, measured in kg of weaned mass produced per hectare (Figure 8), increased across all SR treatments ($P < 0,01$), albeit by only 241 % compared to the 300 % increase in SR. The decrease in individual productivity was evidently offset by the increase in the number of animals in a system (treatment), and the turning point in the response curve of the total system, as predicted

Table 5. The effect of stocking rate on the nutritive value and digestibility of imitated samples obtained from grasses, woody plants and dicotyledonous herbs and forbs (means within a structural group, e.g. grasses, with different superscripts differ significantly at $P < 0,01$ if superscripts are in capital and at $P < 0,05$ if superscripts are in small letters)

Sample n	Field DM %	CP %	Ca %	P %	CF %	ADF %	NDF %	Fat %	Ash %	DOM %	ME MJ/kg
Grasses	125	65,9±23,14	6,8±2,55	0,60±0,480 ^A	0,05±0,026a	35,8±3,51 ^A	41,6±3,27 ^A	2,0±0,82a	8,5±2,33 ^A	52,3±7,89 ^A	7,5±0,94 ^A
	147	64,7±19,87	6,4±2,33	0,54±0,415 ^A	0,05±0,026a	36,5±3,09 ^B	42,4±3,58 ^{A,B}	1,9±0,75a	8,0±2,37 ^A	51,0±9,42 ^{A,C}	7,4±1,21 ^A
	136	68,5±21,58	6,1±2,53	0,30±0,192 ^B	0,04±0,022b	37,3±3,63 ^{B,C}	43,3±4,51 ^B	70,4±6,79 ^B	7,8±2,43 ^A	48,8±8,81 ^B	7,0±1,05 ^B
	136	67,4±20,66	6,5±2,78	0,43±0,309 ^C	0,04±0,032b	37,6±2,97 ^C	43,3±3,20 ^B	72,7±4,40 ^C	7,3±2,48 ^B	49,7±9,45 ^{B,C}	7,1±1,16 ^B
Woody plants	22	65,8±26,07	11,1±4,10	0,87±0,827	0,05±0,025	21,4±4,93	37,8±7,88a	3,9±2,41	8,9±4,71a	46,8±9,38	7,1±1,63
	18	69,9±26,55	12,4±4,12	1,09±0,341	0,06±0,032	22,4±4,81	35,5±7,33a	3,3±2,31	11,0±9,53a	45,9±11,44	6,9±1,61
	15	69,1±23,39	12,0±4,31	1,19±0,213	0,07±0,064	20,8±5,52	33,1±7,89a,b	40,2±8,18b	10,1±8,19a	45,7±8,22	7,2±1,25
	17	82,2±20,06	12,5±3,96	1,56±0,180	0,05±0,040	19,8±6,55	29,2±9,77b	38,5±10,95b	2,8±2,49	19,1±17,19b	48,1±10,20
Dicots	20	43,1±12,99	11,4±2,77	1,73±1,415	0,07±0,028	23,3±8,13	35,1±7,42	3,3±1,31	16,6±8,80	55,9±6,71	8,0±0,95
	15	42,5±12,95	11,8±2,72	1,65±0,742	0,08±0,033	26,6±9,85	35,6±6,58	2,6±0,70	14,7±7,37	56,0±7,43	8,1±1,04
	12	35,4±8,85	12,1±2,01	1,66±0,790	0,10±0,043	22,3±8,03	32,1±5,54	41,0±7,07	21,2±9,83	54,4±10,93	7,6±1,17
	16	40,4±11,44	12,2±3,70	1,60±0,945	0,09±0,036	24,9±7,25	33,1±4,84	42,9±7,36	16,7±6,88	54,0±8,91	7,6±0,92
All imitated samples	167	63,2±23,67	7,9±3,41	0,85±0,978 ^A	0,05±0,027	32,5±7,41a	40,3±5,25	2,4±1,40 ^A	9,5±4,76	52,0±8,26a	7,5±1,07 ^A
	180	63,4±21,07	7,4±3,41	0,73±0,718 ^{A,B}	0,05±0,028	34,5±7,50b	40,8±6,74	2,1±1,10 ^B	8,9±4,63	50,9±9,68a,b	7,4±1,26 ^A
	164	66,2±22,69	7,2±3,68	0,48±0,595 ^C	0,05±0,036	34,5±7,42b	41,4±6,49	65,2±13,38b	9,0±5,43	49,0±9,17c	7,1±1,10 ^B
	170	66,5±21,98	7,7±3,94	0,67±0,768 ^B	0,05±0,037	34,3±6,39b	41,1±5,09	66,2±14,14b	9,3±7,44	50,1±9,61b,c	7,1±1,25 ^B

Stocking rate

Low
Low-medium
Medium-high
High

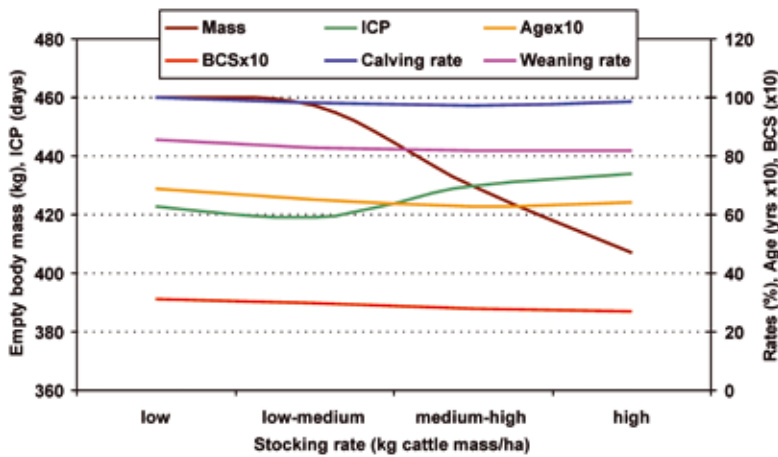


Figure 7. Effect of the stocking rate of cattle on the performance of individual cows, such as their age, body mass, body condition score (BCS) and fertility

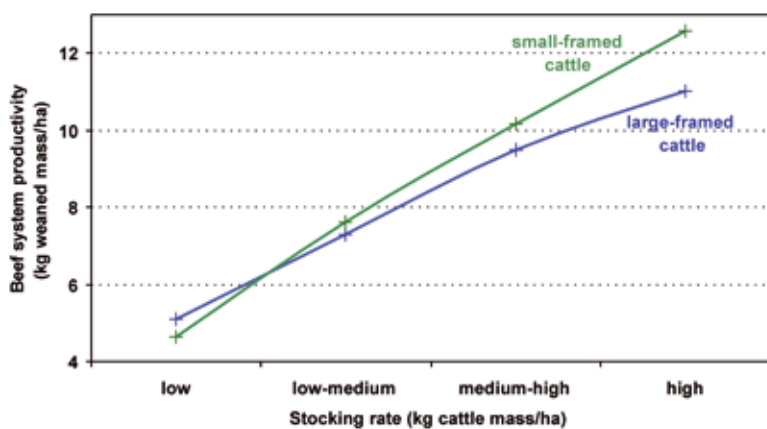


Figure 8. The response of beef system productivity to an increase in the stocking rate of cattle (the arrow indicates the inflection point in the response curve of large-framed cattle)

by Jones and Sandland (1974), was not reached under the conditions of this trial. However, it did appear as if an inflection point was reached in the response curve of large-framed cattle at the medium-high SR, whereas the response curve of small-framed cattle continued increasing linearly (effect of CFS on system productivity: $P < 0,05$). Thus, it appeared that the SR treatment resulted in more stress for large-framed cattle than for their small-framed contemporaries.

CONCLUSION AND RECOMMENDATION

The diet selected by free-ranging cattle in a semi-arid savanna in Namibia was severely affected by the stocking rate of cattle and the season of the year. Only at a low stocking rate could cattle express their true dietary preferences, relying heavily on a small number of highly preferred perennial grass species. As the stocking rate increased, they were forced to make increasing use of previously unpreferred forages, to the extent that their nutritional status and individual productivity declined significantly. Similarly, cattle were forced to make increasing use of browsed forage during the dry seasons of the year, when the grasses are dormant and do not regrow after defoliation. By comparison, the effect of cattle frame size on diet composition was small, although it appeared that small-framed cattle were better able to exploit the available forage resources than large-framed cattle were.

Increasing the stocking rate of cattle had severe effects on rangeland condition. As soon as the stocking rate was increased, the most preferred grass species became weaker and less competitive, and were replaced in the grass sward by less preferred, bulkier grass species with a lower nutritive value. At the highest stocking rate applied in this trial, the threshold towards bush encroachment appeared to be reached as well. Degraded rangeland was less productive and nutritious, and thus less able to support beef production at a high level.

It is therefore recommended that beef producers in the semi-arid savannas of south-western Africa do not exceed a stocking rate of 45 kg cattle mass/ha. At this rate, they can expect relatively high system productivity on a productive, if transformed, grass sward in a savanna that is not yet bush-encroached. At a higher stocking rate, degradation of the range will advance to a higher, more deleterious level that will probably make beef production less sustainable.

Cattle stud breeders that depend on the sale of high-performing live animals are advised not to exceed a stocking rate of 25 kg cattle mass/ha, as only such a low rate will support maximum production of individual animals. Ranching with an adapted, indigenous small-framed breed of cattle will allow ranchers to slightly exceed the above stocking rate recommendations without sacrificing productivity, as the small-framed breed in this trial was more productive and better able to exploit foraging conditions than their large-framed contemporaries.

ACKNOWLEDGEMENTS

The financial assistance of the International Foundation for Science (IFS), Stockholm, Sweden, through its grant B/3183-1, is gratefully acknowledged. The personnel of the Sandveld Research Station are thanked for their assistance in the field, and the staff of the AEZ Laboratory for the analyses of the feed samples.

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