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FORAGE SELECTION OF AFRICAN BUFFALO THROUGH THE LATE DRY SEASON IN THE SATARA REGION OF THE KRUGER NATIONAL PARK

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A research report submitted to the Faculty of Science, University of the Witwatersrand, in partial fulfilment of the requirements for the Degree of Master of Science in Resource Conservation Biology.

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DECLARATION

I declare that this research report is my own work. It is being submitted for the Degree of Master of Science in the University of the Witwatersrand, Johannesburg. It has not been submitted for any degree or examination in any other University.

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(Signature of candidate)

_____ 18 day of March 2003

ABSTRACT

Forage selection by buffalo and the contribution of grass species to buffalo diet were investigated in the granite and basalt landscapes in the Kruger National Park during the late dry season, between July and October in 2002. Two buffalo herds were selected for observation, occupying each of the landscapes. Data on forage selection and dietary contribution were collected by backtracking along the foraging pathways and identifying grazed and not grazed tufts in feeding quadrats. The percentage of green leaves, tuft height and number of stems of each tuft were recorded. Four fixed transects were placed across the catena in each landscape and greenness retention was measured by checking for green leaves in quadrats.

Panicum maximum, *Panicum coloratum*, *Cenchrus ciliaris*, *Heteropogon contortus* and *Digitaria eriantha* were favoured grass species by buffalo. *Urochloa mosambicensis*, *Themeda triandra*, *Eragrostis superba* and *Bothriochloa insculpta* were classified as intermediate, whereas *Cymbopogon* spp. *Setaria* spp., *Pogonarthria squarrosa* and *Aristida congesta barbicolis* were neglected. The acceptance frequency of grass species increased with the progress of the dry season, but only *D. eriantha*, *U. mosambicensis*, *E. superba* and *B. insculpta* recorded significant increases in acceptance between consecutive periods. *P. maximum*, *T. triandra* and *D. eriantha* contributed more to the diet of the herd on the granites than to the diet of the herd on the basalts, whereas *P. coloratum*, *U. mosambicensis* and *C. ciliaris* contributed more to the diet of the herd on the basalts than to the diet of the herd on the granites. Buffalo selected for grass species offering a higher percentage of green leaves and intermediate height. Selection for grass species by buffalo did not differ significantly between the two landscapes.

Landscapes did not differ significantly in the proportions of quadrats retaining green leaves during the dry season. Grass in bottomlands was greener than grass in midslopes or uplands. In July, most feeding sites were located in bottomlands, but with the progress of the dry season buffalo increased the utilization of midslopes and uplands.

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DEDICATION

This research report is dedicated to my mother and brothers for their support and encouragement during my studies.

ACKNOWLEDGEMENTS

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CHAPTER 1. INTRODUCTION

General introduction

Many populations of African buffalo (*Syncerus caffer*) are confined in conservation areas (Sinclair 1977). In these areas, efforts are made to ensure long-term existence of the species. However, despite such efforts there are factors that might undermine conservation efforts for African buffalo. Among the most important threats to conservation are diseases, habitat degradation and predation. The Kruger National Park (KNP) buffalo population has faced the problem of bovine tuberculosis (BTB) since 1990 (Bengis *et al.* 1996). This exotic disease is spreading northward through the Park with the south having the highest prevalence and the north showing the lowest prevalence. The central region has intermediate levels of BTB. Within each region there is variability in the prevalence of the disease between herds.

Owing to the absence of an effective vaccine and/or treatment for the disease, there is a need to deal with the disease not only from an animal health perspective, but also to understand the ecological factors that may influence the transmission rate and the spread of the disease. The transmission and the spread of BTB are related to the movements of the animals, which are influenced by the availability of food, water, shade and predation avoidance. Many management questions related to habitat use and movements can be addressed by understanding the adaptive responses of the animals to the changing environment.

Large herbivores such as buffalo have a diet consisting of a wide range of grass species that differ from each other in terms of their chemical and physical properties. The process of diet selection determines both the quantity and the quality of food consumed and, hence the nutritional status, survival, growth and reproduction of the individuals (Langvatn and Hanley 1993, Hanley 1997). The spatial and temporal distribution of preferred grass species may influence herd movements since buffalo movements reflect adjustments in obtaining resources that fluctuate in availability; particularly food and water (Sinclair 1977).

Studies on forage selection by buffalo have been carried out in different regions of Africa (Field 1976, Sinclair 1977, Taylor 1989, Prins 1996, Perrin and Brereton-Stiles 1999). However, the factors influencing grass species selection, namely grassland species composition, physical characteristics of the grass species and forage availability vary

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spatially and temporally. Grassland species composition changes in response to changes in soil physical and chemical properties, whereas forage availability changes in response to consumption by herbivores and to changes in the growth stages of the grass species. As a consequence, grass species selection and the dietary contribution of each species may also vary from landscape to landscape and from time to time. However, insufficient attention has been paid to the patterns of forage selection by herds foraging in different geological formations during the critical period of food shortage. Therefore, this study was carried out in two different landscapes through the dry season.

The aim of the study was to help understand how food selection may influence buffalo movements. The objectives of this study were:

1. To compare greenness retention between the basalt and granite landscapes.
2. To determine how grass species selection and dietary contribution of grass species change over the dry season in these landscapes.
3. To relate grass species selection by buffalo to grass greenness, grass height and number of stems.

This study is part of the BTB research project of the Kruger National Park (KNP). The aim of the BTB project is to assess which management strategies are the most effective in reducing the prevalence of bovine tuberculosis in the buffalo population. The results will allow predictions of herd movements based on the abundance and distribution of forage species within the home range, which will help understand the ecology of the disease. Thereby the results of this study will contribute towards the overall aims of the BTB research project.

Grassland phenology in savanna landscapes

Water availability is a key factor of savanna ecology (Scholes and Walker 1993) as it determines savanna function by controlling the duration of the period for which processes such as primary production and nutrient mineralisation can occur. Vegetation in savannas is subject to strong water stress that varies in time and space. These savannas undergo a annual dry period of about six months, usually from April to September. Scholes and Walker (1993) pointed out that under the same climate, vegetation structure and composition change with the change from a sandy to a clayey soil due, in part, to the different hydrological characteristics of the two soils. Hydrological characteristics of soils and hence water availability are determined by soil physics, which depends on soil particle size, which in turn depends upon parent material (Scholes and Walker 1993). By determining water availability to plants, the type of geological formation may influence greenness retention during the dry season (Scholes and Walker 1993).

The basalts have higher clay content and tend to be more arid than sandy granites because the small space between the small particles of clay does not allow water to infiltrate. As a consequence, in the basalts more water is lost through soil surface evaporation (Scholes and Walker 1993, Walker 1993). In the granites, mostly with sandy soils characterized by larger particle size and hence larger space between the particles, water from the rainfall infiltrates and concentrates below the soil (Scholes and Walker 1993, R.J. Scholes - pers. commun.). Less water is lost through evaporation and hence more water is still available for use by plants, particularly during the dry season.

Although sandy soils have a very low water-holding capacity (Scholes and Walker 1993), most of the water that infiltrates is available to plants (Walker 1993). On the other hand, heavy-textured clayey soils can hold much more water than sandy soils but they also have a high wilting point, i.e. the soil potential beyond which plants can no longer extract water occurs at a relatively high soil-water content (Walker 1993). The net effect is that in semi-arid regions, sandy soils provide a more favourable soil-moisture regime for plants than do clayey soils. Seghieri et al. (1994) argued that the upper 20 cm in a clayey soil is very dry, and it is where the roots of most grass species lie. Since the processes of nutrient mineralization, transport of nutrients to the roots and uptake by plants are water dependent and dry savannas are water-limited (Scholes and Walker 1993), grass species in sandy soils should retain green leaves for longer. However, during the growing season biomass

production is greater in clayey soils because they are usually nutrient rich and the rate at which plants respond to water supply depends upon soil nutrient content.

Within each landscape, the slope affects moisture effectiveness by determining the proportion of surface runoff to infiltration (White 1997). The soil in uplands tends to be well drained, whereas in bottomlands the soils are generally poorly drained (White 1997). Differences in drainage between different landscape positions give rise to a hydrological sequence from uplands to bottomlands. This can result in differing proportions of green leaves between different landscape positions, with increasing greenness from uplands to bottomlands within the same landscape, particularly during the dry season.

Topography and physical soil properties have a strong effect on water availability for plants and may determine the proportion of green leaves that remains in the sward through the dry season. The availability of green leaves through the dry season is crucial for herbivores because herbivores rely upon green leaves to obtain their main nutrients for survival and reproduction (Owen-Smith 1988). If landscapes differ in the availability of green leaves, herds will be exposed to different conditions in terms of food availability and nutrient acquisition. This may result in different degrees of food shortage, which may result in differences in the grass species utilized through the season.

Forage selection

Animal performance depends on the ability of the animal species to harvest nutrients in an effective and efficient manner (Owen-Smith 1988, Manly *et al*. 1993). Food resources vary not only spatially but also seasonally in response to variable rainfall and soil type (Bell 1982, Walker 1993). They also show seasonal and spatial differences in their nutritional quality and in their overall quantity (Owen-Smith 1982). In contrast, foraging animals require a supply of nutrients above certain thresholds to avoid starvation. Hence, within the landscape herbivores select patches of vegetation in which they feed and within each selected patch, herbivores select their food on a species basis, having preferences for some species and avoidance for others (Arnold 1981, Stuth 1993). Variation in the growth phase of grass species over time can influence the degree to which herbivores discriminate and select among plant species (Bell 1970, Owen-Smith 1982, Augustine *et al*. 1998).

Both leaf production and crude protein concentration are highest during the rainy season. During this season, grazed plants regenerate the parts removed by herbivores, hence reconstituting the patches. However, in most grass species in African savannas, leaf

production ceases during the dry season and forage quality decreases with the maturing and drying out of the grassy vegetation (Owen-Smith 2002). During the dry season, grazed patches are not reconstituted because grass species are in a dormant stage (Owen-Smith 2002). Hence, selective feeding leads to progressive reduction in forage available to herbivores through the dry season.

During the late dry season, food becomes scarce for herbivores; animals lose condition and may die of starvation (Beekman and Prins 1989). Therefore, herbivores develop ways of coping with food scarcity. Options for grazing herbivores include moving to habitats with suitable resources, or changing their diets either by including more grass species or by switching to browse (Beekman and Prins 1989).

Spatial levels of forage selection

Food selection occurs at different hierarchical levels, including landscape, plant community, feeding site/patch, feeding station and plant level (Manly *et al.* 1993, Stuth 1993, O'Reagain 2001). Bailey *et al.* (1996) state that the dimension of these levels of selection is associated with body size and foraging strategy of the herbivore. Furthermore, Senft *et al.* (1987) and Bailey *et al.* (1996) argued that, in order to select, herbivores must perceive differences among plant parts and plant species so that they can discriminate and select among alternatives. However, herbivores selecting food items incur energetic costs associated with travelling and searching another spatial unit. According to optimality theory, a food item should be accepted if the benefit obtained from consuming it outweighs the opportunity cost of searching for and ingesting a more profitable food item within the time entailed to grazing (Owen-Smith 2002).

A feeding station is an area within which the animal can feed without moving its front feet (Owen-Smith 2002). Within each feeding station, selection takes place at plant level. At the plant level selection occurs at three hierarchical levels, namely, plant form, plant species and plant parts, because nutrient concentrations of individual plants and plant parts vary greatly (Owen-Smith 1988). Hence, all herbivores should favour those plant species and plant parts that offer the highest intake rate and nutrient content at any given time (Owen-Smith 1988). Staddon (1983) in Bailey *et al.* (1996) argued that through the process of momentary maximization, animals select the best available alternative at any given time. Senft *et al.* (1987) and Bailey *et al.* (1996) maintained that the threshold of acceptance of a particular food is based on physiological state and recent experience.

Therefore, the threshold of acceptance should change according to the nutritional value of plants encountered recently, presumably during the last few bouts.

Large herbivores may shift between habitat types that are different in the resource attributes they present (McNaughton 1985). For instance, Owen-Smith (1988) indicated that in Hluhluwe-Umfolozi Park, South Africa, white rhinoceros (*Ceratotherium simun*) shifted their grazing location from the short grass grassland favoured in the wet season towards grasslands offering a higher food biomass during the dry season. McNaughton (1985) found that the diet of ungulates in Serengeti changed with season. These seasonal diet shifts consisted of changes in the proportion of grass species in the diet as a result of ungulates moving to grasslands that had different relative availability of grass species as the dry season progressed.

Factors influencing forage selection

Forage selection by grazers is influenced by a combination of chemical and physical characteristics of grasses as well as by behavioural, morphological and physiological features of the grazing animal (Illius and Gordon 1990, Bailey *et al.* 1996).

Species Composition

Selection of forage presumes morphological and nutritional differentiation among plants (Senft *et al.* 1987, Van Soest 1987, Barnes *et al.* 1993, Stuth 1993). Van Soest (1987) states that forage selection is influenced by plant species available, the environment for plant growth, and the age and maturity of the forage. Stuth (1993) and O'Reagain (2001) pointed out that animals respond to landscape heterogeneity at the plant level by selecting for certain species while avoiding others within a feeding station. Furthermore, Stuth (1993) maintained that selection depends on the availability and diversity of the forage, thus it is diminished by high grazing pressure and uniformity of the sward. High grazing pressure reduces the availability of suitable food and hence reduces selection. In a homogeneous grass layer the nutrient concentrations between different plant species do not differ greatly, therefore food selection is less pronounced. Laca *et al.* (1993) argued that when grazing heterogeneous swards cattle are able to detect very small differences between plants in a feeding station. The vegetation in the tropics is heterogeneous in food for herbivores, because vegetation in the tropics encompasses different plant forms and plant species with different chemical and physical properties, which results in selection

(McNaughton 1983). In temperate grasslands food selection at the grass species level is less pronounced because these grasslands are less diverse.

Physical and chemical characteristics of the grass species

Although plant nutrient contents are important in determining grass species selection (Field 1976), dietary selection by grazers could not be predicted on the basis of nutritional factors alone. This is because secondary compounds and physical features of the grass such as greenness, stemminess, leaf table height, the presence of hairs, leaf texture, as well as the seasonal changes in the growth stages of the available grass species, also play an important role in grass species selection (Heady 1964).

- Leaf table height

Leaf table height is another factor that might affect grass species acceptability by grazing ungulates. The intake rate is influenced by sward height and density (Illius and Gordon 1990; Hanley 1997) and increases asymptotically with sward height (Laca *et al.* 1999, O'Reagain 2001) because with increasing grass height, bite size increases as animals prehend a bigger volume of herbage through increased bite depth (Illius and Gordon 1990, O'Reagain 2001). Nevertheless, increases in grass height are coupled with a reduction in the nutritional quality of the sward because grass growth and maturity are accompanied by the accumulation of structural carbohydrates in the stems, which are less digestible (Van Soest 1987). Therefore, although the energy content of the sward increases with height, the digestibility of that energy declines (Van Soest 1987, Wilmshurst *et al.* 1999). Energy intake is constrained by forage availability and by the physical capacity of the ruminant digestive system (Wilmshurst *et al.* 1999). Therefore there is a trade-off between bite size and bite quality. For example, Owen-Smith (2002) stated that nutritious short grasses may be neglected by large grazers because they yield an inadequate intake rate. This indicates that there is also a threshold in grass height for acceptance by grazers.

Under dry season conditions, tall grass is not necessarily of poor nutrient content due to the absence of regrowth (Wilmshurst *et al.* 1999). So, ruminant grazers should concentrate on tall grass patches offering high intake rate if digestibility does not decline with increases in grass height (Wilmshurst *et al.* 1999). In addition, studies on forage selection by grazers have shown that diets of herbivores broaden during the dry season (Casebeer and Koss 1970). This broadening of the diet can be either by including more grass species in the diet or selecting for different species as the season progresses.

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- Greenness and stemminess

Diet quality for grazers is strongly correlated with the proportion of green leaf in the diet. Therefore grazing animals select leaf in preference to stem, and green in preference to dry/brown or dead material (O'Reagain 2001). Studies on ruminant grazers such as cattle demonstrated that plant species selection was highly correlated with the proportional availability of leaf tissues among the available food plants because leaves contain the photosynthetic enzymes and are highest in protein and minerals (Bell 1970, Field 1976, Minson 1981, McNaughton 1983). Conversely, a negative correlation existed between grass species selection and the number of stems of the tuft (Magome 1991, Stuth 1993). High number of stems leads to plant rejection since a high intake of fibrous stem material would restrict the rate of food passage through the digestive system, increase the retention time and reduce the net rate of food intake (Owen-Smith 1982). Therefore, grazers should select species based on the balance between nutrient content and energetic costs of harvesting and processing (mastication and digestion) a particular food or species (O'Reagain 2001). Owen-Smith (2002) suggested that the relative preference for grass species by grazing ungulates may change seasonally, depending on varying greenness and leaf:stem ratio. Owen-Smith (1982) stated that grass leaves contain high levels of crude protein only when they are young, exceeding 15-20% of dry matter. As leaves age, the protein contents decrease and structural carbohydrates increase (Minson 1981). Despite the importance of green leaves as source of nutrients, their proportion in herbivores diet drops through the dry season (McNaughton 1985).

The presence of secondary compounds such as tannins and phenols has been a strong reason for plant rejection among browsing ungulates (Arnold 1981, Owen-Smith and Novellie 1982, Owen-Smith and Cooper 1987a). However, secondary compounds are relatively rare among grass species, which suggests that, although these compounds influence species selection among grazing herbivores (O'Reagain 2001), their relative importance is less than in browsers. Grass species containing secondary compounds such as *Bothriochloa* spp. and *Cymbopogon* spp. are generally neglected by ruminant grazers.

Animal Species

The animal species is another factor in the food selection process (Van Soest 1987). Sympatric ungulates tend to use the food resources in their environment in different ways (Voeten and Prins 1999). Differences in feeding behaviour are determined by morphological and physiological features of the animal, particularly body size, the

structure of the mouth parts and dentition, gut morphology and function, sex and reproductive state (Hanley 1982, Owen-Smith 1982, Van Soest 1987, Gordon 1989). For instance, large grazers have wide muzzles and are less selective than small grazers with narrow muzzles. Small sized animals have higher metabolic requirements than large mammals and they are likely to be limited by small gut volume. Therefore they should select food items of higher quality. Large herbivores have greater gut capacity relative to energetic requirements (Illius and Gordon 1990, Hanley 1997) and they tolerate poor quality food (Illius and Gordon 1990, Bailey *et al.* 1996). Ability for selection varies with animal species and the need may be regulated by hunger and the availability of food. Generally a starving animal selects more for quantity than for quality because it is less capacity-limited (Van Soest 1987). During the late dry season, when high quality food is available nowhere and herbivores run the risk of starvation, they end up eating less nutritious food.

- African buffalo

Buffalo are water-dependent grazers (Sinclair 1977, Beekman and Prins 1989, Taylor 1989, Prins 1996). They are relatively non-selective grazers when all grass species in the sward are green (Beekman and Prins 1989) but prefer green food when the sward is of mixed phenological stages (Taylor 1989). Beekman and Prins (1989) and Prins (1996) observed two foraging tactics in buffalo, namely, bulk feeding when food is abundant and of good quality, or when food is abundant but of relatively poor quality; and plant species and plant part selection when food is abundant but of mixed quality or when food is scarce and of poor quality. The most limiting nutrient for herbivores is protein (Van Soest 1987, Prins 1996) since it influences the digestibility of food. The protein requirements for buffalo depend upon their physiological state. For example, Prins (1996) argued that non-lactating cows require a minimum crude protein concentration of 6.2% for maintenance. Above maintenance requirement levels, an additional supply of nutrients is needed for production either as growth or reproduction. For example, according to Prins (1996), lactating cows require at least 8.5% of crude protein concentration in their food.

Studies of diet composition by mean of rumen samples (e.g. Sinclair 1977) have revealed that buffalo select for leaves and reject stems, particularly during the wet season. However, prehending the grass tuft with the tongue prevents buffalo from efficiently selecting leaves from stems. Therefore, through the dry season the proportion of leaves in the diet decreases while the proportion of stems shows the opposite trend (Sinclair 1977).

Increases in the proportion of stems in the diet indicate that although food selection is still evident, its effect decreases as food availability declines progressively.

According to Perrin and Brereton-Stiles (1999), buffalo prefer tall grass species, but they can graze short and generally more nutritious grasses. Short leaf height results in small bite size and therefore yields reduced food intake. Sinclair (1977) and McNaughton (1983) stated that buffalo avoid grass species with secondary compounds such as *Cymbopogon excavatus*. However, Field (1976) in Rwenzori National Park in Uganda found that buffalo eat the new growth of *Cymbopogon* spp. and *Bothriochloa* spp. after a burn. Field (1976) found that buffalo favour *Chloris gayana*, *Cynodon* spp., *Panicum repens*, *Sporobolus* spp., *Themeda triandra* and *Hyparrhenia filipendula*. The same author indicated that buffalo show selective avoidance of certain grasses during most of the year, but graze them at the height of the dry season. McNaughton (1985) argues that buffalo have a similar diet in the wet and dry seasons, although the proportions of grass species in the diet change with season. This change consists of a decline in the proportion of preferred species and increase in the proportion of less preferred species. Prins (1996) found that in Lake Manyara National Park in Tanzania, buffalos favour *Cynodon dactylon*, *Enneapogon cenchroides*, *Chloris gayana*, *Urochloa pullulans*, *Panicum maximum* and *Eragrostis superba*. Funston *et al.* (1994) observed that in the Sabi Sand Wildtuin in South Africa, buffalo selected for *Themeda triandra* and *Panicum maximum*. Fibrous grasses such as *Aristida* spp. were neglected.

Hypotheses

The hypotheses being tested in this study were:

1. During the dry season the granite landscape retains more green leaf than the basalt landscape.

2. Buffalo include more grass species in their diet and increase their acceptance of each grass species as the dry season progresses. The dietary contribution of preferred species declines while the dietary contribution of intermediate and neglected species increases with time..

3. Buffalo favour grass species offering a high proportion of green leaves and tall grass species, and neglect grass species with a high number of stems.

Study Area

Location

Satara is located in the central section of the Kruger National Park, South Africa (24°23' S; 31°47' E). This was a suitable area for this study because in this region buffalo occur in herds of several hundreds of individuals. Furthermore, the prevalence of bovine tuberculosis (BTB) in buffalo is increasing in this region, so that it is important to understand different factors that influence buffalo movements and the transmission rate of the disease. Specifically, the study was carried out in the home ranges of two buffalo herds, namely, the Timbavati herd with a home range extent of approximately 29000 ha mainly in the granite landscape (90% of the home range), and the Mavumbye herd, with a home range extent of approximately 15000 ha in the basalt landscape. The home range of the Timbavati herd is located in the south-western direction from the Satara camp to the north of the Sweni River. The home range of the Mavumbye herd is located in the north-eastern direction from the Satara camp to the north of the Sweni River.

The study area has the following physical characteristics:

Geomorphology: Like the entire KNP, the Satara region is geologically characterized by predominantly granite formations in the western half and basalts in the eastern half. The granite landscape is dominated by sandy soils, whereas the basalts are dominated by clayey soils (Gertenbach 1983). A narrow belt of Karoo sediments (shale and sandstone) divides

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the two main geological formations. The basalt landscape is almost flat whereas the granite landscape is more undulating.

In the western half of the study area, there is also an area dominated by another volcanic rock, gabbro, which is a dark-colored, coarse-grained intrusive igneous rock very similar to the basalt in its mineral make up, therefore contrasting with the dominant granitic system in the Timbavati area.

Climate: The climate of the central KNP is semi–arid, with a hot wet season and a mild dry season. The mean annual rainfall in Satara is about 548 mm (Gertenbach 1980). About 85-90% of the annual precipitation falls during the wet season months from October to March. The average daily maximum temperature is at its highest between November and March (± 32° C), with temperatures reaching up to 44°C. The lowest average daily minimum temperature is in June and July (± 6°C) (du Toit 1988).

Vegetation: The two main landscapes in the study area are Lebombo South, and *Sclerocarya birrea/Acacia nigrescens* savanna (Gertenbach 1983). The eastern half of the study area is an open tree savanna with the woody vegetation dominated by *Sclerocarya birrea* and *Acacia nigrescens*, while the grass layer is dominated by *Panicum* spp., *Urochloa mosambicensis, Themeda triandra* and *Bothriochloa* spp.. The western half is a relatively more densely wooded savanna with the woody vegetation dominated by *Combretum apiculatum* and *Pterocarpus rotundifolius*, whereas the grass layer is dominated by *Panicum maximum, Themeda triandra, Digitaria eriantha, Eragrostis* spp. *and Cymbopogon plurinodis*, plus fibrous less palatable grass species such as *Pogonarthria squarrosa* (Gertenbach 1983).

Experimental approach

The fieldwork was conducted during the late dry season (July - October 2002). Grass species composition and forage production differ between landscapes, hence forage selection may also differ between herds foraging in different landscapes. Therefore, two herds were selected for observation, one with the home range in the basalts and one with about 90% of the home range in the granites. The last herd also foraged occasionally in the gabbro, Karro sediments and basalts. In each of the selected herds, about 20 individuals had been fitted with radio collars by the research team working on the BTB research

project. The receiver and aerial were provided by the BTB research project. Therefore, radio telemetry was used to locate the herds daily in the morning (5:30 AM).

After locating the herd, the foraging pathway of buffalo during previous hours was located and data on grass species selection and dietary contribution were collected by backtracking along the foraging pathway. In each herd, data collection was carried out during four to seven days per period of three weeks. The four defined periods were: 7 – 24th July, 27th August – 13th September, 17th September – 5th October and 7 – 25th October. The information sought was changes in grass species selected, differences in grass species selection between herds foraging in the two landscapes, as well as changes in the acceptance of each grass species and the changes in the dietary contribution of each grass species with time. Data were collected during two consecutive days for each herd, followed by two days of sampling the foraging pathway of the herd foraging in the other landscape.

During the late dry season, fires are frequent in the lowveld and usually herds tend to move to the burned section of the home range to graze the highly nutritive green grass regrowing after the burn. Indeed, a section of the home range of the Timbavati herd was burned during this study, but the occurrence of fire did not affect the entire buffalo home range. The herd was not located grazing on burned areas during the sampling days because in these areas the grass was still too short to harvest. Therefore, herds were followed and vegetation sampled only in the unburned section of the home range.

Methods of data collection and analysis

Comparison of grass greenness between the landscapes
Data collection
Four fixed line transects were placed across the catena within each landscape. In the granites two transects started along the Sweni River and two along the Timbavati River. In the basalt landscape two transects started along the Mavumbye River and two along the Gudzani River. Along each defined transect, greenness was measured in August and again in September. Data collection consisted of walking across the catena from bottomlands to uplands, and establishing sampling points systematically 10 paces apart along the line transect. At each point, a 0.7 m x 0.7 m quadrat was placed. Each quadrat was checked for the presence of green leaves, recorded as present or absent. In each landscape, quadrats with green leaves were counted and the landscapes were compared in terms of proportion

of quadrats that retained green leaves. In each quadrat, the grass species that retained green leaves was recorded. Other grass species found in quadrats along the transect were listed to record which species were present but dry. Data collection was repeated after three weeks.

The GPS position was taken every 200 m along each transect to ascertain that approximately the same line transect was monitored to detect changes in the proportion of quadrats with green leaves over time.

Data analysis

Greenness retention was compared to find any significant difference between landscapes, time periods and landscape positions. To test for dependence or independence between greenness (green and not green), time period, landscape and landscape position, four-factor log linear analysis was performed using the number of quadrats with and without green leaves (categorical data) for each of the factors included in the analysis. Backward elimination was done to identify significant interactions associated with greenness retention. Log linear analysis was performed using STATGRAPHICS software at 95% significant level.

Determination of diet selection and dietary contribution

Data collection

After locating the herds, the foraging path of the herd was identified through the presence of fresh dung and fresh footprints. Along the foraging pathway of the herd, foraging paths and feeding stations of individual buffalos were located through the presence of tracks and fresh bites. Each day four foraging sites (10 m x 20 m) were located systematically 100 m apart along the foraging path of the herd. This was done by walking along the foraging path of the herd and locating signals of recent grazing after every 100 m. Within each foraging site, two almost parallel foraging pathways of individual buffalos were identified through the observation of fresh bites. Fresh grazing was identified by the presence of a bright and whitish colour at the surface of incision of stems and middle vein of the leaves. These foraging pathways had their starting points on parallel feeding stations. Five 0.7 m x 0.7 m quadrats were placed systematically 5 m apart along each of the foraging pathways of individual buffalos. If the foraging pathway of an individual buffalo was no longer clearly visible, the nearest foraging pathway was followed. In total, ten 0.7 m x 0.7 m quadrats were sampled to document grass species availability and selection within each foraging site. Thus, in total 40 quadrats were sampled per day.

Within each 0.7 m x 0.7 m quadrat the following data were recorded:

1. the grass species present - binoculars were sometimes used to increase the resolution of the naked eye in observing some differentiating features of the grass species, especially the presence or absence of hairs in the nodes of the grass;

2. the grass species grazed;

3. the total number of tufts present, and the number of tufts that were grazed for each grass species.

Data analysis

The availability of grass species was assessed by their frequency of occurrence. This was calculated by dividing the number of quadrats in which the species was present by the 40 quadrats sampled per day. In order to assess the relative selection of grass species by buffalo, two indices were calculated; the frequency of acceptance and the forage ratio. The frequency of acceptance was calculated by dividing the number of quadrats where the species was eaten by the total number of quadrats in which the species was present (quadrats were the replicates assuming that successive quadrats 5 m apart represented independent choices).

To calculate the forage ratio, the relative use and the relative availability of each species needed to be estimated. The relative use of each grass species was estimated by dividing the number of grazed tufts for each species by the total number of grazed tufts for all species recorded within quadrats during the dry season and during each of the defined periods. The relative availability, which gives the expected proportion of utilization for each grass species was estimated by dividing the number of tufts of each species by the total number of tufts for all species recorded within quadrats during the dry season and during each of the defined periods. Following Owen-Smith and Cooper (1987b) forage ratios (FR) were calculated by dividing the relative use of the species by its relative availability. Thereafter forage ratios were transformed to a logarithmic scale.

The proportional contribution of each grass species to the diet of buffalo was estimated by counting the number of tufts of that species that were grazed and dividing this by the total number of grazed tufts of all species added together for that day. The dietary contribution of each grass species within each defined period was determined by averaging the results obtained from each day within each period and study herd.

Four-factor log linear analysis was applied to detect differences in acceptance frequency among 10 grass species, among four time periods and between two landscapes. Only the 10 grass species that showed sample size greater than five quadrats for each of the factors were included in the analysis to ensure adequate sample size. The null hypotheses for statistical testing were 1) the acceptance for each species was not significantly different from the mean acceptance considering all species, 2) grass species acceptance did not change from one period to another, 3) the acceptance frequency of grass species did not differ between herds foraging in different landscapes. Backward elimination was performed to identify the significant factors or interaction of factors in the analysis. This started off with the saturated model, which fits perfectly. Interactions were sequentially removed and the change in model fit after removing the interaction as indicated by the chi-squared test and the p-value, was noted. Backward elimination continued until the removal of the interaction led to a significant loss in model fit. If the removal of the interaction led to a significant loss in model fit, the interaction had a significant effect in the model. Log linear analysis was performed at 95 % significance level using STATGRAPHICS software.

According to the forage ratio index, grass species resulting in forage ratio greater than one ($\log_{10}$ FR > 0) were considered favoured, whereas those yielding forage ratios less than one ($\log_{10}$ FR < 0) were neglected. Grass species with forage ratios not significantly different from one were classified as intermediate in preference. To identify forage ratios statistically different from one, following Byers and Steinhorst (1984), simultaneous Bonferroni confidence intervals were determined for the observed proportions of utilization of each grass species. Bonferroni confidence intervals were calculated to test whether the selection of a particular grass species depended on its availability in feeding quadrats. In using this technique, expected proportion of utilization (based upon the availability of each grass species) not lying within the confidence interval indicated that the use of this species was significantly different from its availability in feeding quadrats (p<0.05). If the expected proportion of utilization was below the confidence interval the species was favoured, whereas if the expected proportion of utilization was above the confidence interval the species was neglected. Grass species whose expected proportion of use lied within the confidence interval were classified as intermediate species (Byers and Steinhorst 1984).

The contribution of each of the most common grass species to the diet of buffalo was compared between the two landscapes and among the four time periods using two-way analysis of variance (ANOVA). Days were considered as the replicates. Daily dietary

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proportions (proportion of grazed tufts) were subjected to *arcsin* transformation for normality (Zar 1984, Quinn and Keough 2002). This test was done in STATISTICA package at 95% significant level.

Determination of the factors influencing grass species selection

Data collection

Within each feeding quadrat, for each of the species present, grass height, greenness and steminness were estimated. Grass height was recorded following the method used by Winkler (1992). It consisted of measuring the height of the tallest basal leaf above ground level for each grass tuft. Following Perrin and Brereton-Stiles (1999), the height to which buffalo grazed the grass, and the height of nearby ungrazed tufts of the same species, were measured. Ungrazed height within the site/patch indicated the leaf table height available to buffalo on arrival at a site, whereas freshly grazed height represented the level of herbage available after the buffalo had eaten. If ungrazed tufts were not available nearby, the previously grazed height (old bites) was recorded; these bites were distinguished by the dark colour at the surface of incision. Leaf table height of the species in each quadrat was classified in the following height classes: 1-10, 11-30, 31-50, 51-70, >70 cm.

The proportion of leaves of each grass species that were still green was estimated subjectively. These estimates were checked by removing leaves of tufts of each grass species, and counting the number of leaves and determining the percentage of leaves that were green, in two out of every 10 quadrats in each foraging site. In other eight quadrats greenness was estimated subjectively. Greenness for the species present in each quadrat was classified in the following classes: 0, 1-10%, 11-25%.

Steminess was assessed for each grass species by counting the number of emerging stems in each grass tuft. Stemminess for the species present in each quadrat was classified in the following classes: 0, 1 – 2, 3 – 4, 5 + stems.

Habitat variables recorded at each foraging site included landscape position (upland, midslope or bottomland), tree and shrub cover, and the presence of termite mounds. This information was collected because these factors can influence grassland species composition and grass phenology. Woody vegetation within the foraging site was classified as a tree if the height was greater than 2.5 m and as a shrub if the height was less than 2.5m (Scholes *et al.* 2001). The canopy cover of the foraging site covered by trees or by shrubs was estimated subjectively, and classified in the following classes: 0%, 0-10%, 10-20%, 20-30%, etc.

Data analysis

The strength of the relationship between species acceptance and each of the measured physical characteristics of the grass (greenness, height and number of stems) was estimated by performing correlation analysis. This test was done for each of the study periods to accommodate possible changes in the mean greenness, grass height, number of stems as well as in the acceptance frequency of each grass species over time, which could change the strength of the relationship between these continuous variables. The percentage of green leaves was subjected to logarithmic transformation to approximate a normal distribution of the data. The analysis was performed in STATISTICA software at 95% significant level.

Overview of the project

Forage selection of buffalo was assessed in the basalt and granite landscapes in the Kruger National Park using frequency of acceptance and forage ratio. The limitation of the forage ratio index is that it divides the use of a particular species by its availability in the environment. Thus, it tends to underrate the most common food species. The dietary contribution was determined using the proportion of grazed tufts of each species. The shortcoming of the procedure used to estimate dietary contribution is that grazed tufts were counted regardless of the size and degree of utilization of each grazed tuft.

The project also assessed the influence of physical characteristics of the grass species on their acceptance by buffalo. Besides the measured physical characteristics (grass greenness, grass height and number of stems), other factors such as differences in nutrient content among grass species may have influenced their acceptance by buffalo. Nonetheless, nutritional analysis of grasses was not part of my study, as it was being done by other members of the research team studying the factors influencing habitat selection by buffalo.

Another achievement of this study was the comparison of the retention of green leaves through the dry season in the two landscapes. Data on greenness were recorded as presence or absence of green leaves within quadrats, and the landscapes were compared in terms of proportion of quadrats retaining green leaves. A better comparison of greenness retention between landscapes would have been achieved perhaps by estimating and comparing the proportion of green leaves within quadrats in the two landscapes. In

addition, differences in grass species composition may have influenced the overall greenness retention in the two landscapes because the ability to withstand drought and retain green leaves varies among grass species. However, comparing greenness at a fine scale was not part of my study due to shortage in time available for data collection.

It was also initially planned to document the dietary contribution of grass species by means of microhistological analysis of faecal samples. The limitation of microhistological analysis of dung is the differential digestibility of food items. Furthermore, I started the analysis with a "learn by doing" approach without an experienced adviser. This delayed the learning process and made the progress very slow. Only about 50% of the epidermal fragments in the slides were identifiable. The technique proved to be very time consuming; at least 2 h were needed for the analysis of each faecal sample from the digestion process to the identification of 50 fragments per composite faecal sample. Hence, the results obtained from this technique were not included in the main results of this study. The results obtained using this technique were similar to those obtained by direct observations (proportion of grazed tufts) in terms of changes between periods in the dietary contribution of each grass species as well as in terms of contribution of each grass species to the diet of buffalo in the two landscapes.

The main results obtained from this study are presented in the next chapter in a format of a manuscript prepared for submission for publication. Other information is presented in Appendices.

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Forage selection of African buffalo (*Syncerus caffer*) through the late dry season in the Satara region of the Kruger National Park

Abstract

Forage selection by buffalo and the contribution of grass species to buffalo diet were investigated comparing two herds occupying the granite and basalt landscapes of the Kruger National Park during the late dry season, between July and October in 2002. Grass greenness retention did not differ significantly between the two landscapes. Grass was greener in bottomlands than in midslopes or uplands. Forage selection and dietary contribution of different grass species were recorded by backtracking along foraging pathways and identifying grazed and not grazed tufts. Physical characteristics of each grass species were also recorded. *Panicum maximum, Panicum coloratum, Cenchrus ciliaris* and *Heteropogon contortus* were species highly acceptable to buffalo. These favoured grass species offered a high proportions of green leaves and were of intermediate height. The acceptance frequency for these species remained high throughout the dry season. However, their dietary contribution declined with the progress of the dry season owing to seasonal decline in the available biomass of these grass species. The acceptance frequency as well as the dietary contribution of *Urochloa mosambicensis, Digitaria eriantha, Eragrostis superba* and *Bothriochloa insculpta* increased with time. *P. maximum, Themeda triandra* and *D. eriantha* contributed more to the diet of the herd on the granites than to the diet of the herd on the basalts, whereas *P. coloratum, U. mosambicensis* and *C. ciliaris* contributed more to the diet of the herd on the basalts than to the diet of the herd on the granites. In accordance with expectations from foraging theory, buffalo expanded the range of grass species accepted, changed the proportions of grass species in the diet and changed their grazing locations in terms of both plant communities and position in the landscape.

Introduction

The availability of forage for herbivores in savannas varies not only spatially but also seasonally in response to variable rainfall and soil type (Bell 1982; Walker 1993). Forage resources also show seasonal and spatial differences in nutritional quality. As the dry season progresses, crude protein concentration declines while the levels of structural carbohydrates increase in grass tissues (Owen-Smith 1982). Foraging animals require a supply of nutrients above certain thresholds to avoid starvation. Hence, from the array of grass species on offer, herbivores prefer to eat some grass species and avoid others (Barnes *et al.* 1993).

The retention of green leaves through the dry season is important for herbivores because green leaves are high in proteins, minerals, vitamins and photosynthetic enzymes (Bell 1970, Field 1976). These nutrients are essential for growth, reproduction and survival of the animals. Sandy soils lose less rainfall water due to surface evaporation than do clayey soils (Scholes and Walker 1993). Hence, during the dry season the granite landscape should retain more green leaves than the basalt landscape. The availability of green leaves declines during the dry season, but forage availability in terms of biomass remains adequate. Thus, during the dry season the most limiting factor for grazing herbivores is forage quality.

By feeding selectively herbivores cause a progressive decline in the standing biomass of favoured species, so that harvestable stands of these species become scarce towards the end of the dry season. Options for grazing herbivores when favoured species become scarce include increasing the time and energy expended searching for preferred food, which reduces daily food intake (Malecheck and Balph 1987), or expanding their diet by feeding on less preferred forage species, and hence minimizing the time spent searching for food. The proportion of the diet made up by each grass species may also change with season, as a result of changing availability due to consumption and/or to movements of herbivores into areas with different relative availability of grass species.

The quality of forage available is the most critical factor influencing the daily food intake by ruminants (Prins 1996). Buffalo change the proportion of time spent grazing and ruminating through the seasonal cycle (Prins 1996). During the late dry season, high quality food is available nowhere within the landscape. Thus, buffalo consume low quality food, which reduces grazing time but increases ruminating time. This is because buffalo are constrained by their ruminant digestive system in that the intake of poor quality food

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reduces fermentation rate and increases retention time, thereby reduces the overall daily food intake.

Consequently, during the late dry season buffalo lose condition due to shortage in protein and energy in grass tissues, and they may die from starvation (Beekman and Prins 1989, Prins 1996). Buffalo herds may move long distances searching for preferred food (Sinclair 1977). These changes in movement patterns and social organization can potentially increase the risk of predation (Malecheck and Balph 1987), and the spread of diseases like bovine tuberculosis. Other options include changing their diet either by including more grass species or by switching to browse as the dry season progresses (Beekman and Prins 1989). Food distribution within the landscape may influence buffalo movements, as herds tend to exploit sections of the home range where favoured species are available in adequate amounts. Therefore, understanding food selection during the critical period of food shortage may help understand herd movements.

In this study I compared greenness retention between the basalt and granite landscapes. I compared the changes in grass species selection by buffalo and in the contribution of each grass species to the diet of buffalo during the dry season in the two landscapes. Furthermore, relationships between the acceptance frequency of grass species and physical characteristics of the grass species were addressed. I hypothesized that grass on the granite landscape should be greener than grass on the basalt landscape as the granite loses less water due to evaporation than the basalt landscape. I also hypothesized that with the progress of the dry season buffalo would increase their acceptance for usually neglected grass species. The contribution of favoured species to the diet of buffalo was expected to decline while the dietary contribution of neglected species was expected to increase since the available biomass of the most favoured grass species declines with the progress of the dry season. Finally, I expected that buffalo would favour greener and tall grass species provided that the consumption of these species result in an adequate intake of protein and energy within the time assigned to grazing.

Methods

Study Area

The study was conducted near the Satara rest camp in the central section of the Kruger National Park, South Africa (24°23' S; 31°47' E). Geologically the area is characterized by predominantly basalt formations in the eastern half and granite formations in the western

half (Gertenbach 1983). In the western half of the study area, there is also an area dominated by another volcanic rock, gabbro; which is similar to but coarser than basalts. The home range extent of the buffalo herd on the granites comprising about 350 individuals was approximately 29000 ha. The home range extent of the buffalo herd on the basalts including about 800 individuals was approximately 15000 ha.

In the basalts the grass layer is dominated by *Panicum* spp., *Urochloa mosambicensis, Themeda triandra* and *Bothriochloa* spp.. In the granites the sward is dominated by *Panicum maximum, Themeda triandra, Digitaria eriantha, Eragrostis* spp. *and Cymbopogon plurinodis,* plus fibrous less palatable grass species such as *Pogonarthria squarrosa* (Gertenbach 1983).

The climate is semi–arid, with hot wet season (October – March) and mild dry season (April – September). The mean annual rainfall in Satara is about 548 mm (Gertenbach 1980), with approximately 85-90% of the annual rain falling during the wet season months.

Experimental approach

Two buffalo herds, one herd living on the basalts and one living on the granites were pre-selected for observation. These herds were observed during the late dry season (July - October 2002). The herds were located using radio telemetry each morning and data collected by backtracking along the foraging pathway. For each herd, data collection was carried out during four to seven days per period of three weeks. Feeding observations were supported by comparing greenness retention between the two landscapes.

Grass greenness in the two landscapes

Four fixed line transects were placed across the catena within each landscape. Along each transect, greenness was measured twice, in August and then in September. The sampling procedure consisted of walking across the catena from bottomlands to uplands, and establishing sampling points every 10 paces along the line transect. At each sampling point, a 0.7 m x 0.7 m quadrat was placed. Each quadrat was checked for green leaves, recorded as present or absent.

Feeding observations

Along the foraging pathway of the herd, foraging paths and feeding stations of individual buffalos were located through the presence of fresh dung, tracks and fresh bites. Each day,

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four foraging sites (10 m x 20 m) were located systematically 100 m apart along the foraging path of the herd. Within each foraging site, two parallel foraging pathways of individual buffalos were identified through the observation of fresh bites. Five 0.7 m x 0.7 m quadrats were placed systematically 5 m apart along each of the foraging pathways of these buffalos. In total, ten 0.7 m x 0.7 m quadrats were sampled to document grass species availability and selection within each foraging site. Thus, 40 quadrats were sampled each day. The landscape position of each feeding site was also recorded.

Within each 0.7 m x 0.7 m quadrat, grazed and ungrazed grass species were identified. The total number of tufts and the number of freshly grazed tufts were counted for each grass species. Grass height was recorded by measuring the height of the tallest basal leaf above ground level for each grass tuft and data were grouped into five height classes: 1-10, 11-30, 31-50, 51-70, >70 cm. The proportion of green leaves of each grass species was estimated subjectively and classified into three greenness classes: 0, 1-10%, 11-25%. The number of emerging stems in each grass tuft was counted and classified into four stem classes: 0, 1 – 2, 3 – 4, 5 + stems. Grass height, greenness and number of stems of each grass species were averaged for each of the sampling periods.

Calculations.

The proportion of quadrats that retained green leaves was calculated by dividing the number of quadrats that retained green leaves by the total number of quadrats recorded for each landscape type and position during each sampling period.

The availability of grass species was estimated by their frequency of occurrence, calculated by dividing the number of quadrats where each species was present by the 40 quadrats sampled per day. The relative selection for grass species was assessed both by frequency of acceptance and by forage ratio. The frequency of acceptance was calculated by dividing the number of quadrats where the species was eaten by the total number of quadrats in which the species was present. Following Owen-Smith and Cooper (1987), forage ratios (FR) were calculated by dividing the relative proportion of grazed tufts of each species by its relative availability. Thereafter forage ratios were transformed to a logarithmic scale. The dietary contribution of each grass species was estimated for each day's sample by counting the number of tufts of that species that were grazed and dividing this by the total number of grazed tufts of all species added together for that day. Dietary proportions were expressed as mean ± standard error.

Statistical analysis

The proportion of quadrats that retained green leaves was compared between two landscapes, two time periods and three landscape positions by four-way log linear analysis. This was done using the number of quadrats with and without green leaves for each of the factors included in the analysis (landscapes, time periods and landscape positions). Backward elimination was done to identify the significant interactions associated with greenness retention.

Differences in acceptance frequency among 10 grass species, among four time periods and between two landscapes were assessed by four-way log linear analysis. Only the 10 grass species that showed a sample size greater than five quadrats for each of the factors were included in the analysis to ensure adequate sample size. Backward elimination was done to identify the significant interactions affecting the acceptance of grass species. Starting off with the saturated model, i.e. the model that fits perfectly, interacting factors were sequentially removed and the change in model fit after removing the interaction as indicated by the chi-squared test and the p-value, was noted. Backward elimination continued until the removal of the interactions led to a significant loss in model fit. If the removal of the interaction led to a significant loss in model fit, the interaction had a significant effect in the model. Log linear analysis was performed at 95% significant level (p-value<0.05) using STATGRAPHICS software.

Grass species with forage ratios (i.e. proportional use over availability) significantly greater than one ($\log_{10}$ FR > 0) were considered as favoured, whereas those yielding forage ratios significantly less than one ($\log_{10}$ FR < 0) were regarded as neglected. Grass species with forage ratios not significantly different from one were regarded as intermediate in preference. To identify forage ratios statistically different from one, simultaneous Bonferroni confidence intervals were determined (eg. Byers and Steinhorst 1984).

The dietary contribution of each grass species was compared between landscapes and time periods using a two-way ANOVA. Daily dietary proportions were *arcsin* transformed for normality (Zar 1984, Quinn and Keough 2002). Correlation analysis was performed to measure the relationship between species acceptance and physical characteristics of the grass species. The percentage of green leaves was log transformed. Grass species with 0% of green leaves were changed to 0.1% to allow for the log transformation. Two-way ANOVA and correlation analysis were done using STATISTICA software at 95% significant level (p-value<0.05).

Results

Comparison of greenness retention between landscapes

During the dry season both landscapes retained a small proportion of quadrats with green leaves. In August, the mean proportion of quadrats with green leaves in the basalt landscape was 0.13 ±0.04, 0.05±0.007 and 0.04±0.012 in bottomlands, midslopes and uplands, respectively. In the granite landscape, the proportions were 0.10±0.01 in bottomlands, 0.06±0.007 in midslopes and 0.004±0.004 in uplands. In September, the proportions of quadrats with green leaves had declined. In the basalts the proportions were 0.08±0.03 in bottomlands, 0.031±0.002 in midslopes and 0.02±0.009 in uplands, whereas in the granites the proportions were 0.07±0.01, 0.05±0.007 and 0 in bottomlands, midslopes and uplands, respectively (Figure 1).
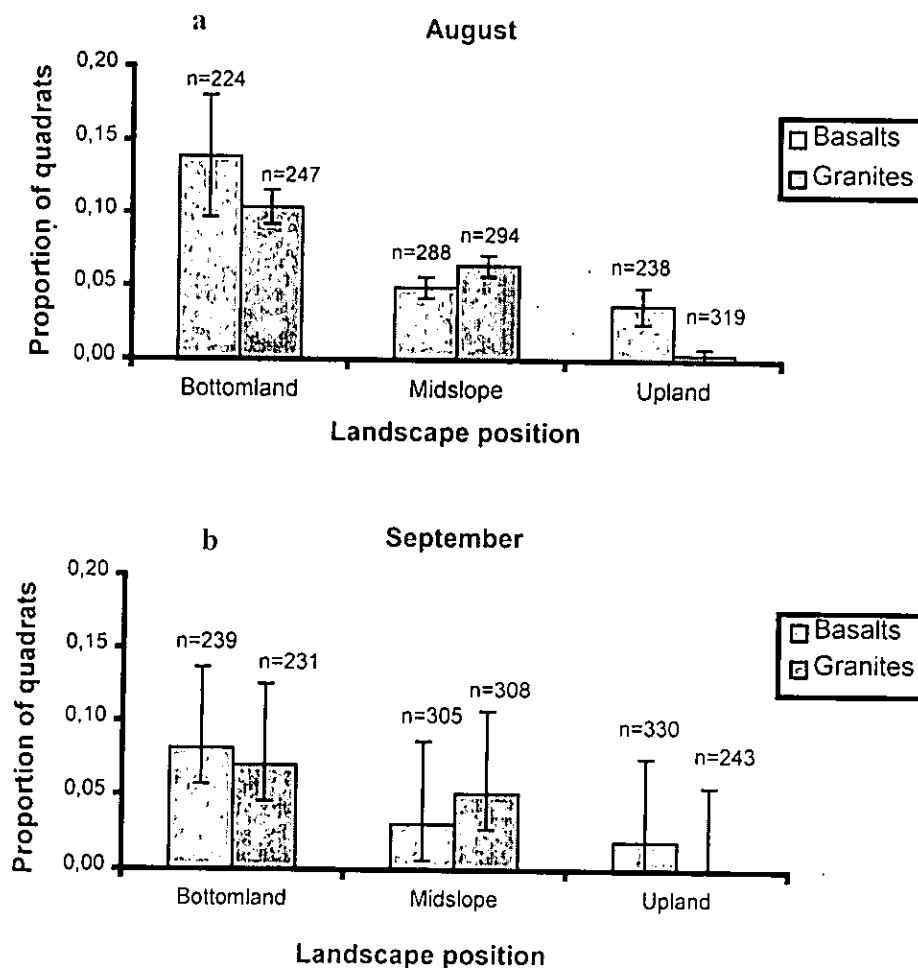
Figure 1. Proportion of quadrats with green leaves within each landscape and landscape position in (a) August and (b) September. Vertical bars indicate standard error.

Landscapes did not differ significantly in their overall greenness retention (χ^2=3.77, df=2, p=0.15). Within each landscape, landscape position influenced greenness retention with bottomlands retaining a higher proportion of quadrats with green leaves than midslopes or uplands (χ^2=14.4, df=2, p=0.008). In both landscapes, the decline in grass greenness from August to September was small and not significant (χ^2=2.48, df=1, p=0.11). The proportion of quadrats with green leaves as well as the proportion of green leaves for each grass species increased in October following the first rains, but it was not measured because this study was concerned with greenness retention during the dry season.

Utilization of landscape positions

The proportion of feeding sites in each landscape position changed as the dry season progressed. The herd on the basalts favoured bottomlands and midslopes from July to early October, but switched to uplands in late October. The herd on the granites was most commonly found feeding in midslopes or in uplands (Figure 2).

Grass species selection

In total 27 grass species were encountered by buffalo in the two landscapes during the dry season (Appendix I). The buffalo herds in the two landscapes did not differ significantly in their acceptance for particular grass species (χ^2= 4.4, df=3, p=0.221). A significant difference in acceptance frequency of the 10 grass species that showed sample size greater than five quadrats for each of the factors was observed among time periods (χ^2=126.34, df=27, p<0.001). In both landscapes and all time periods, the acceptance frequency differed significantly among grass species (χ^2=95.95, df=9, p<0.001). Because landscape type was not a significant factor in the acceptance of grass species by buffalo, frequencies of acceptance were grouped regardless of the landscape.
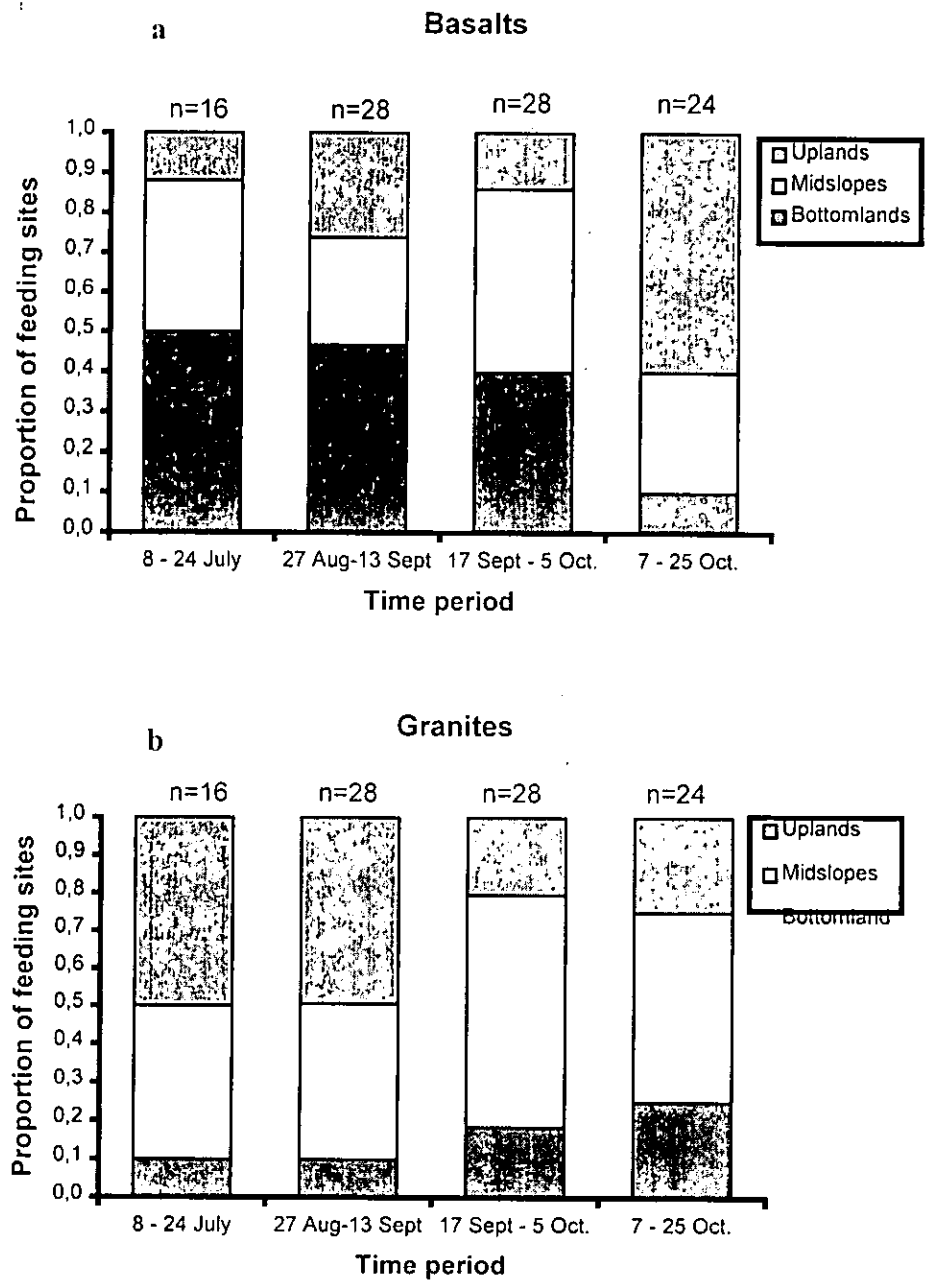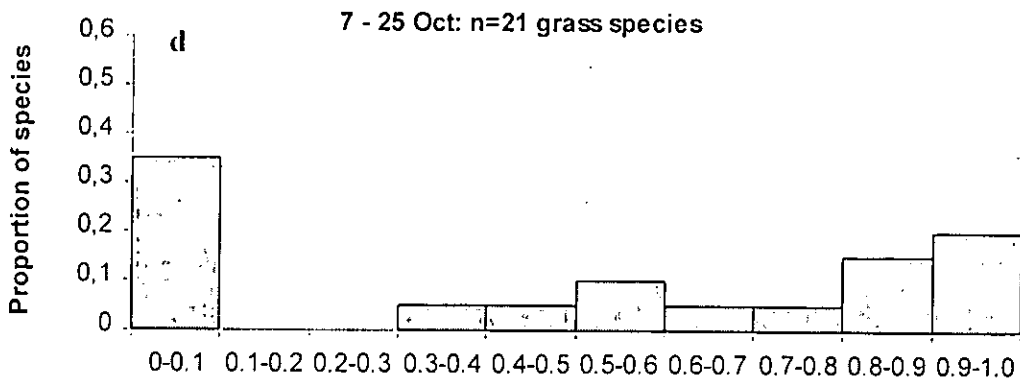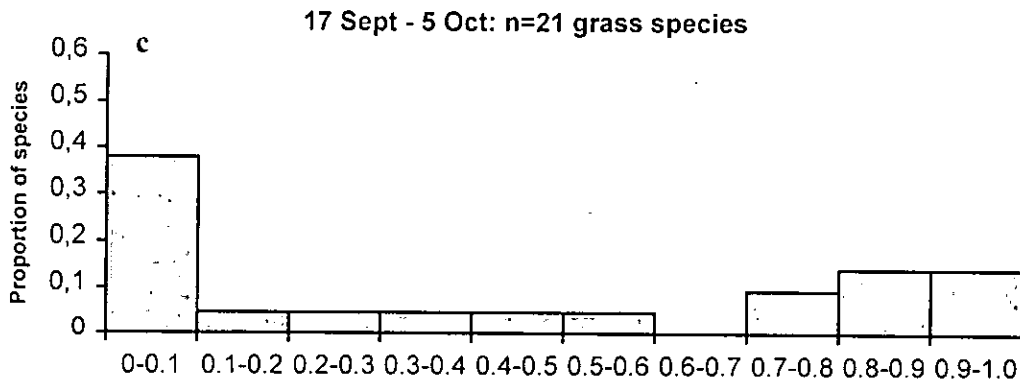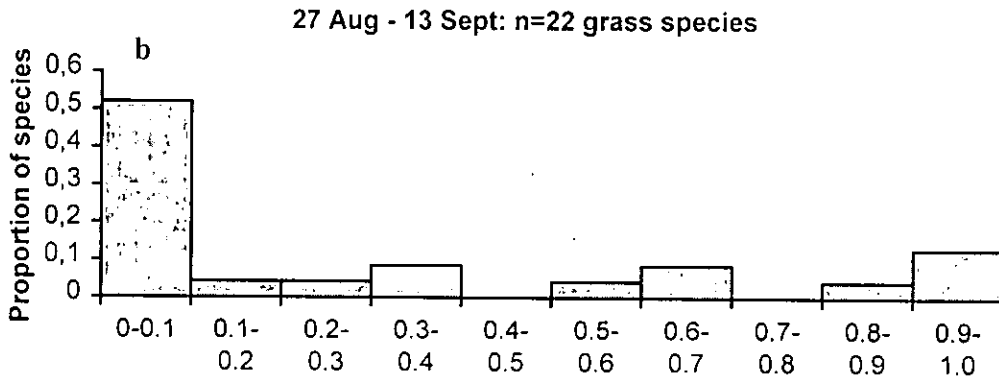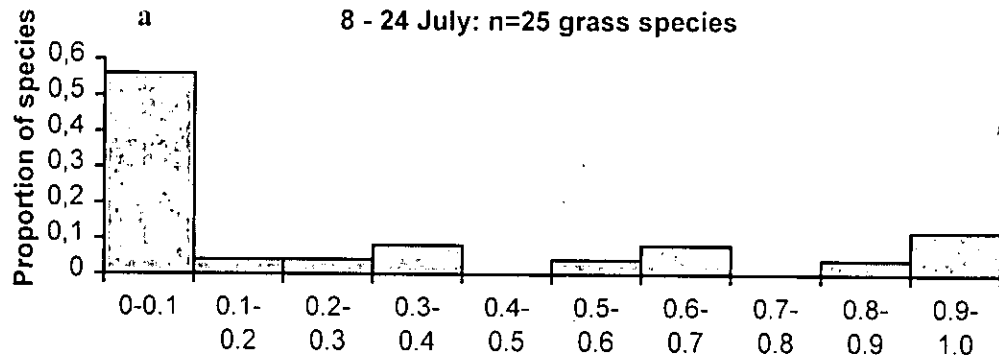
Basalts

Granites

Figure 2. Changes between periods in the proportion of feeding sites located in different landscape positions in the (a) basalts and (b) granites.

With the progression of the dry season, the proportion of grass species with acceptance frequency greater than 0.6 increased, while the proportion of species with acceptance frequency less than 0.1 decreased (Figure 3). This is an indication that more grass species were included in the diet and that the buffalo increased their acceptance for particular grass species as the dry season progressed.

The acceptance frequency differed among grass species (Figure 4). Grass species yielding high acceptance values (>0.5) during July, i.e. *P. maximum*, *P.coloratum*, *C. ciliaris* and *H. contortus* remained highly acceptable throughout the dry season. Most grass species that were of low acceptance frequency in July showed increasing acceptance with the progress of the dry season. The acceptance of *D. eriantha*, *U. mosambicensis*, *U. oligotricha* and *T. triandra* increased to above 0.5 from late August until late October, whereas the acceptance frequency of *E. superba*, *E. ciliaris* and *B. insculpta* increased only in late October. At the end of the dry season almost all grass species showed high acceptance frequency. Only *Cymbopogon* spp., *Setaria* spp., *Pogonarthria squarrosa*, *Tricholaena monachne*, *Chloris virgata* and *Aristida congesta barbicolis* remained neglected throughout this study (Figure 4).

Of all grass species encountered by buffalo, increases in acceptance frequency among time periods were statistically significant for *Digitaria eriantha*, *Urochloa mosambicensis*, *Eragrostis superba* and *Bothriochloa insculpta*. The acceptance frequency of *D. eriantha* increased significantly from 0.37 of the 94 quadrats recorded in July to 0.63 of the 147 quadrats encountered in late August and then to 0.85 of the 137 quadrats found with this species in late September ($\chi^2 = 67$, df=3, p<0.001). In July buffalo grazed *Urochloa mosambicensis* in only 0.1 of the 98 quadrats encountered, but the proportion of grazed quadrats increased to 0.29 of the 227 quadrats found in late August and then to 0.66 of the 151 quadrats recorded with this species in late September ($\chi^2 = 165.7$, df=3, p<0.001). The acceptance frequency of *Eragrostis superba* increased significantly from 0.18 of the 83 quadrats in late August to 0.46 of the 62 quadrats found in late September and then to 0.75 of the 72 quadrats encountered with this species in late October ($\chi^2 = 82.9$, df=3, p<0.001). Buffalo started grazing *Bothriochloa insculpta* in late September by grazing only 0.04 of the 53 quadrats recorded, but the acceptance frequency of this species increased to 0.47 of the 192 quadrats recorded with this species in late October ($\chi^2 = 99.6$, df=3, p<0.001). Non-overlapping binomial confidence limits suggest significant difference in acceptance frequency between consecutive periods (Figure 5). These binomial confidence limits were calculated following the Department of Agriculture of the United

States of America on the calculation of binomial confidence limits for proportions and sex ratios (www.wcrl.ars.usda.gov/cec/java/sexratio.htm).

a 8 - 24 July: n=25 grass species

27 Aug - 13 Sept: n=22 grass species

b

17 Sept - 5 Oct: n=21 grass species

c

7 - 25 Oct: n=21 grass species

d

Acceptance category
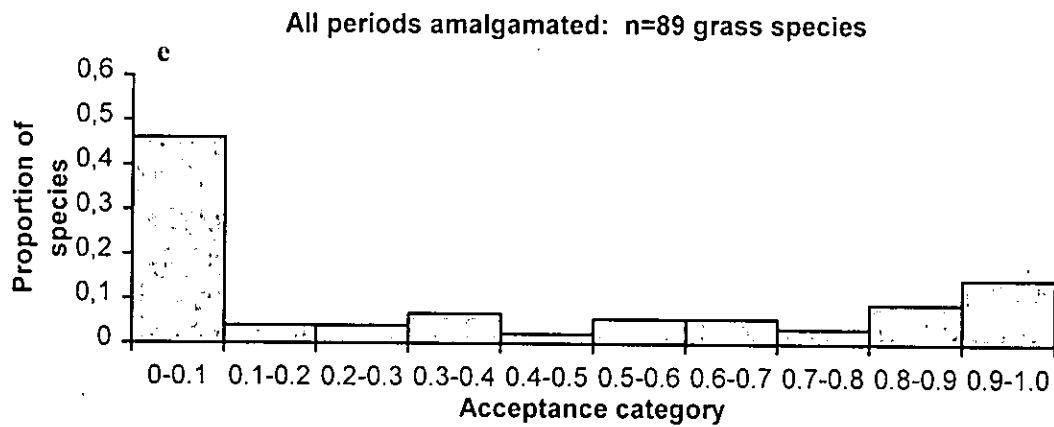
All periods amalgamated: n=89 grass species

Figure 3. Proportion of grass species in different acceptance categories with the progress of the dry season.

Changes in the availability of grass species over time

At the beginning of the study in July buffalo selected feeding sites with high availability of *Panicum* spp., but from late August onwards *U. mosambicensis* also became more commonly found in feeding sites. A decline in the availability of both *Panicum* spp. was noted from late August onwards. The availability of *B. insculpta* in feeding sites increased markedly in late October (Figure 6).

Acceptance frequency showed no significant relation with availability (Appendix III). Some species frequently encountered by buffalo, such as *D. eriantha* and *U. mosambicensis*, were not highly accepted at the beginning of the study, while uncommon grass species such as *Sporobolus ioclados*, *Ischaemum fasciculatum* and *Cenchrus ciliaris*, recorded high acceptance frequencies.
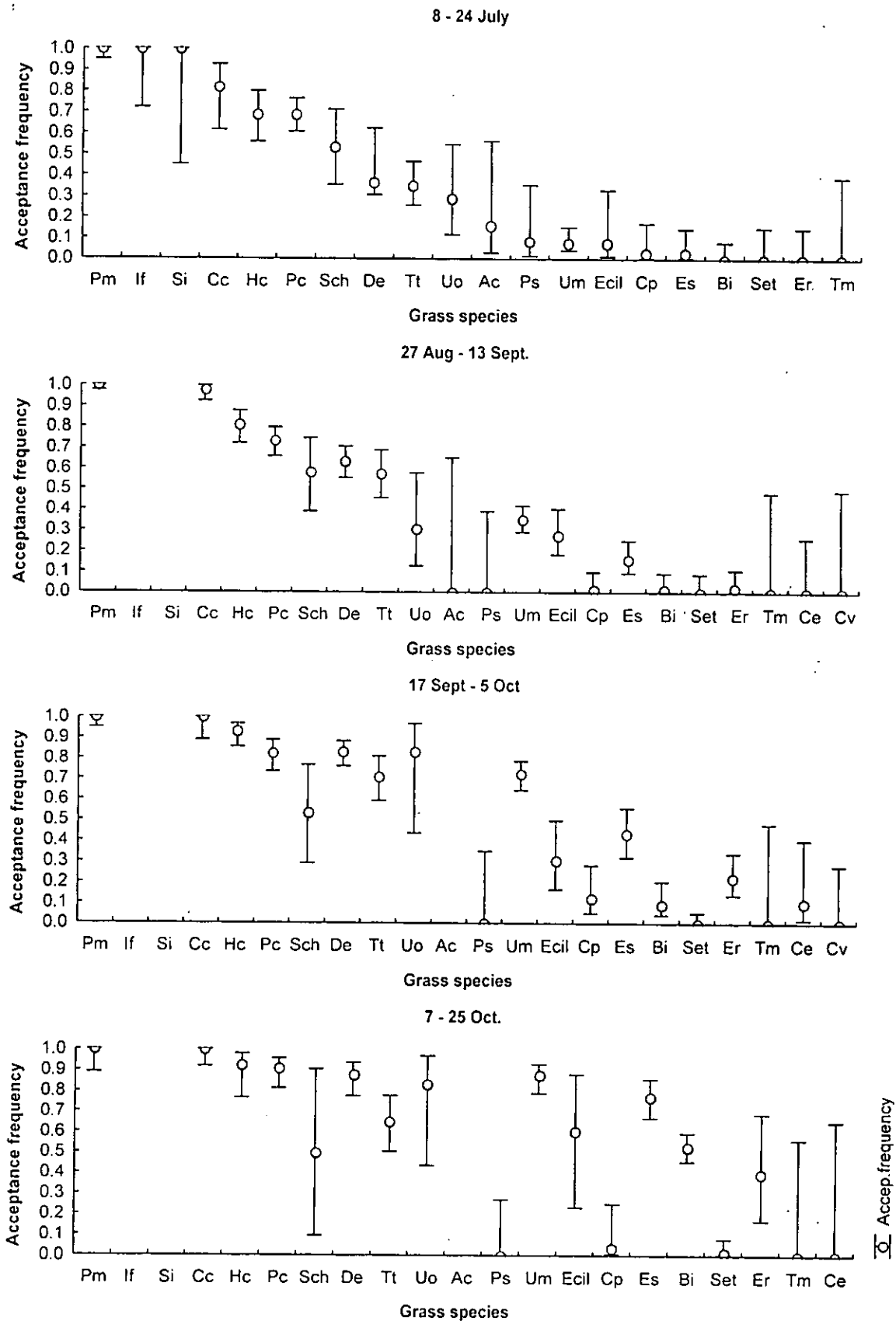
Figure 4. Changes between periods in the acceptance frequency of each grass species. Vertical lines indicate 95% binomial confidence limits. Acronyms are identified in Appendix I.
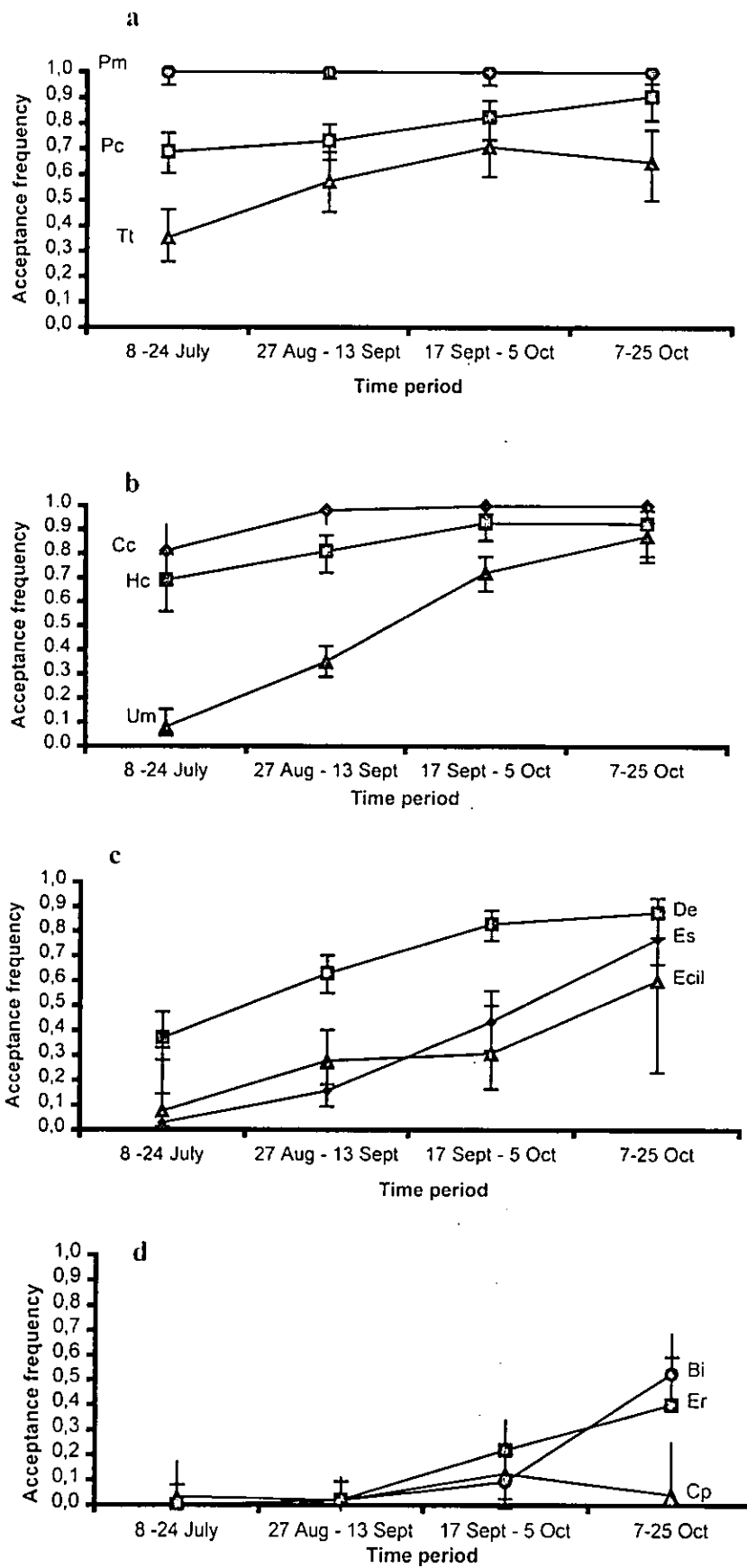
Figure 5. Changes between periods in the acceptance frequency of (a) Pm-*Panicum maximum*, Pc-*Panicum coloratum* and Tt-*Themeda triandra*; (b) Cc-*Cenchrus ciliaris*,

Hc-*Heteropogon contortus* and Um-*Urochloa mosambicensis*; (c) De-*Digitaria eriantha*, Es-*Eragrostis superba* and Ecil-*Eragrostis ciliaris*; and (d) Bi-*Bothriochloa insculpta*, Er-*Eragrostis rigidior* and Cp-*Cymbopogon plurinodis*. Vertical lines indicate 95% binomial confidence limits.

Dietary contribution

The diet obtained by buffalo changed in its grass species composition with the progression of the dry season. Five species showed significant changes in dietary contribution between time periods. In July *P. maximum* made up 0.25±0.08 of the diet in the basalts and 0.46±0.12 of the diet in the granites but the contribution of this species dropped significantly to 0.06±0.02 in both landscapes in late October (F=12.47, p<0.001, df=3). *P. coloratum* showed a similar pattern to *P.. maximum*. The contribution of *P. coloratum* to the diet of buffalo was 0.22±0.38 and 0.25±0.12 in the basalts and granites, respectively in July, but declined to 0.14±0.04 in the basalts and to 0.06±0.02 in the granites in late October (F=3.12, p=0.03, df=3) (Figure 7).

In contrast, the dietary contribution of *U. mosambicensis*, *E. superba* and *B. insculpta* increased with the progression of the dry season. From July to October the contribution of *U. mosambicensis* to the diet of buffalo increased significantly from 0.02±0.02 to 0.32±0.08 in the basalts and from 0.01±0.01 to 0.13±0.04 in the granites (F=7.7, p<0.001, df=3). *E. superba* did not contribute to the diet of buffalo in July, but an increase to 0.15±0.06 in the basalts and to 0.07±0.02 in the granites was observed in late October (F=11.35, p<0.001, df=3). *B. insculpta* showed a similar pattern to *U. mosambicensis* and *E. superba*. This species contributed nothing to the diet in both landscapes in July, but the dietary contribution increased significantly to 0.21±0.07 in the basalts and to 0.18±0.08 in the granites in late October (F=17.46, p<0.001, df=3) (Figure 7). The dietary contribution of *C. ciliaris* increased significantly with time only in the granite landscape. *C. ciliaris* made up 0.01±0.01 of the diet in the granites in July but the dietary contribution of this species increased significantly to 0.14±0.07 in late October (F=4.49, df=3, p=0.008). In both landscapes, the dietary contribution of *T. triandra*, *D. eriantha*, *H. contortus* and *S. pappophoroides* did not change significantly throughout the study period.
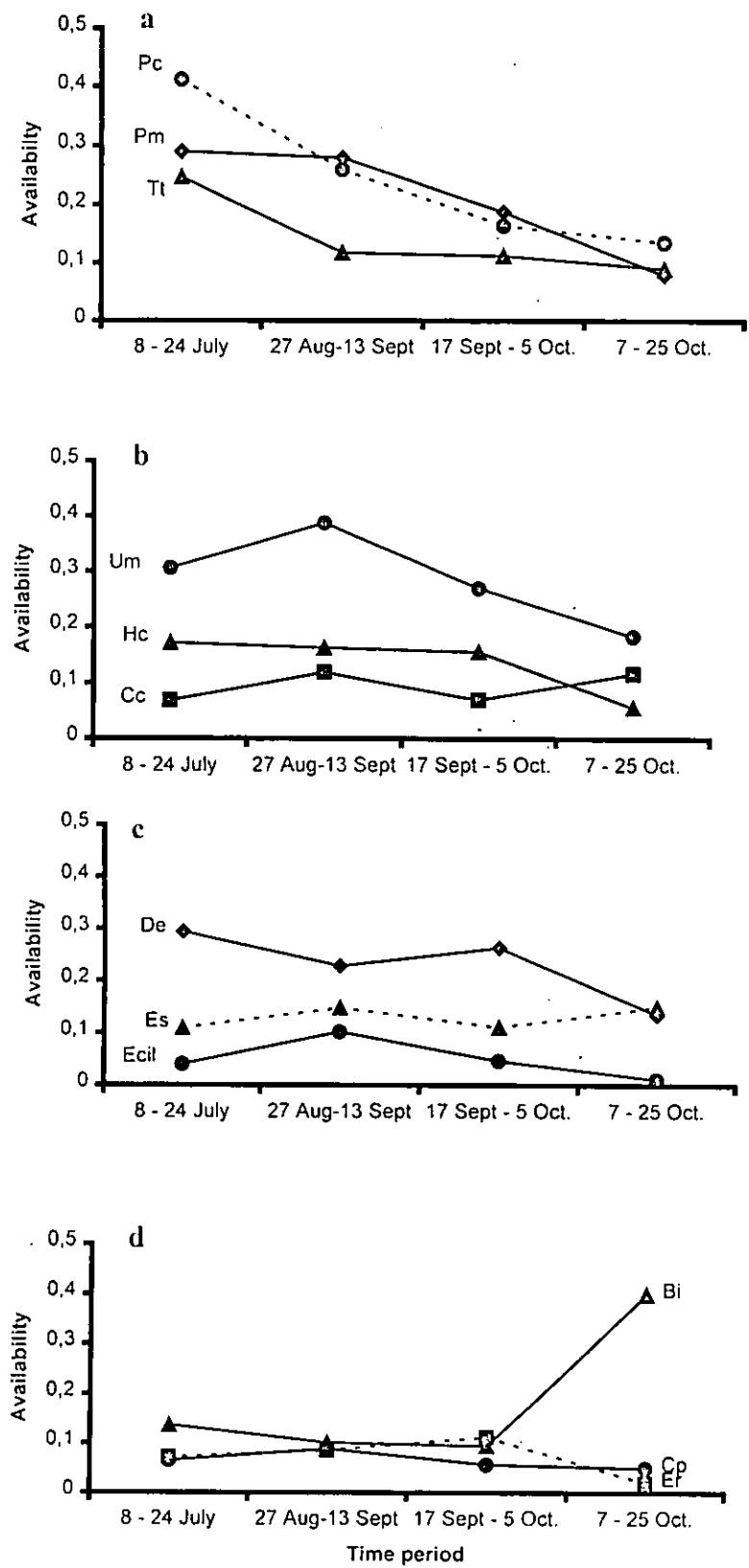
Figure 6. Changes in the availability of grass species in feeding quadrats over time (n=8, 14, 14 and 12 days during the four study periods, respectively). Acronyms for section (a), (b), (c) and (d) are identified in Figure 5.

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The overall dietary contribution of *P. maximum*, *T. triandra* and *D. eriantha* from July to October was significantly greater in the granites than in the basalts. *P. maximum* contributed significantly more in the granites (0.26) than in the basalts (0.14) (n=24, F=11.24, p<0.001, df=1). *T. triandra* made up 0.08 of the diet in the granites and 0.03 of the diet in the basalts. The difference between these two means was statistically significant (n=24, F=6.24, p=0.01, df=1). The dietary contribution of *D. eriantha* was significantly more in the granites (0.24) than in the basalts (0.10) (n=24, F=8.9, p=0.004, df=1) (Table 1).

The proportions of *U. mosambicensis*, *P.coloratum* and *C. ciliaris* in the diet of buffalo during the dry season were significantly greater in the basalts than in the granites. *U. mosambicensis* made up 0.18 of the diet in the basalts but only 0.07 of the diet in the granites. The difference between these two means was significant (n=24, F=10.27, p=0.01, df=1). In the basalts, 0.17 of the diet was made up by *P. coloratum*, whereas in the granite landscape the contribution of this species was 0.12. These means differed significantly (n=24, F=4.16, p=0.04, df=1). The overall proportional contribution of *C. ciliaris* to the diet of buffalo in the basalts was 0.09 and 0.04 in the granites. The two means were statistically significant (n=24, F=11.49, p=0.001, df=1). The dietary contribution of *H. contortus*, *E. superba*, *S. pappophoroides* and *B. insculpta* did not quite differ significantly between landscapes (Table 1).

Other species contributed a small amount to the diet in only one of the landscapes. For instance, *Eragrostis rigidior* and *Cymbopogon plurinodis* contributed to the diet in the granites, whereas *Eragrostis ciliaris* contributed only to the diet in the basalts. These species were encountered by buffalo in only one landscape.

Factors influencing grass species selection

Grass species acceptance was positively correlated with the percentage of green leaves offered by each species in all four periods (Figure 8). The correlation between grass species acceptance frequency and grass height was positive but weak from July to early September. This correlation became negative from late September to the end of the dry season because the acceptance of short grass species (*D. eriantha* and *U. mosambicensis*) increased while tall species (*Cymbopogon* spp. and *Setaria* spp.) remained neglected (Appendix IV). The acceptance frequency of grass species was weakly, negatively and not

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significantly correlated with the number of stems, which indicated that the number of stems was not a significant factor in the selection of grass species by buffalo.

Generally brown/dry and short species such as *E. rigidior*, *D. eriantha*, *U. mosambicensis* and *S. pappophoroides* as well as tall species such as *Setaria* spp. and *C. plurinodis* recorded lower acceptance values than species with relatively high proportion of green leaves and intermediate height such as *P. maximum*, *P. coloratum*, *C. ciliaris* and *H. contortus* (Figure 9). Grass greenness appeared to be more important than grass height in influencing species acceptance. For instance, *C. plurinodis*, *T. triandra* and *Setaria* spp. were species of almost the same height, but *Themeda* was more acceptable probably because this species was slightly greener than the other two species.

Classification of grass species

Following Owen-Smith (2002), *P. maximum* and *P. coloratum* were classified as staple food for buffalo because these species were both highly acceptable and of high availability. However, the dietary contribution of these species declined seasonally due to declining availability in feeding quadrats indicating that buffalo changed plant communities where to graze. Other highly acceptable grass species such as *Cenchrus ciliaris*, *Heteropogon contortus*, *Sporobolus ioclados* and *Ischaemum fasciculatum* contributed less to the diet owing to their low availability. *Urochloa mosambicensis* and *Digitaria eriantha* appeared to be reserve resources, as buffalo turned to them later in the dry season. *Bothriochloa insculpta* and *Eragrostis superba* could be classified as buffer resources, because these grass species were neglected during most of the season, but became much more acceptable and contributed more to the diet just at the end of the dry season. The relative proportions of grass species in the diet of buffalo changed as herd shifted from grazing *Panicum* spp. and *U. mosambicensis* dominated grassland types earlier in the season to increase the utilization of patches dominated by *Bothriochloa* spp. at the end of the dry season.
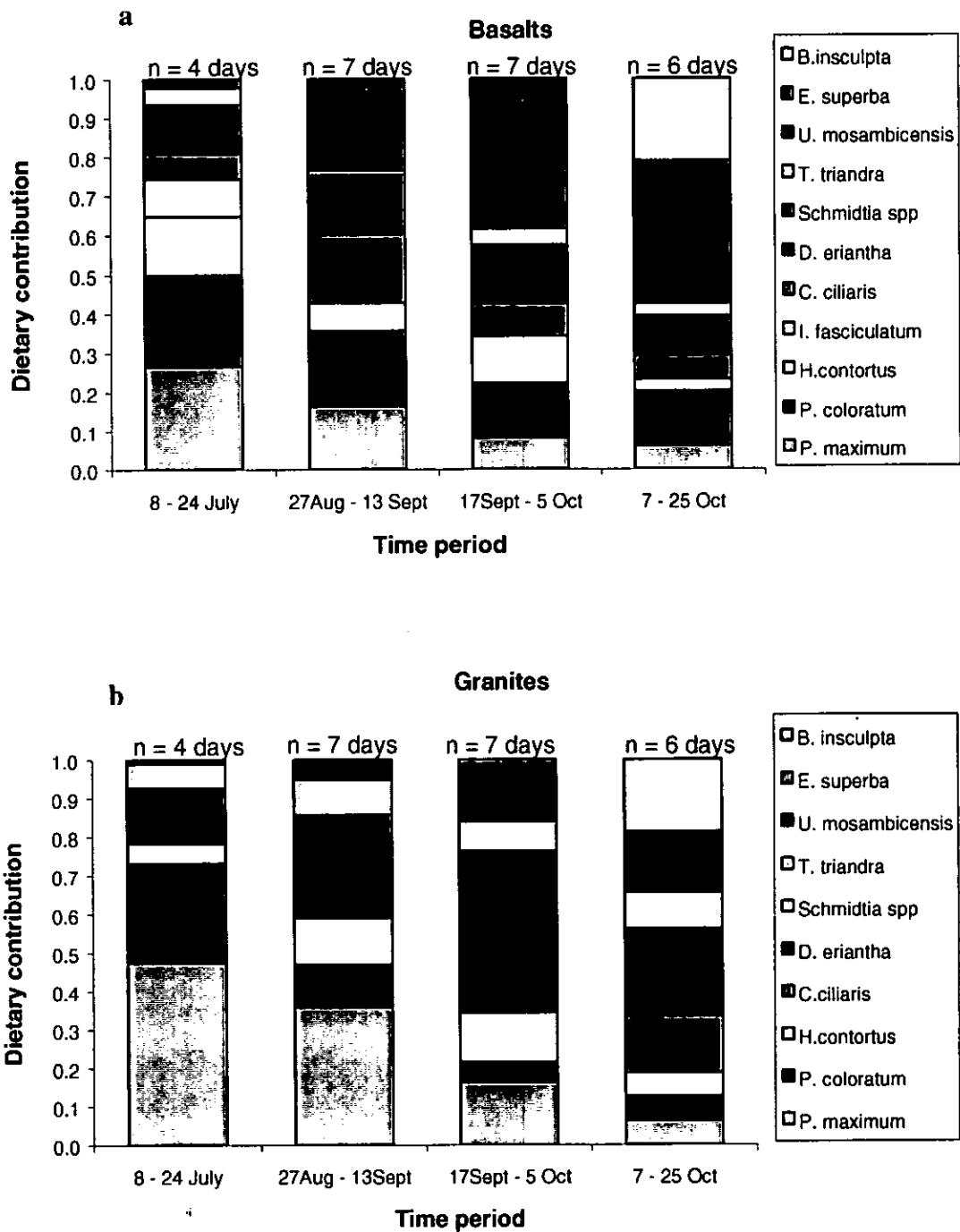
Basalts

Granites

Figure 7. Changes between periods in the contribution of each grass species to the diet of buffalo in the (a) basalts and (b) granites.
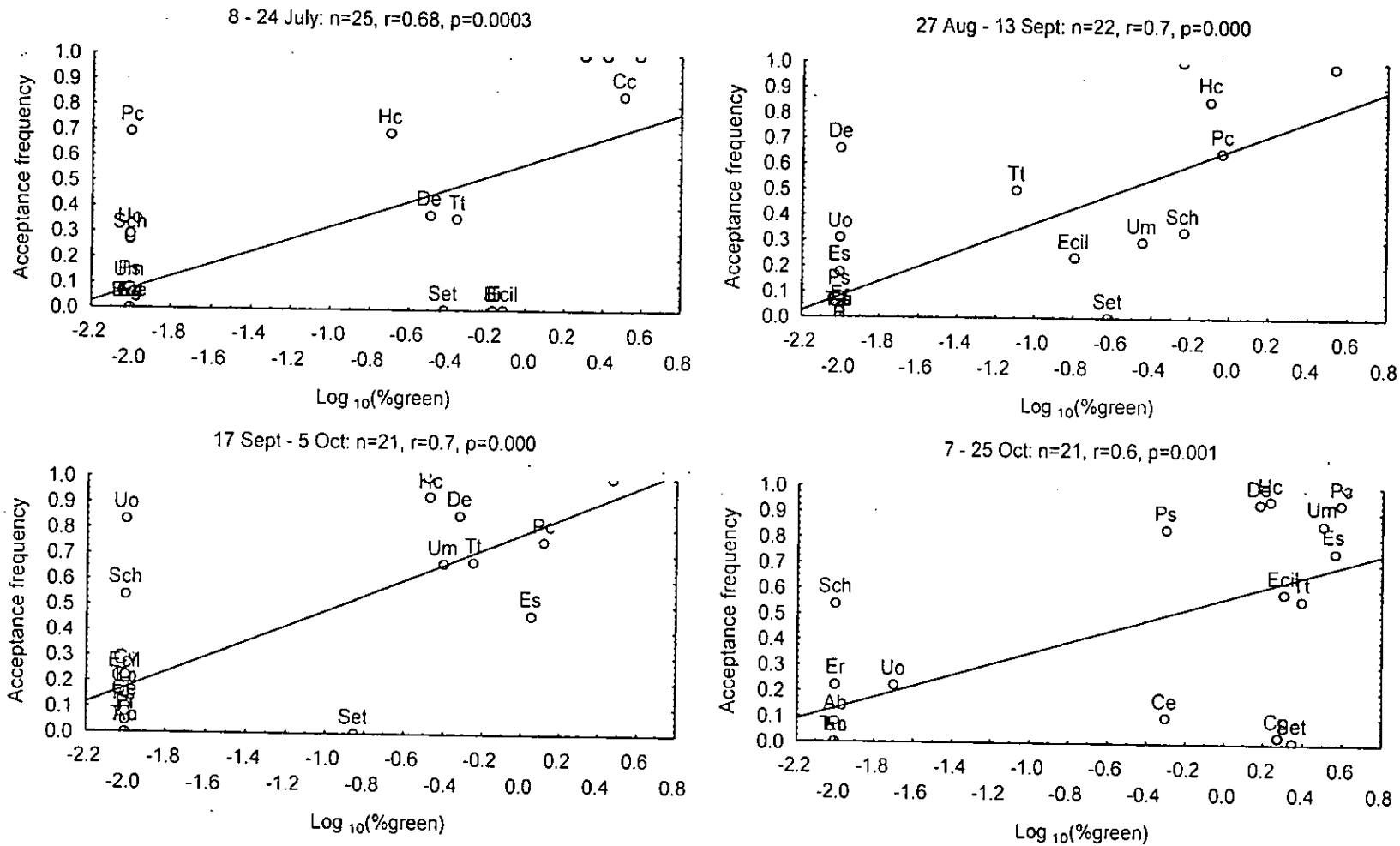
Figure 8. Relationships between acceptance frequencies for grass species and proportion of green leaves in each period. Acronyms are identified in Figure 5.
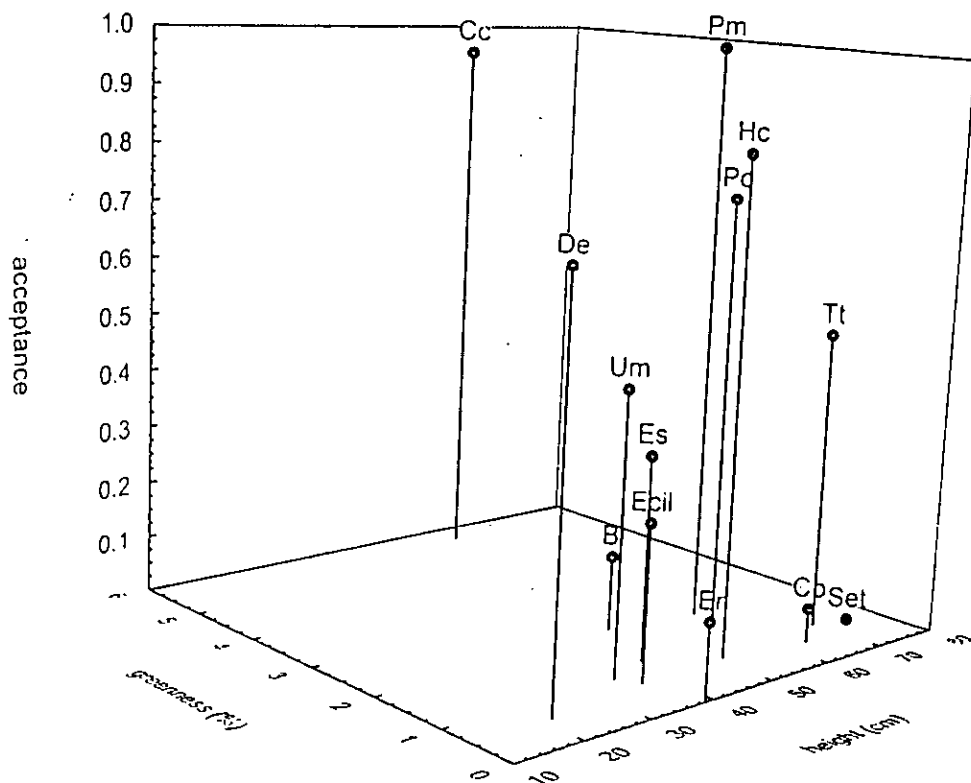
Figure 9. Three dimensional plot showing the relationship between the average over the dry season in acceptance frequency, greenness and grass height of each grass species. Acronyms are identified in Figure 5.

According to acceptance frequency, *P. maximum, P. coloratum, H. contortus, C. ciliaris, D. eriantha* and *I. fasciculatum* were the most favoured grass species for buffalo. *U. mosambicensis, T. triandra, S. pappophoroides* and *E. superba* were intermediate species, whereas *B. insculpta, Setaria spp, Cymbopogon spp, E. rigidior, P. squarrosa, T. monachne* and *A. congesta barbicolis* were neglected (Table 1).

U. mosambicensis appeared an intermediate species according to the frequency of acceptance but fell within the neglected category according to the forage ratio. This difference in classification is because the forage ratio tends to underrate very common species as it divides the use by the availability.

Table 1. Overall dietary contribution, acceptance frequency and forage ratio of grass species through the dry season months.

	Dietary contribution		Relative selection				
	Basalts	Granites					
Acronyms	Mean	Mean	N (quadrats)	Acc. freq. (bin. CL)	Expect. use	Log FR	Bonferroni interval
Pm	0.14	0.26***	384	1 (0 –0.01)	0.1	0.28	0.17≤p ≥0.215
Pc	0.17*	0.12	442	0.77 (0.04 - 0.035)	0.1	0.14	0.116≤p ≥0.15
De	0.1	0.24**	443	0.68 (0.046 - 0.04)	0.15	0.09	0.17≤p ≥0.21
Um	0.18**	0.07	564	0.49 (0.04 - 0.04)	0.15	-0.07	0.11≤p ≥0.144
Hc	0.09	0.09	264	0.84 (0.05 - 0.04)	0.06	0.18	0.08≤p ≥0.11
Cc	0.09***	0.04	188	0.97 (0.034 - 0.02)	0.04	0.26	0.05≤p ≥0.078
Tt	0.03	0.08**	251	0.55 (0.06 - 0.056)	0.06	-0.01	0.04≤p ≥0.06
Es	0.06	0.02	252	0.39 (0.058 - 0.06)	0.05	-0.15	0.027≤p ≥0.04
Bi	0.05	0.05	346	0.32 (0.04 - 0.05)	0.08	-0.30	0.03≤p ≥0.04
Sch	0.02	0.01	67	0.55 (0.12 - 0.115)	0.015	0.00	0.009≤p ≥0.02
Er	0	0.01	143	0.13 (0.046 - 0.06)	0.03	-0.66	0.003≤p ≥0.01
Ecil	0.02	0	105	0.28 (0.07 -.09)	0.019	-0.33	0.004≤p ≥0.01
Set			202	0.005 (0.04 - 0.27)	0.04	-1.88	0.0005≤p ≥0.002
Cp			138	0.05 (0.025 - 0.05)	0.03	-1.07	- 0.0002≤p ≥0.004
Ab			99	0.11 (0.09 - 0.32)	0.018	-1.52	0.0005≤p ≥0.002
Ps			35	0.028 (0.02 - 0.12)	0.007	-1.40	- 0.0005≤p ≥0.001
Tm			17	0 (0 - 0.18)	0.003		
If			12	1 (0 – 0.26)	0.003	0.29	0.004≤p ≥0.013
Ce			36	0 (0 - 0.09)	0.006		
If, Si, Uo, Ps, Ab	0.04	0.02					

* denotes p<0.05   ** denotes p<0.01   *** denotes p<0.001

Abbreviations used as column headings in Table 1:

Mean: overall mean dietary contribution of each grass species to the diet of buffalo in the basalt and granite landscape

N: number of quadrats encountered with the grass species throughout the study period

Acc. freq. (bin. CL): proportion of quadrats where the species was grazed (binomial confidence limits)

Expect. use: Expected use of each grass species according to its availability in the sward

log FR: logarithmic transformation of the forage ratio

Bonferroni interval: Simultaneous Bonferroni confidence intervals for the observed proportion of utilization of each grass species

Discussion

Buffalo were selective for particular grass species and their selection for species changed over the dry season. Grass species made up different proportional contributions to the diet of buffalo and these proportions changed seasonally. Buffalo favoured grass species offering a high proportion of green leaves and grass species of intermediate height. Landscapes did not differ significantly in the proportion of quadrats retaining green leaves. Grass was greener in bottomlands than in midslopes or uplands.

Panicum spp. were favoured and constituted a great part of the diet of buffalo. This finding is in accordance with the study of Field (1976), Funston *et al.* (1994) and Perrin and Brereton-Stiles (1999). On the other hand, buffalo avoided *Setaria* spp. and *Cymbopogon* spp. as also found by Field (1976) and Perrin and Brereton Stiles (1999). Field (1976) identified the aromatic smell of *Cymbopogon* spp. attributed to its high content in essential oils as the likely reason for the rejection of this species during his work in Uganda.

Buffalo did not highly favour *Themeda triandra*. This grass species was not important for buffalo in terms of both acceptance frequency and dietary contribution. This observation is in accord with the finding of Field *et al.* (1973) in Uganda. McNaughton (1985) also reported that in Serengeti buffalo did not favour patches dominated by *Themeda* during the dry season. However, it has been reported that *Themeda trianda* is among the most favoured grass species by a similar grazer, cattle (Field *et al.* 1973, O'Reagain and Mentis 1989, Stoltsz and Danckwerts 1990).

Despite the aromatic smell of *Bothriochloa*, buffalo grazed this species at the end of the dry season, but the aromatic smell may explain the low acceptance observed during most of the dry season. Field (1976) also reported that the overall acceptance of *Bothriochloa* by buffalo was very low. Buffalo avoided *Bothriochloa* in July, but grazed this species in October when this grass species was dominant in feeding sites and when this species offered a high proportion of green leaves in response to the first rains. Perrin and Brereton-Stiles (1999) also found that buffalo rejected *Bothriochloa* during the early dry season months (May-July).

Buffalo favoured grass species offering a higher proportion of green leaves, but when nutrient rich green material was not available, buffalo consumed brown material. For instance, the significant increase in the acceptance of *Digitaria eriantha*

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and *Urochloa mosambicensis* with the progression of the dry season was not related to changes in greenness because these species remained dry almost throughout this study. A reason for the increase in acceptance frequency and dietary contribution of these species is probably the decline in the availability of the greener and more palatable grass species. In addition, *Digitaria* and *Urochloa* have soft leaves and stems (pers. observation), which indicate lower concentration of structural components in the tissues of these grass species. Hence, these species are of high digestibility even when dry (Oudtshoorn 1999). Taylor (1989) also observed that buffalo select green leaves when the sward is of mixed phenological stages, but become relatively non-selective when the sward is very dry.

Buffalo were selective for grass species of intermediate height because these species secure adequate bite size. In July buffalo were more selective for medium-tall grass species such as *Panicum* spp., but turned to shorter species such as *Digitaria eriantha* and *Urochloa mosambicensis* later in the season. Likewise, Perrin and Brereton-Stiles (1999) observed that in Hluhluwe-Umfolozi Park buffalo favoured tall grass species during the early dry season months. O'Reagain and Mentis (1989) found that the acceptance of grass species by cattle was positively correlated with leaf table height and negatively correlated with number of stems. The expected negative significant correlation between acceptance frequency and number of stems was not revealed in this study as it was observed that *Heteropogon contortus* and *Eragrostis superba* were accepted despite being the stemmiest grass species.

The basalt and granite landscapes appeared with very low availability of green leaves through the dry season. This finding is in discrepancy with previous research during the dry season (Seghieri *et al.* 1994) reporting that clayey soils show a more severe aridity than sandy soils. In July, herds favoured bottomlands and midslopes where relatively more green leaves could be found, but as the dry season progressed, herds increased the use of uplands probably due to the decline in forage biomass in bottomlands and midslopes.

Foraging theory predicts that diets should be widened as food availability declines (Owen-Smith 2002). In accordance with this theory, buffalo widened the range of grass species they ate as the dry season progressed. The diet of buffalo changed markedly through the season in terms of species selected as well as in terms of contribution of each grass species to the diet. The available biomass of preferred species declined in feeding sites at the end of the dry season as a result of

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consumption and/or shifts in grazing locations in terms of both plant communities and landscape position. Thus, buffalo adapted to the changing circumstances by incorporating more grass species in the diet and by increasing the contribution of the previously neglected and hence abundant grass species to the diet. Buffalo widened their diet with the progression of the season, but being ruminants they are constrained by forage quality (Prins 1996). Thus, unpalatable species such as *Pogonarthria squarrosa*, *Cymbopogon* spp., *Aristida congesta barbicolis* and *Setaria* spp. (Oudtshoorn 1999) were consistently avoided.

Conclusion

Buffalo coped with the food restrictions during the dry season by widening the diet in terms of grass species eaten and by changing the proportions of each grass species in the diet. Herds changed their grazing location in terms of both landscape position and plant communities. The availability of green leaves for the herds was very low in both landscapes during the dry season. Buffalo selected for grass species offering a higher proportion of green leaves and for grass species of intermediate height. Although selective for green leaves and intermediate height, with the progress of the dry season buffalo increased the consumption of the most available brown/dry leaves and short grass species. Despite differences in botanical composition of grass species, herds did not differ in their acceptance for particular grass species. However, differences in relative availabilities of grass species between landscapes may have accounted for the observed differences in the contribution of each grass species to the diet of the herds in the two landscapes.

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**Appendix I.** Grass species encountered by buffalo in feeding sites.

Scientific names	Common names	Acronyms
Panicum maximum	Buffalo grass/guinea grass	Pm
Panicum coloratum	Small buffalo grass	Pc
Digitaria eriantha	Common finger grass	De
Themeda triandra	Red grass	Tt
Heteropogon contortus	Spear grass	Hc
Urochloa mosambicensis	Bushveld signal grass	Um
Cenchrus ciliaris	Foxtail buffalo grass	Cc
Eragrostis superba	Saw-tooth love grass	Es
Eragrostis rigidior	Broad curly leaf	Er
Eragrostis ciliaris	Wooly love grass	Ecil
Eragrostis curvula	Weeping love grass	Ec
Eragrostis gummiflua	Gum grass	Eg
Bothriochloa insculpta	Pinhole grass	Bi
Urochloa oligotricha	Perennial signal grass	Uo
Ischaemum fasciculatum	Hippo grass	If
Sporobolus ioclados	Pan dropseed	Si
Schmidtia pappophoroides	Sand quick	Sch
Pogonathria squarrosa	Herringbone grass	Ps
Tricholaena monachne	Blue-seed grass	Tm
Hyparthelia dissoluta	Yellow thatching grass	Hd
Eneapogon cenchroides	Nine-awned grass	Ene
Cymbopogon plurinodis	Narrow-leaved turpentine grass	Cp
Cymbopogon excavatus	Broad-leaved turpentine grass	Ce
Setaria spp	Bristle grass	Set
Chloris virgata	Feather-top chloris	Cv
Aristida congesta barbicolis	Spreading three-awn	Ab
Aristida congesta congesta	Tassel three-awn	Ac

| 7 - 25 Oct	n=12 days	n=480 quadrats		
Species	mean	mean	SE	Binomial confidence intervals
Bi	0.4(0.1-0.7)	0.47	0.06	0.07 - 0.07
Cc	0.12(-0.01-0.24)	1.00	0	
Cp	0.05(-0.05-0.16)	0.03	0.01	0.035 - 0.21
De	0.14(-0.01-0.28)	0.94	0.03	0.10 - 0.06
Ecil	0.01(-0.01-0.03)	0.58	0.03	0.37 - 0.28
Er	0.02(-0.04-0.08)	0.22	0.09	0.23 - 0.29
Es	0.15(0.02-0.28)	0.75	0.05	0.10 - 0.09
Hc	0.06(-0.003-0.12)	0.94	0.03	0.16 - 0.05
Pc	0.14(0.029-0.24)	0.93	0.03	0.09 - 0.05
Pm	0.08(0.025-0.13)	1.00	0	
Sch	0.004 (-0.005-0.01)	0.50	0.2	0.41 - 0.41
Set	0.14(0.03-0.25)	0.01	0	0.01 - 0.07
Tt	0.09(-0.01-0.19)	0.56	0.1	0.15 - 0.13
Um	0.18(0.05-0.32)	0.86	0.04	0.8 - 0.05

Appendix III. Comparison between acceptance frequency and availability of grass species over the dry season.
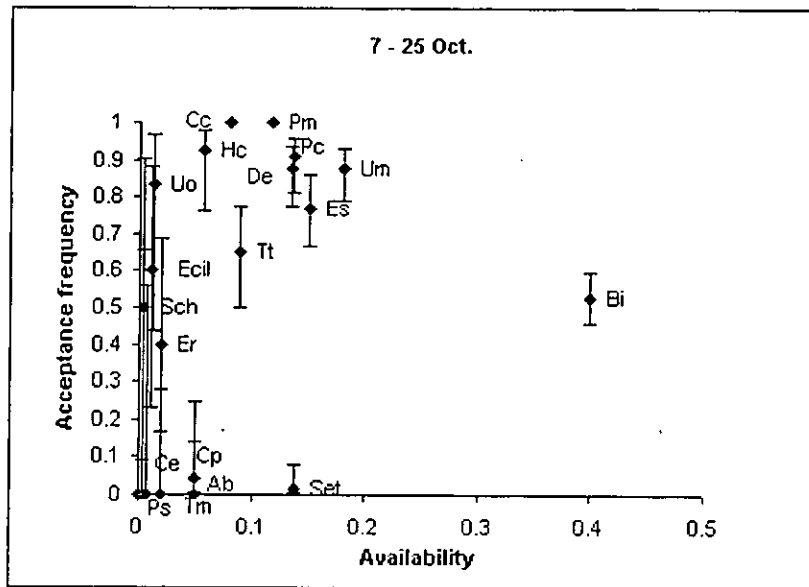

8- 24 July
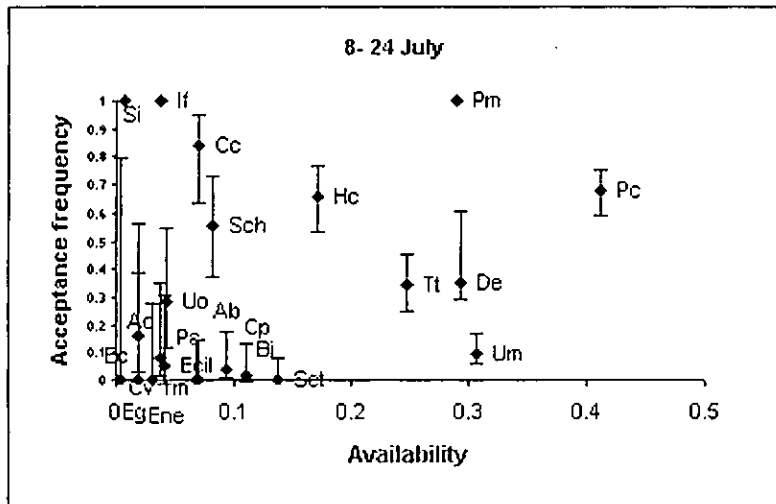
Correlation analysis: n=25, r=0.3164, p=0.123. Vertical lines indicate 95% binomial confidence limits

27 Aug - 13 Sept.
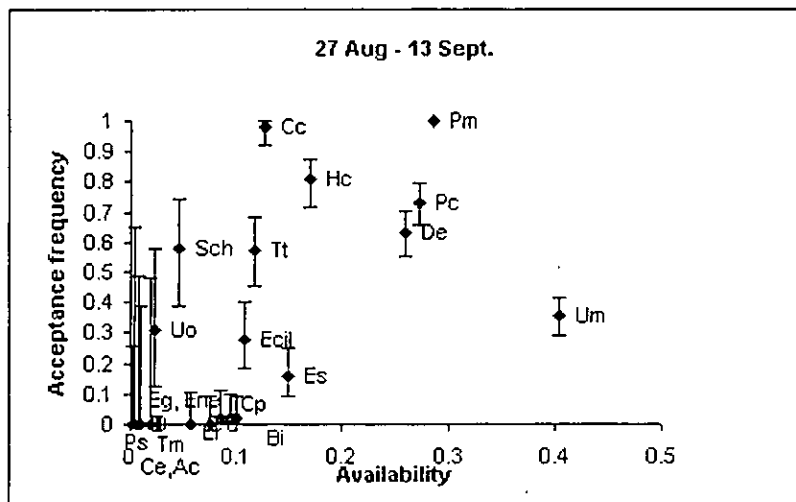
Correlation analysis: n=22, r=0.6298, p=0.001. Vertical lines indicate 95% binomial confidence limits
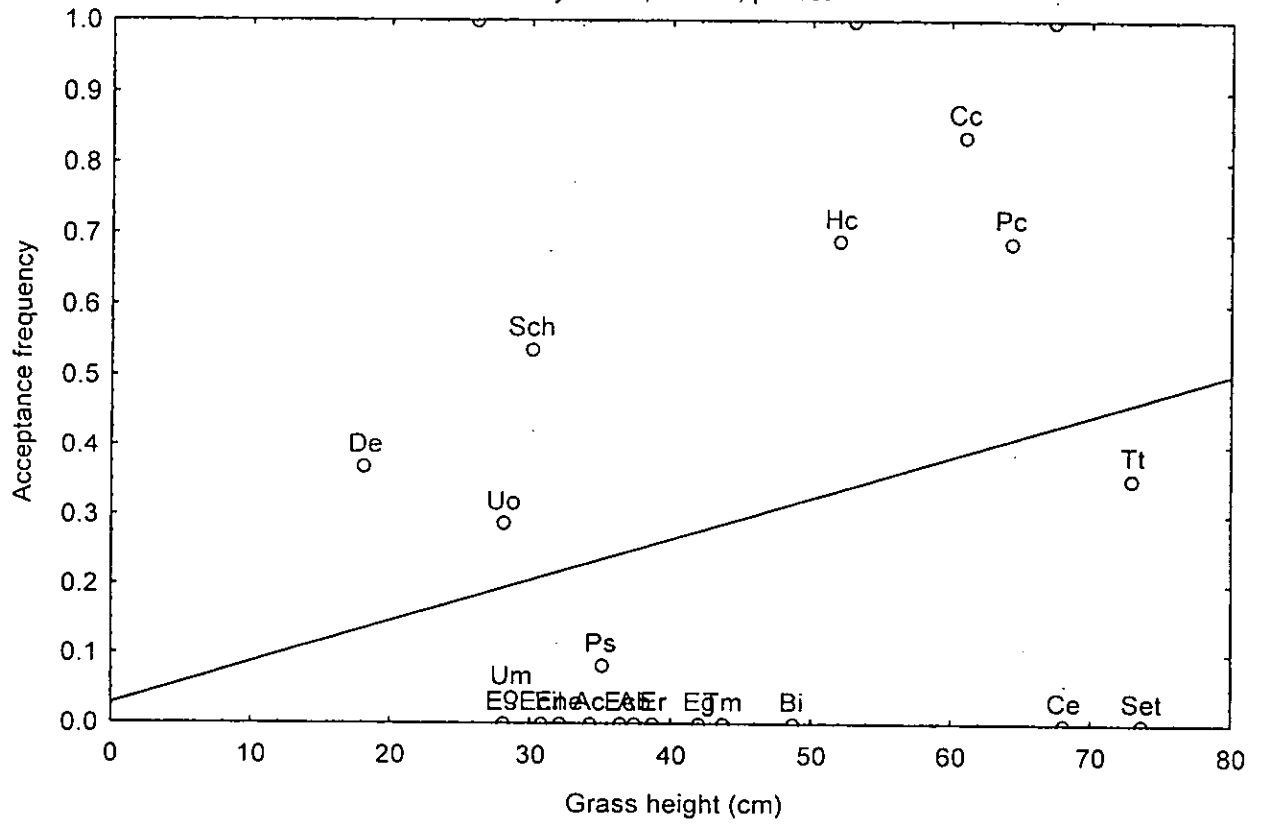
57

17 Sept - 5 Oct.
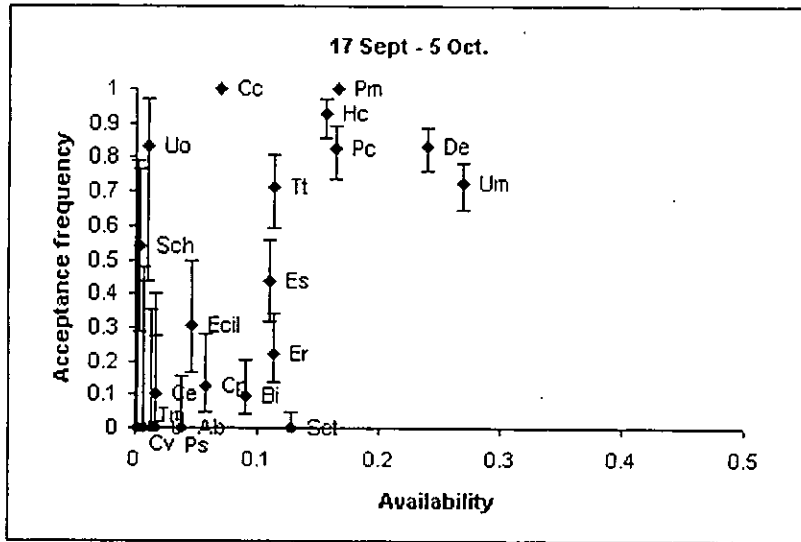
Correlation analysis: n=21, r=0.567, p=0.007. Vertical lines indicate 95% binomial confidence limits
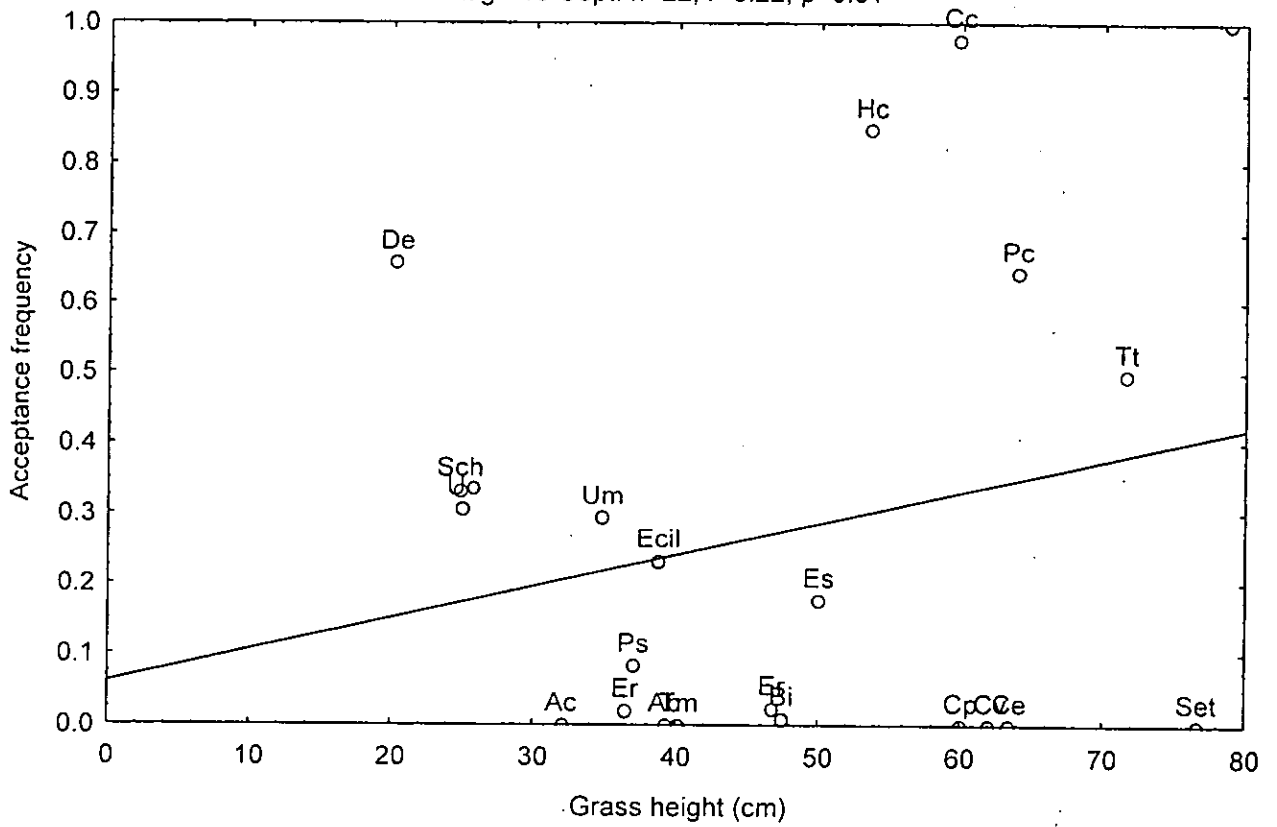

7 - 25 Oct.

Correlation analysis: n=20, r=0.33, p=0.15. Vertical lines indicate 95% binomial confidence limits.

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Appendix IV. Relationships between acceptance frequencies of grass species, grass height and number of stems in each sampling period.
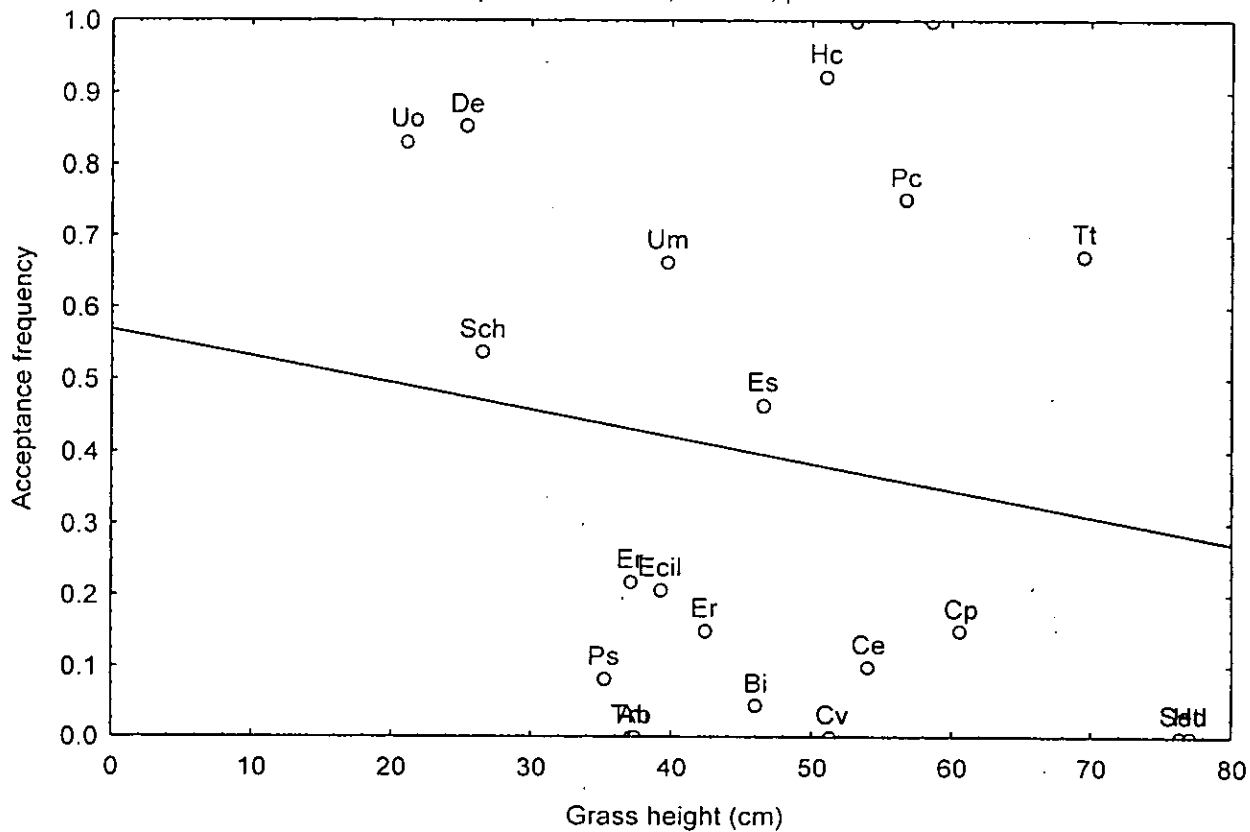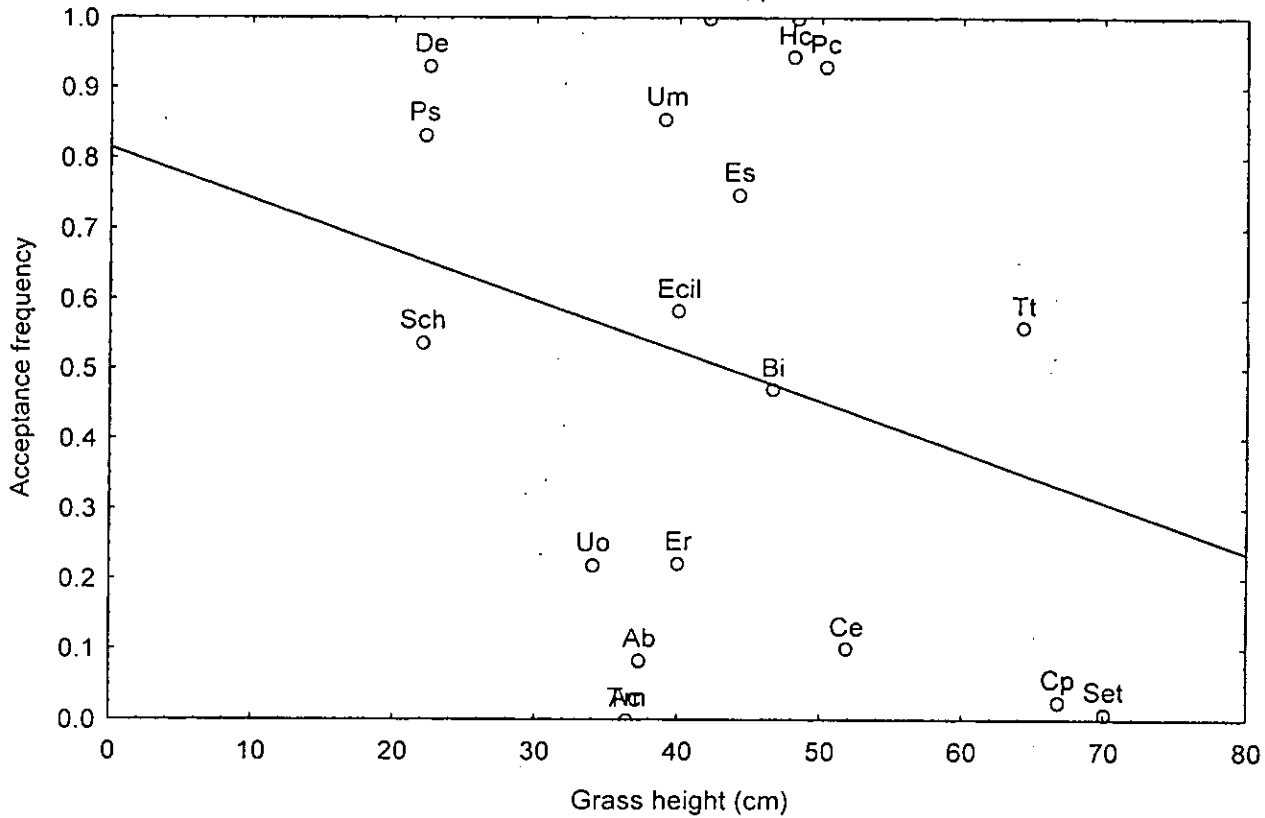

8 - 24 July: n=25, r=0.26, p=0.23

27 Aug - 13 Sept: n=22, r=0.22, p=0.31

17 Sept - 5 Oct: n=21, r=-0.15, p=0.50

7 - 25 Oct: n=21, r=-0.25, p=0.28

8 - 24 July: n=25, r=-0.08, p=0.69

Acceptance frequency vs Nº of stems

Data points labeled: Cc, Pc, Hc, Sch, De, Uo, Tt, Um, Ps, Ene, Bi, Ecil, Es, Ce

27 Aug - 13 Sept: n=22, r=-0.24, p=0.29

Acceptance frequency vs Nº of stems

Data points labeled: Cc, Hc, De, Pc, Tt, Sch, Um, Uo, Ecil, Es, Ps, Bi, Cp, Er, Er, Ho, Um, ASet, Ce
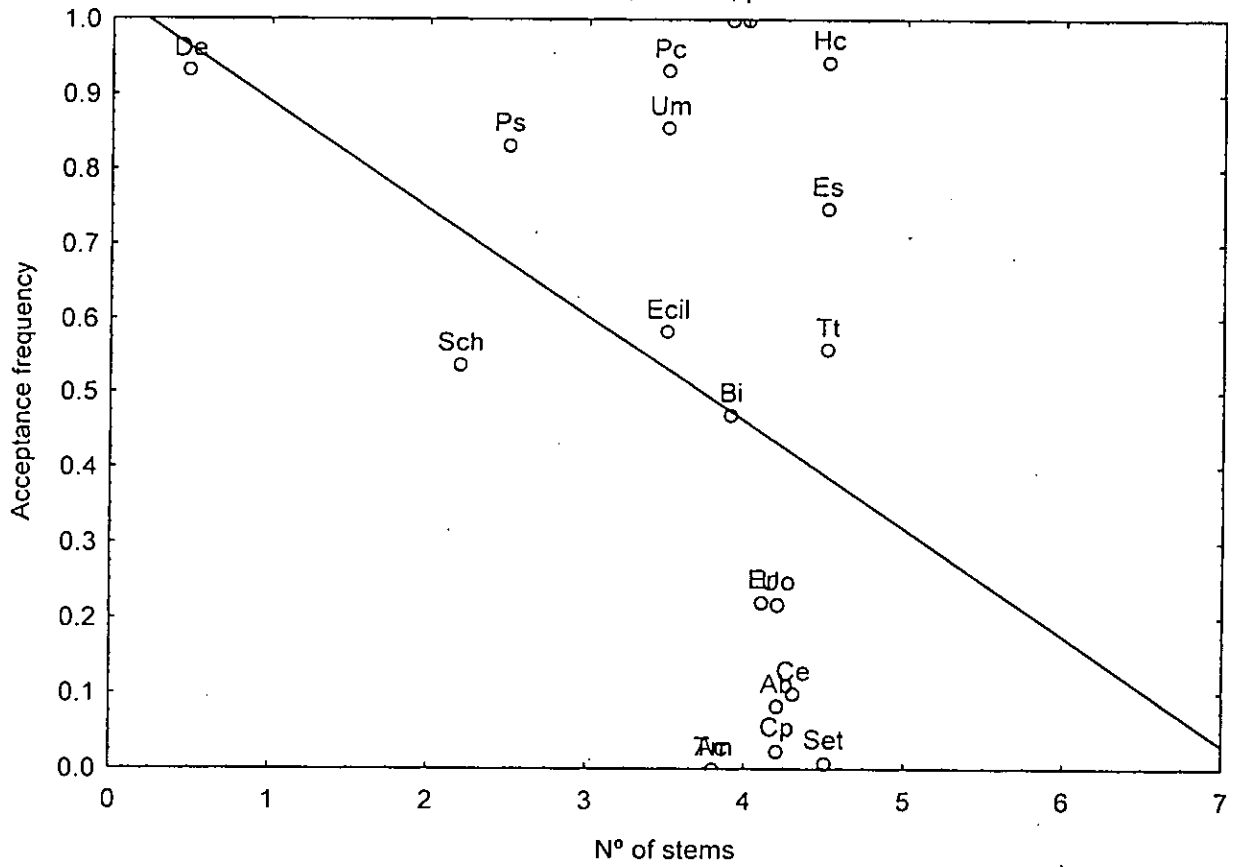
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17 Sept - 5 Oct: n=21, r=-0.27, p=0.22
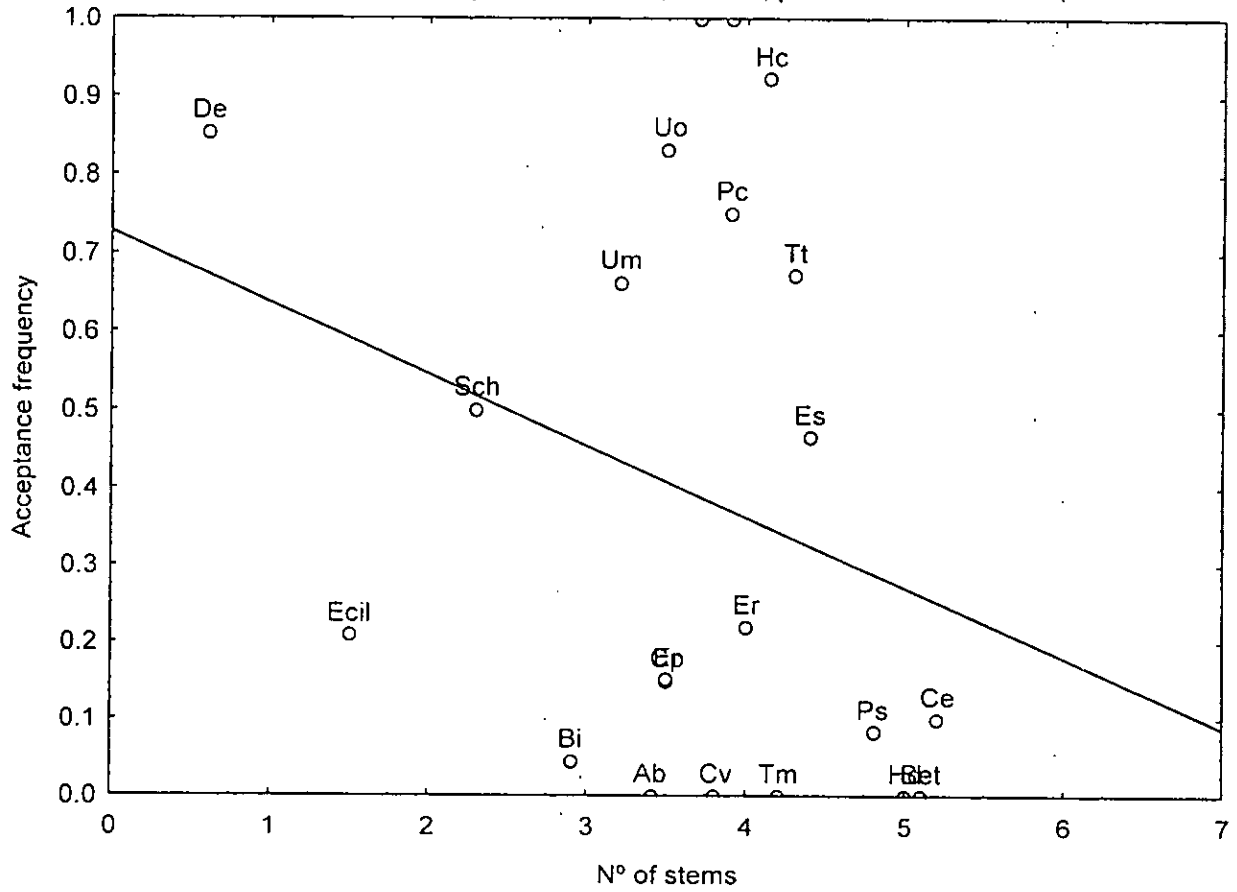
7 - 25 Oct: n=21, r=-0.36, p=0.12

Appendix V. Microhistological analysis of faecal samples

The contribution of grass species to buffalo's diet was also estimated by microhistological analysis of faecal material. This method of determining the botanical composition of large herbivore diets relies on the examination and identification of epidermal fragments of plants in the faeces of the animals by mean of a light microscope (Holechek *et al.* 1982, Monro 1982, McInnis *et al.* 1983, Henley *et al.* 2001).

Preparation of reference slides

The twelve most common grass species in the study area were collected in October 2002 to prepare key reference slides. The grass species collected included; *Panicum maximum, Panicum coloratum, Urochloa mosambicensis, Digitaria eriantha, Themeda triandra, Cenchrus ciliaris, Heteropogon contortus, Eragrostis superba, Eragrostis rigidior, Eragrostis ciliaris, Bothriochloa insculpta* and *Cymbopogon plurinodis*.

Following Stewart (1967), Field (1972), Monro (1982) and Bartolomé *et al.* (1998), the preparation of the key reference slides consisted of treating fresh plant material with nitric acid. The treatment process consisted of cutting a piece of grass leaf (about 2 cm in length), adding 4 ml of nitric acid (55%) in a glass cup and heating for 2-3 minutes in a boiling water-bath. Thereafter, 100 ml of distilled water were added and the mixture was boiled to complete the clearing process. The supernatant fluid was removed and the piece of leaf was mounted (fixed) on a glass slide using DPX (a water-white polystyrene solution in xylene with a plasticiser added) and covered with cover slip.

This treatment removed the opaque mesophyll tissue from the epidermis such that the structures of the epidermis, such as the silica bodies, the stomata, the hairs and the papillae could be visible and identifiable.

Preparation of faecal samples and identification of epidermal fragments

From each herd, ten fresh faecal samples from the same day were collected in a paper bag and amalgamated to form one composite sample. Four composite samples were collected during each sampling period of three weeks from each herd. Following Hansen *et al.* (1985) and Henley *et al.* (2001), the samples were oven-dried at 65°C and milled through a

1 mm screen to avoid the effect of different fragment sizes on identification, which could bias results towards larger fragments.

From each composite sample, 1 g was placed in 4 ml of nitric acid (55%) within a glass cup and heated for 2-3 minutes in a boiling water bath and then cleared with 100 ml of distilled water. The mixture was boiled and then left for 2-3 minutes to allow fragments to settle and concentrate. After removing the supernatant fluid, sub-samples were spread on slides and covered by coverslips. Slides with faecal material were examined under a light microscope at 100X and 400X magnification (Bartolomé et al. 1998).

The identification of fragments was based on the shape of the silica bodies, shape and size of the silica cells, form of the stomata and presence or absence of hairs. About 40 – 50% of the fragments per slide could be identified. From the composite faecal sample of each day, fifty fragments were identified at grass species level. Only fragments above certain minimum size, arbitrarily chosen, were considered for identification. This was necessary to avoid bias in favour of grass species that break up into smaller and more numerous fragments during the digestion process. Unidentifiable fragments were classified as monocots or dicots based on the disposition of the cells of the leaf. The proportion of each grass species in the diet was estimated for each day's sample by counting the number of identified fragments of that grass species and dividing this by 50 fragments identified per day for all grass species.

The grass species composition of the diet of buffalo changed with the progress of the dry season. This was shown by the changing proportion of epidermal fragments in the faeces of buffalo (Table 2). The results obtained using this technique were similar to those obtained by direct observations in terms of changes between periods in the dietary contribution of each grass species as well as in terms of contribution of each grass species to the diet of buffalo in the two landscapes (granites and basalts).

Table 2. Changes over time in the proportion of identifiable epidermal fragments of each grass species in faeces of buffalo, plus the subdivision of unidentifiable fragments between monocots and dicots.

Basalts

Grass species	27Aug - 13 Sept n=4 days mean±SE	17Sept - 5 Oct n=4 days Mean±SE	7 - 25 Oct n=4 days mean±SE
Pm	0.15±0.003	0.13±0.002	0.09±0.001
Pc	0.22±0.006	0.28±0.002	0.15±0.002
Um	0.24±0.002	0.26±0.004	0.13±0.002
De	0.03±0.002	0.1±0.003	0.05±0.003
Hc	0.1±0.003	0.07±0.002	0.04±0.002
Tt	0.07±0.003	0.03±0.002	0.04±0.002
Cc	0.11±0.002	0.08±0.001	0.10±0.003
Bi	0.01±0.001	0.01±0.001	0.28±0.002
Es	0.07±0.004	0.04±0.004	0.12±0.003
Unidentifiable fragments			
Monocots	0.967	0.98	0.973
Dicots	0.033	0.02	0.027

Granites

Grass species	27Aug - 13 Sept n=4 days mean±SE	17Sept - 5 Oct n=4 days Mean±SE	7 - 25 Oct n=4 days mean±SE
Pm	0.16±0.003	0.19±0.004	0.11±0.002
Pc	0.14±0.002	0.13±0.003	0.11±0.004
Um	0.18±0.003	0.11±0.003	0.08±0.002
De	0.36±0.008	0.33±0.004	0.17±0.003
Hc	0.03±0.002	0.06±0.003	0.10±0.003
Tt	0.04±0.002	0.03±0.001	0.06±0.003
Cc	0.02±0.001	0.04±0.002	0.08±0.004
Bi	0.01±0.001	0.05±0.002	0.22±0.006
Es	0.06±0.004	0.06±0.004	0.07±0.003
Unidentifiable fragments			
Monocots	0.974	0.966	0.952
Dicots	0.026	0.034	0.048

Acknowledgements

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