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Diet Composition of Wildebeest, Waterbuck and Reedbuck in Relation to Food Quality in a Moist Savanna of Tanzania

Diploma thesis in Environmental Sciences 2006

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Title page: Male waterbuck (*Kobus ellipsiprymnus)*
Photograph: Jean-David Gerber

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Summary

In order to analyse differences in feeding strategies between wildebeest, waterbuck and reedbuck in different seasons (early dry vs. late dry) and different regions (Mkwaja North and Saadani North) of a coastal savanna in Tanzania, I analysed the diet compositions of these herbivores by examining fragments of plant species in dung samples. Whether plant species were eaten or not was examined in relation to leaf nitrogen and phosphorus concentrations and dry matter digestibility. It was expected that these grazing antelope species of varying size differ in their food selection strategy and hence diet composition, and that this differentiation is related to body size. Further differences between seasons and regions were expected because of the changing quality of the food.

Diet overlap between the three herbivores was very high in the early dry season (> 95 %) and decreased in the late dry season, although the diet overlap between waterbuck and wildebeest remained high (> 90 %).

In the early dry season the grass species *Panicum infestum* was the major component of the diet for all three study animals. In the late dry season waterbuck and wildebeest also included *Heteropogon contortus* in large proportions, while the small-bodied reedbuck switched to feeding mainly on dicotyledonous plants and, to a lesser extent, on *Heteropogon contortus*. The number of plant species in the diet and diet breadth were lowest for reedbuck.

Regional differences in the diet composition were observed in the late dry season. Waterbuck included significantly less *Panicum infestum* in Mkwaja North and reedbuck included a higher proportion of dicots than in Saadani North, suggesting a higher nutritional constraint especially on small herbivores in Mkwaja North.

Preference for forage species could not be explained by nutritional quality: *Panicum infestum* and *Heteropogon contortus* did not have higher nitrogen or phosphorus concentrations than other plant species, and dry matter digestibility of *Panicum infestum* was very low (36 %) compared to that of other species. Hence, the results are contrary to traditional explanations of food preference. Other quality factors of the food or its spatial distribution may be important in evaluating why animals prefer certain plant species.

Zusammenfassung

Diese Arbeit untersucht Unterschiede in den Ernährungsstrategien von Gnu, Wasserbock und Riedbock, sowie Unterschiede zwischen Jahreszeiten (frühe Trockenperiode gegenüber später Trockenperiode) und Regionen (Mkwaja Nord und Saadani Nord) einer feuchten Küstensavanne in Tanzania. Zu diesem Zweck habe ich die Nahrungszusammensetzung dieser Herbivoren mittels Dungproben bestimmt. Ob Pflanzenarten gefressen wurden oder nicht wurde in einen Zusammenhang mit den Stickstoff- und Phosphorkonzentrationen sowie der Verdaubarkeit der Blätter gebracht. Es wurde erwartet, dass die drei verschieden grossen, grassfressenden Antilopenarten abweichende Ernährungsstrategien verfolgen und somit auch eine unterschiedliche Nahrungszusammensetzung aufzeigen, welche mit der Verschiedenheit ihrer Körpergrösse zusammenhängen. Des Weiteren, wurden Unterschiede zwischen Jahreszeiten und Regionen erwartet, da unter solchen Umständen die Futterqualität von Pflanzen sich verändert.

Die Übereinstimmung in der Ernährung der drei Herbivoren war sehr hoch in der frühen Trockenperiode (> 95 %) und nahm in der späten Trockenperiode ab. Die Überlappung zwischen Wasserbock und Gnu blieb jedoch auch dann hoch (> 90 %).

In der frühen Trockenperiode bildet die Grassart *Panicum infestum* den Hauptanteil der Nahrung von allen drei Tieren. In der späten Trockenperiode fressen Wasserbock und Gnu auch *Heteropogon contortus* in grossen Mengen, während der kleine Riedbock vor allem auf dicotyledone Pflanzen und geringere Mengen *Heteropogon contortus* umstellt. Die Anzahl an verschiedenen Arten in der Nahrungszusammensetzung und die Breite des Nahrungsspektrums ("diet breadth") waren am niedrigsten beim Riedbock.

Regionale Unterschiede in der Nahrungszusammensetzung wurden für die späte Trockenperiode beobachtet. Der Wasserbock frass signifikant weniger *Panicum infestum* in Mkwaja Nord, und der Riedbock ernährte sich von grösseren Proportionen an dicotyledonen Pflanzen als in Saadani Nord. Dies weist auf einen höheren Mangel an Nährstoffen in Mkwaja Nord hin, vor allem für kleine Herbivoren.

Die Präferenz von Futterpflanzen konnte nicht durch ihren Nährwert erklärt werden: *Panicum infestum* und *Heteropogon contortus* zeigten keine höhere Stickstoff- und Phosphorkonzentrationen und eine sehr tiefe Verdaubarkeit (36 %) im Vergleich zu anderen Pflanzenarten. Meine Resultate widersprechen daher traditionellen Erklärungen von Futterpräferenzen. Andere Qualitätsfaktoren der Futterpflanzen oder ihre räumliche Verteilung könnten wichtig sein, um zu erklären, warum bei den Tieren eine Präferenz für bestimmte Pflanzenarten besteht.

Contents

Introduction

The coexistence of woody plants and grasses is an important characteristic feature of savanna ecosystems. In moist savannas with a mean annual rainfall greater than 650 mm the coexistence of grasses and woody cover is maintained by disturbances such as fire and herbivory (Scholes & Archer 1997, Van Langevelde et al. 2003, Sankaran et al. 2005). Savannas support a high diversity and biomass of ungulate herbivores (i.e. hoofed mammals), which may consume up to 65 % of the net foliage production (Sinclair 1975, Frank et al. 1998). Ungulate herbivores are often classified into "grazers" that eat primarily grasses and sedges, and "browsers" that prefer forbs, leaves of woody plants and fruit. This classification is not always consistent in the literature. These herbivores have a large impact on the savanna vegetation by altering and maintaining ecosystem properties such as productivity, nutrient cycling and plant species composition (Georgiadis & McNaughton 1990, Augustine & McNaughton 1998, Anderson et al. 2006). There are a great variety of ungulate herbivores with diverse feeding strategies that may have different impacts on the savanna vegetation and other ecosystem properties. In order to assess this impact it is important to study the feeding behaviour of different herbivores in various savanna ecosystems. Such feeding studies are necessary, for instance, to enable estimates of the carrying capacities for these systems (Ben-Shahar 1991, Bodenstein et al. 2000). Knowledge on the feeding behaviour is limited for many herbivore species, and most information on plant-herbivore interactions in savanna ecosystems was obtained in semi-arid regions. These interactions may be different in moist savannas where rainfall and water availability are not the only factors maintaining ecosystem characteristics (Sankaran et al. 2005).

In ruminant herbivores three major morphological parameters determine the optimal feeding behaviour and degree of selectivity: body size, volume of digestive system, and mouth size (Hanley 1982, Illius & Gordon 1993).

Body size is the most important factor determining the metabolic rate and food requirement. Large-bodied mammals have higher absolute food requirements since they have higher costs of maintenance and production compared to smaller mammals (Geist 1974, Hanley 1982). Small mammals have higher relative metabolic rates and require food of high quality (high protein and nutrient levels) (Geist 1974, Hanley 1982). Whereas large ruminants need big quantities of nutrients per day, they require fewer nutrients per unit body weight than small ruminants (Geist 1974, Hanley 1982). This results in two opposing factors restricting ungulates: (a) small-bodied ungulates are limited by forage quality; (b) large-bodied ungulates are limited by forage quantity (Hanley 1982, Illius & Gordon 1993). Therefore, small herbivores need to search for high quality food and select the nutrient richest forage (selective feeding strategy). Large herbivores require large amounts of forage and cannot afford to spend time searching only high quality forage (bulk feeding strategy). Unselective feeding behaviour seems to be limited by body size; ungulates with less than 90 kg bodyweight need to feed selectively on a high quality diet in order to survive (Van Soest 1996).

The volume of the digestive system increases linearly to body size, while the energy requirements only increase by three quarters. This allometric relationship enables large-bodied animals to tolerate low quality food thanks to their longer and more efficient digestive system (Geist 1974, Du Toit & Owen-Smith 1989, Wilsey 1996, Kamler et al. 2003, Clauss & Hummel 2005).

Mouth size is also an important feature determining the possible degree of selective feeding. Animals with small mouths and narrow muzzles are more capable of selecting individual plants or plant parts within a community (Hanley 1982, Van Soest 1996).

Feeding patterns of ungulate herbivores differ between seasons. Nutrient levels vary between grass species, and they decrease with age. As the growing season progresses and plants get older, the available food quality decreases (Mowat et al. 1965, Georgiadis & McNaughton 1990). However, in some species this happens more quickly than in others. This means that a comparatively nutrient poor grass species in the wet season may become relatively nutrient rich, and hence more attractive for herbivores, later in the dry season when other grasses age and die (Mowat et al. 1965, Prins & Beekman 1989, Georgiadis & McNaughton 1990, Ben-Shahar & Coe 1992). This explains why grass species composition in the diet of ungulates was found to vary between seasons in a number of studies (Prins & Beekman 1989, Ego et al. 2003, Macandza 2004, Omphile et al. 2004).

Studies in semi-arid and moist savannas showed contrasting patterns of diet overlap among ungulate herbivores between wet and dry seasons. In semi-arid savanna ecosystems the dietary overlap of herbivores increased in the dry season, coinciding with decreasing quality of available forage (Ego et al. 2003, Omphile et al. 2004). In a moist savanna, diet overlap between the three browsing herbivores red duiker, common duiker and suni decreased in the dry season (Prins et al. 2006).

It seems that the two alternative feeding strategies (selective and bulk) may lead to different shifts in plant species included in the diet during the progression of the dry season. Hence, diet overlap is likely to be larger between herbivores with the same feeding strategy. Herbivores with bulk feeding behaviour are limited to habitats that provide a certain overall average of nutritive quality (i.e. above a critical value of 4 % of crude protein (Sinclair 1975)) as well as sufficient quantity that yields enough energy to meet their direct metabolic requirements. The reason for this is that most large herbivores are unable to rely on fat reserves, unlike a few species such as the white rhinoceros (Shrader et al. 2006). This might imply larger seasonal shifts in grazing patches at the landscape scale, and as a consequence a greater seasonal variation of plant species included in the diet for bulk feeders compared to selective feeders (cf. Ben-Shahar 1991, Wilmshurt et al. 1999).

The number and proportion of plant species included in the diet indicate the breadth of an animal's food niche and represent diet diversity (Omphile 2004, Prins et al. 2006). Results of previous studies of herbivore diets in savanna ecosystems are inconsistent with respect to seasonal changes in diet breadth. Diets of zebra and wildebeest in a semi-arid savanna were more diverse in the dry than in the wet season (Ben-Shahar & Coe 1992). In contrast, goats and sheep in a semi-arid savanna have a less diverse diet in the dry season compared to the wet season (Omphile et al. 2004). Prins et al. (2006) found the same pattern of decreasing diet breadth in the dry season in three ungulate browsers in a moist savanna system. Hence, it is unclear how diet breadth differs among seasons and whether there are differences between bulk and selective feeding herbivores.

During the dry season, the metabolizable energy of non-grass species, such as leaves of woody plants and forbs (i.e. dicots), is generally higher than that of most grasses (Owen-Smith 1997). In African ungulates it has been frequently observed that the proportion of dicots in the diet tends to increase during the dry season (Tomlinson 1980, Owen-Smith 1997, Ego et al. 2003). As selective feeders depend on sufficient food quality and seem to select the nutrient richest forage, they may not only shift their diet in terms of grass species composition, but might also consume higher proportions of dicots than bulk feeders. This, however, needs to be confirmed by field studies.

The aim of this study was to investigate differences in the diet composition and diet quality between selective and bulk feeding herbivores in a coastal moist savanna ecosystem in Tanzania. I selected reedbuck, wildebeest and waterbuck as my study animals because of their morphological features and abundance in the study area. Reedbuck is a selective feeder, which would be expected to pick out the nutrient richest plant species and plant parts. Wildebeest (a well-studied ruminant herbivore in semi-arid savannas) is an example of a large bulk feeder, which would be expected to feed on large quantities of average quality food. Waterbuck has been reported to be a selective feeder to some degree (Tomlinson 1980, East 1984, Melton 1987), although its body mass could indicate a tendency towards a bulk feeding strategy.

The objectives of the study were:

1. To determine the diet composition of three herbivores differing in body size and feeding behaviour; i.e. wildebeest (260 kg), waterbuck (200 kg) and reedbuck (45 kg).

2. To examine seasonal differences in the diet composition; i.e. early dry season vs. late dry season.

3. To examine differences in the diet composition between two diverse savanna ecosystems in the Saadani National Park with different land-use history; i.e. Mkwaja North (former intensive cattle ranch) and Saadani North (former arable land).

4. To evaluate if the difference between plant species that are eaten and those which are not eaten by the study animals can be explained from differences in food quality (i.e. nitrogen content, phosphorus content and dry matter digestibility).

The following hypotheses were tested:

1. Reedbuck chooses its diet selectively and therefore feeds on a smaller number of plant species than waterbuck and wildebeest.

2. The diet overlap between reedbuck, waterbuck and wildebeest is higher in the early dry season than in the late dry season.

3. All study animals eat higher proportions of dicots in the late dry season than in the early dry season. Reedbuck eats proportionally more dicots than waterbuck and wildebeest since dicots have a higher nutritional quality.

4. Reedbuck shows a diet composition of plant species with a higher nutritional value (i.e. high nitrogen and phosphorus concentrations, high digestibility) than plant species included in the diet of waterbuck and wildebeest.

Materials and methods

Study area

The study area is located in the Saadani National Park, which lies on the coast of Tanzania (East Africa), approximately 160 km north of Dar es Salaam. Mean annual temperature of the region is 25°C, with an annual range of 5°C and a daily range of 8°C (Tobler et al. 2003). Mean annual rainfall is 900 mm, but there has been much variation in the last 50 years with rainfall ranging from 500 mm to 1700 mm (Tobler et al. 2003). There are two main rainy seasons, a short one from October to December, with intense rainfall and monthly averages exceeding 100 mm, and a longer one from March to June followed by a dry period. Due to its coastal location, the area around Saadani National Park experiences a relatively short period without rain. In August and September the vegetation can become extremely dry and bush fires may occur (Tobler et al. 2003).

The Saadani National Park was founded in 2002. It consists of regions with different land-use histories and vegetation (Tobler et al. 2003). In this study I concentrate on two regions: Mkwaja North and Saadani North (Figure 1). These regions were chosen because they represent two diverse moist savanna ecosystems with considerable differences in former land-use, vegetation characteristics, animal species composition and proportion of trees.

Mkwaja North (240 km^2) was run as an intensive cattle ranch from 1953 to 2000 and was stocked with 13 000 cattle at its peak (Tobler et al. 2003). The area was organized in a paddock (boma) system consisting of 13 paddocks, where up to 1’500 cattle were herded at night. It contains many water dams. During the day herds of 200-400 cattle were led to grazing pastures. This intensive grazing led to bush encroachment, which together with problems of cattle diseases finally forced the ranch to shut down in 2000 (Ford & Blaser 1971, Tobler et al. 2003, Gross et al. 2005). Now, in 2006, Mkwaja North is a moist savanna system with a small-scale mosaic structure of nutrient poor tall grass savanna, nutrient rich short grass savannas in the former paddocks and dense acacia woodland (Halsdorf 2002).

Saadani North (110 km^2) has been a game reserve since 1969 and was formerly used for agricultural purposes, mainly for sisal plantation. With the introduction of large grazing herbivores (e.g. wildebeest) areas with short vegetation were maintained and created (i.e. grazing lawns). The vegetation of Saadani North is a large-scale mosaic of vast open grassland plains dotted with occasional palm trees, patches of evergreen bush and open acacia woodland (Halsdorf 2002).

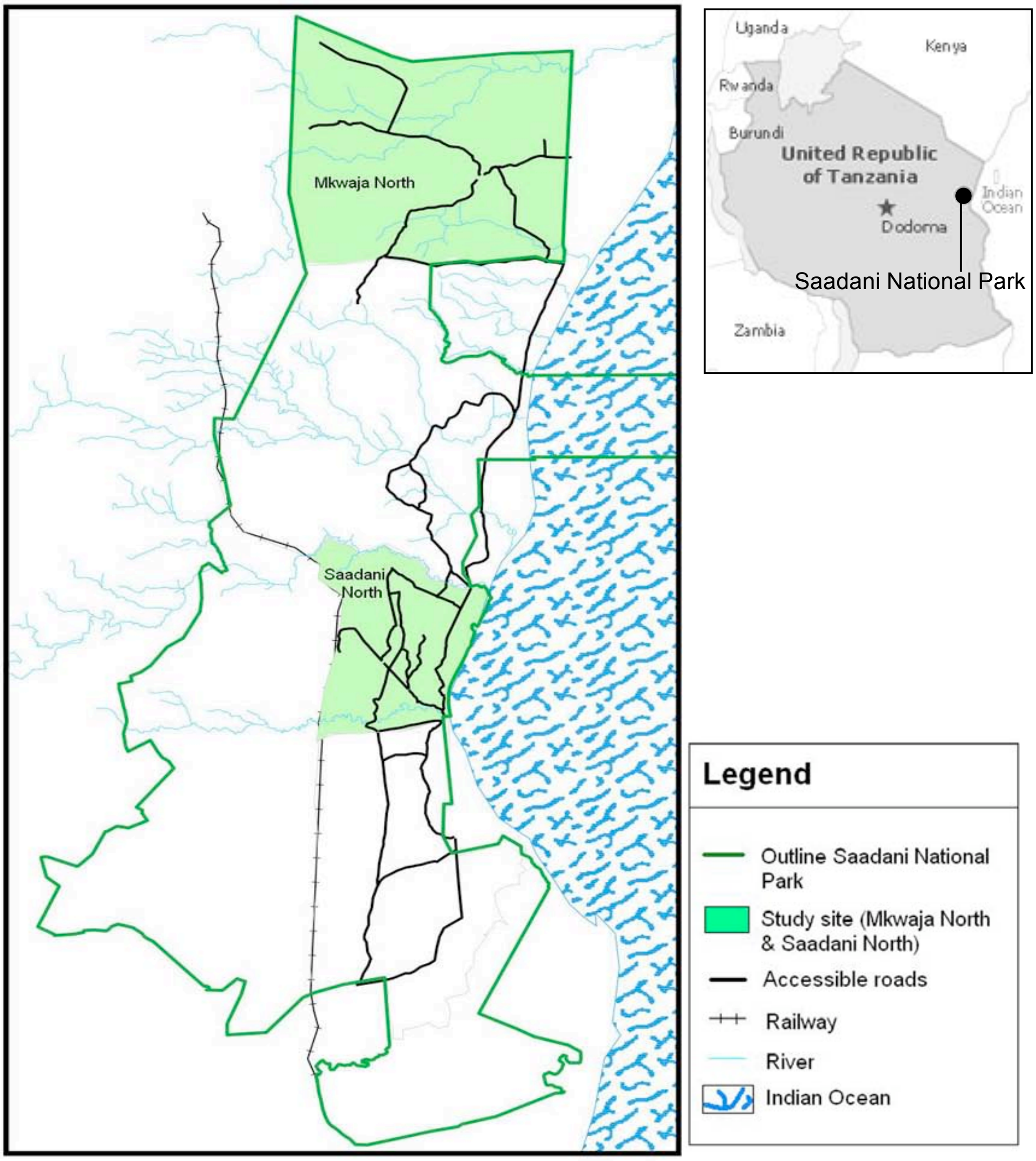


Figure 1: Map of Saadani National Park, Tanzania.

Mkwaja North has an undulating topography with several small hills of Mesozoic limestone unlike Saadani North, which is predominantly flat (Klötzli 1980, Tobler et al. 2003). Furthermore, the savanna is less open in Mkwaja North than in Saadani North because of the enhanced bush encroachment. The percentage of grassland in Saadani North is four times higher than in Mkwaja North, and the proportion of woodland is five times smaller (Tobler et al. 2003). For both regions four different habitat types were defined as follows: paddock centre (PC), paddock margin (PM), tall grass savanna (Tall) and acacia woodland (Aca) for Mkwaja North and, respectively, grazing lawn (GL), black cotton plain (BC), tall grass savanna (Tall) and acacia woodland (Aca) for Saadani North (Figure 2, Table 1).

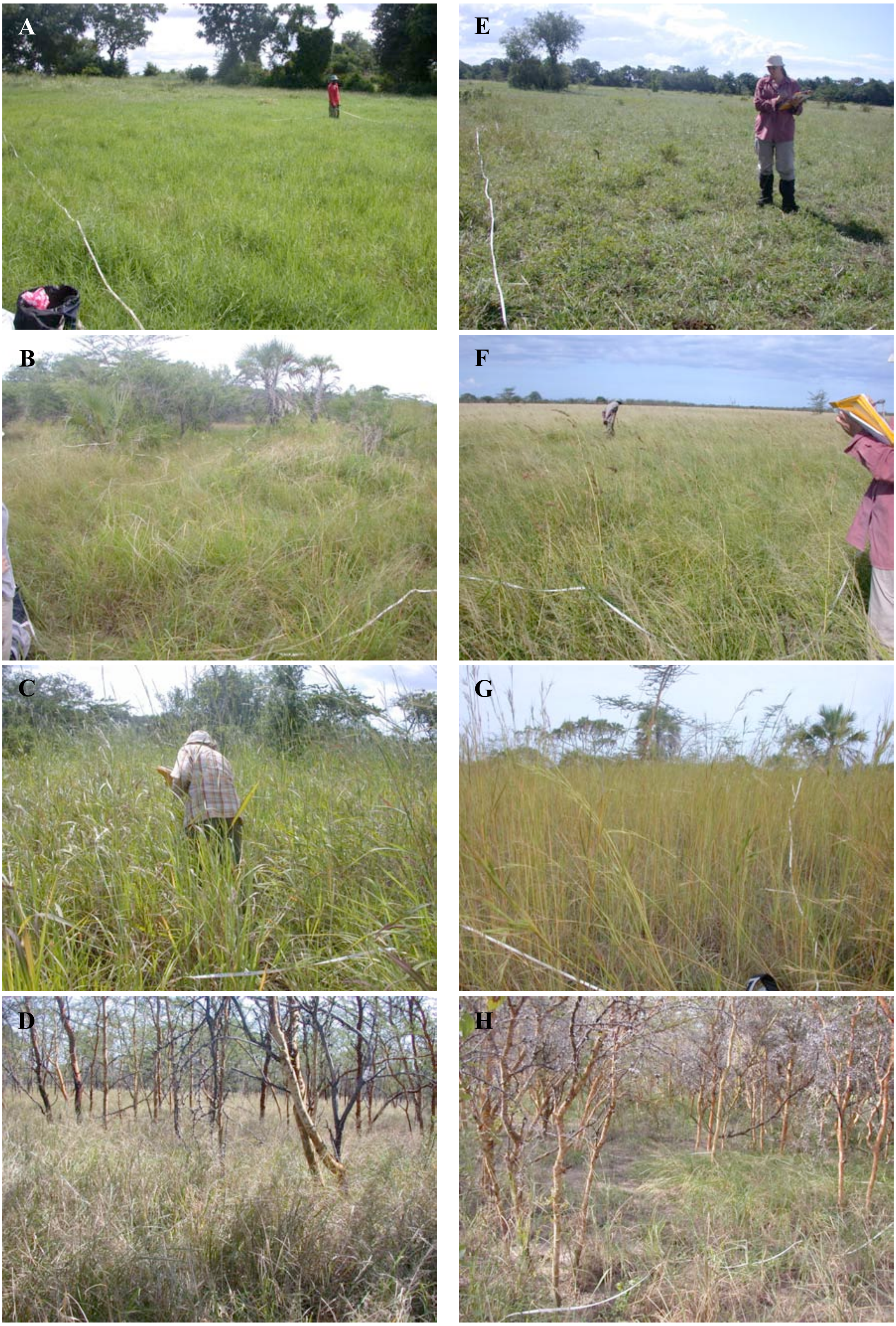


Figure 2: Habitat types in Mkwaja North: A= Paddock centre, B= Paddock margin, C= Tall grass, D= Acacia; and in Saadani North: E= Grazing lawn, F= Black cotton, G= Tall grass, H= Acacia.

Table 1: Dominant plant species in major habitat types in Mkwaja North and Saadani North. Data is based on five vegetation surveys per habitat type from the early dry season.

Mkwaja North	
PC:	Former paddock, where cattle were herded at night and strongly fertilised the soil. Dense grassy vegetation characterized by the following species: *Cynodon dactylon* (> 90%), *Paspalum dilatatum* (-5%) and *Panicum infestum* (-5%). Vegetation cover 100%, height 50-75 cm.
PM:	Areas surrounding paddock centres. Vegetation consisting of *Panicum infestum* (-80%), *Heteropogon contortus* (-80%), *Eragrostis superba* (-30%) and many other species. Dense to patchy vegetation cover, height 70-110 cm.
Tall:	Areas with tall grass. Ground vegetation characterized by *Andropogon gayanus*, *Cymbopogon caesius*, *Hyperthelia dissoluta*, *Diheteropogon amplectens* (all > 40%) and containing other species. Patchy vegetation (75% cover) reaching a height of 120-150 cm. Palm trees occur regularly in habitat.
Aca:	Areas dominated by acacia trees (*Acacia zanzibarica*). Ground vegetation consisting of *Sporobolus pyramidalis* (> 50%), *Panicum infestum* (> 50%), *Heteropogon contortus* (-30%) and other species. Vegetation dense to patchy (84% cover), height 75-95 cm.
Saadani North	
GL:	Open areas with short grass. Ground vegetation characterized by *Digitaria milanjiana* (-50%), *Diheteropogon amplectens* (-50%), *Chloris mosambicensis* (-20%), *Panicum infestum* (-20%) and other species. Vegetation dense, height 20-40 cm.
BC:	Large open areas with black cotton soil. Vegetation consisting of *Panicum infestum*, *Setaria incrassata*, *Sporobolus pyramidalis* (all -70%), *Bothriochloa* sp. (-15%), *Cymbopogon caesius* (-15%), *Heteropogon contortus* (-15%) and other species. Very dense vegetation cover (98%), height 70-100 cm.
Tall:	Areas with tall grass. Ground vegetation characterized by *Cymbopogon caesius* (-40%), *Hyperthelia dissoluta* (-40%), *Diheteropogon amplectens* (-20%), *Andropogon gayanus* (-20%) and other species. Vegetation dense to patchy, height 110-180 cm.
Aca:	Areas dominated by acacia trees (*Acacia zanzibarica*). Vegetation containing *Panicum infestum*, *Sporobolus pyramidalis* (both -50%), Chloris mosambicensis (-20%) and other species. Very patchy vegetation (54% cover), height 60-75 cm.

The composition and population densities of ungulates differ between Mkwaja North and Saadani North. There is a higher diversity of animal species and larger populations in Saadani North than Mkwaja North (Table 2), partly due to the former competition by cattle and greater poaching activity in the north of the National Park (Baldus et al 2001). In Mkwaja North, mostly non-migratory species are found (Tobler et al. 2003). However, in the late dry season large herbivores (e.g. elephants) may migrate to Mkwaja North from Saadani, as the water dams carry a constant water supply. In the late 1970s some animals were introduced into the moist savanna system in the Saadani Game Reserve such as wildebeest and zebra, originally adapted to semi-dry savanna systems and previously not occurring in the Saadani area (East 1984, Baldus et al 2001). To date, these animals have not been spotted in Mkwaja North.

Table 2: Estimates of animal populations in Saadani National Park.

		Treydte (2004)[1]		Air survey 2004[2]	Body weight (kg)[3]
Common name	Scientific name	MN	SGR	SGR	
African buffalo	*Syncerus caffer*	0	38	461	500
Bohor reedbuck	*Redunca redunca*	28	333	258	45
Bushbuck	*Tragelaphus scriptus*	3	4	9	60
Bushpig	*Potamochoerus larvatus*	0	4	xxx	70
Eland	*Taurotragus oryx*	0	31	276	600
Greater kudu	*Tragelaphus strepsiceros*	0	11	xxx	215
Grey duiker	*Sylvicapra grimmia*	2	1	xxx	20
Giraffe	*Giraffa camelopardalis*	14	121	286	1180
Hartebeest	*Alcelaphus buselaphus*	0	85	692	185
Harvey's duiker	*Cephalophus harveyi*	14	5	46	14
Sable antelope	*Hippotragus niger*	0	0	9	230
Suni	*Neotragus moschatus*	1	0	xxx	5
Waterbuck	*Kobus ellipsiprymnus*	11	137	101	200
Warthog	*Phacochoerus africanus*	20	151	350	75
Wildebeest	*Connochaetes taurinus*	0	574	3766	260
Zebra	*Equus quagga boehmi*	0	22	xxx	250

[1] Treydte (2004)	Recorded animal numbers during transect surveys
[2] Air survey (2004)	Arial survey data obtained from TAWIRI, estimated values
[3] Body weight (kg)	Kingdon (1997)
MN	Mkwaja North
SGR	Entire Saadani Game Reserve
xxx	No data available

Table 3: Food type preference of study animals on grazing-browsing gradient.

	Reedbuck	Waterbuck	Wildebeest
Hofmann & Stewart (1972)[2]	Fresh grass grazer dependent upon water	Fresh grass grazer dependent upon water	Fresh grass grazer dependent upon water
Estes (1991)[1]	Grazer, may eat forbs and leaves of woody plants in dry season	Protein rich grass, dicots for additional protein intake when green grass scarce	Feeds on short grass with rapid regrowth
Kingdon (1997)[1]	Exclusive grazer	Grazer, leaves of woody plant or fruit if grass scarce	Grazer, leaves of woody plant in very harsh conditions
Gagnon & Chew (2000)[1]	Obligate grazer, > 95% monocots 5% dicots	Variable grazer, 84% monocots 15% dicots 1% fruit	Variable grazer, 87.5% monocots 12% dicots 0.5% fruit
Cerling et al. (2003)[3]	Hypergrazer, > 95% grass	Grazer 70-95% grass	Hypergrazer, > 95% grass

[1] Classification based on observations, literature review.
[2] Classification based on the stomach-structure of animals.
[3] Classification based on stable carbon isotope analysis of tooth, hair and hoof material.

Study animals

Three abundant ungulate herbivore species of different body size were chosen as study animals: reedbuck, waterbuck and wildebeest (Figure 3). While reedbuck and waterbuck are native to the Saadani area, wildebeest was introduced from semi-arid savanna ecosystems.

The reedbuck (*Redunca redunca*) is a small antelope adapted to moist savannas (East 1984, Kingdon 1997). Feeding activity takes place mostly after dark in open areas (Kingdon 1997, Pérez-Barberia et al. 2001). Females generally group in home ranges during the wet season when most young are born and males tend to be scattered in the area. During the dry season females search the best remaining grazing areas and male reedbucks compete for the females, which possibly results in submissive males having to feed in inferior grazing areas (Kingdon 1997).

The waterbuck (*Kobus ellipsiprymnus*) is a large antelope adapted to moist savanna ecosystems with a permanent water supply (East 1984, Kingdon 1997). Waterbuck prefer open habitats with a short to medium sward height for grazing (Wirtz & Kaiser 1988, Pérez-Barberia et al. 2001, Traill 2004). Males show territorial behaviour, but bachelor males are often tolerated (Estes 1991, Kingdon 1997).

The wildebeest (*Connochaetes taurinus*) is a large antelope adapted to relatively dry savannas (East 1984, Kingdon 1997). It is dependent on feeding areas with short grass and shows migratory behaviour from one feeding ground to the next (Wilmshurst et al. 1999, Traill 2004). Wildebeest are social grazers and are organized in large permanent herds (Estes 1991, Kingdon 1997).

While only little is known about the biology and feeding behaviour of reedbuck, waterbuck and especially wildebeest are much-studied animals. African ungulates are often classified according to their preferred food type on a grazing-browsing gradient, however contradictive classifications are found in literature for the three study animals (Table 3).

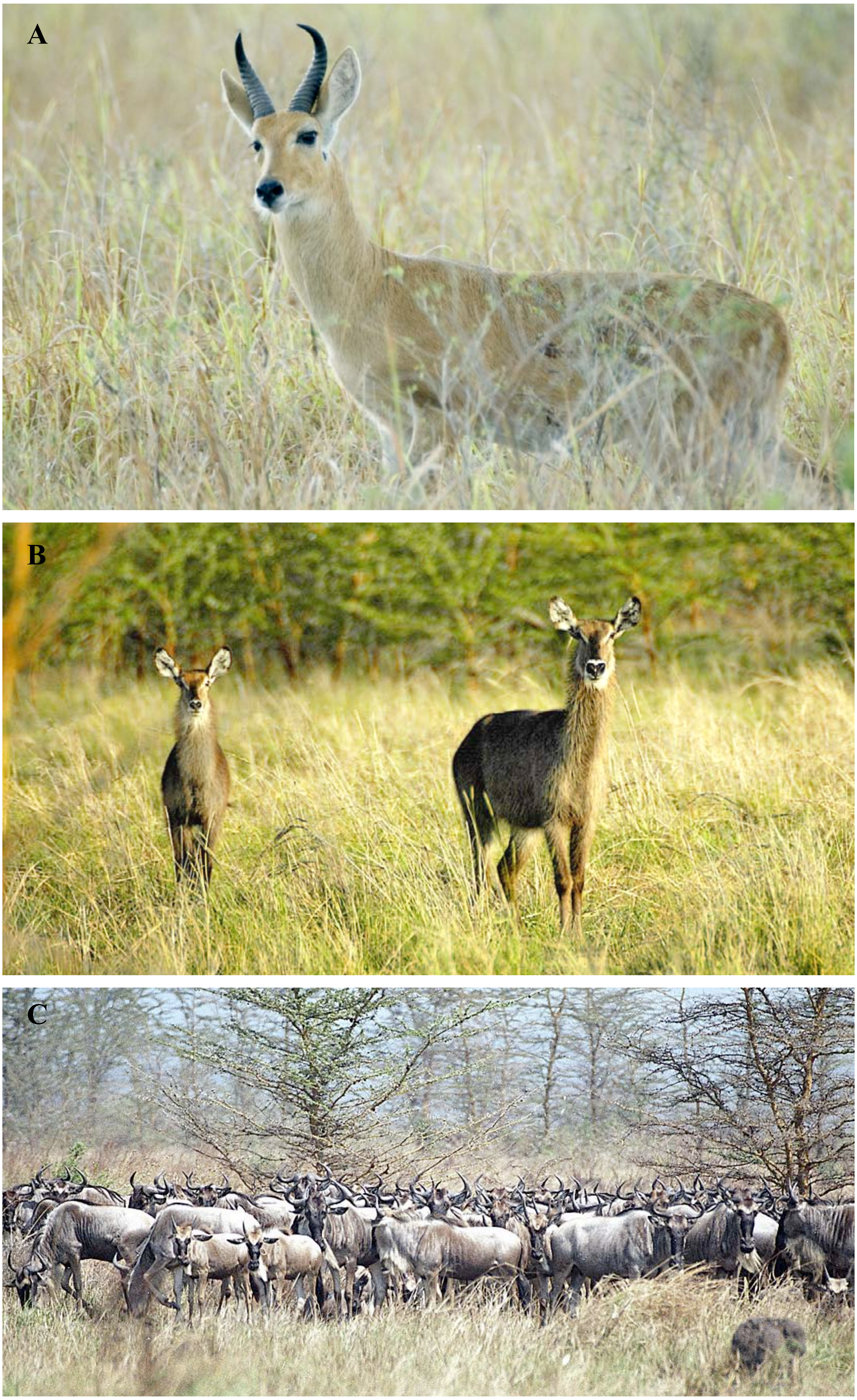


Figure 3: A= Male reedbuck (*Redunca redunca*), B= Female waterbuck (*Kobus ellipsiprymnus*) with young, C= Wildebeest (*Connochaetes taurinus*); Photographs by Jean-David Gerber.

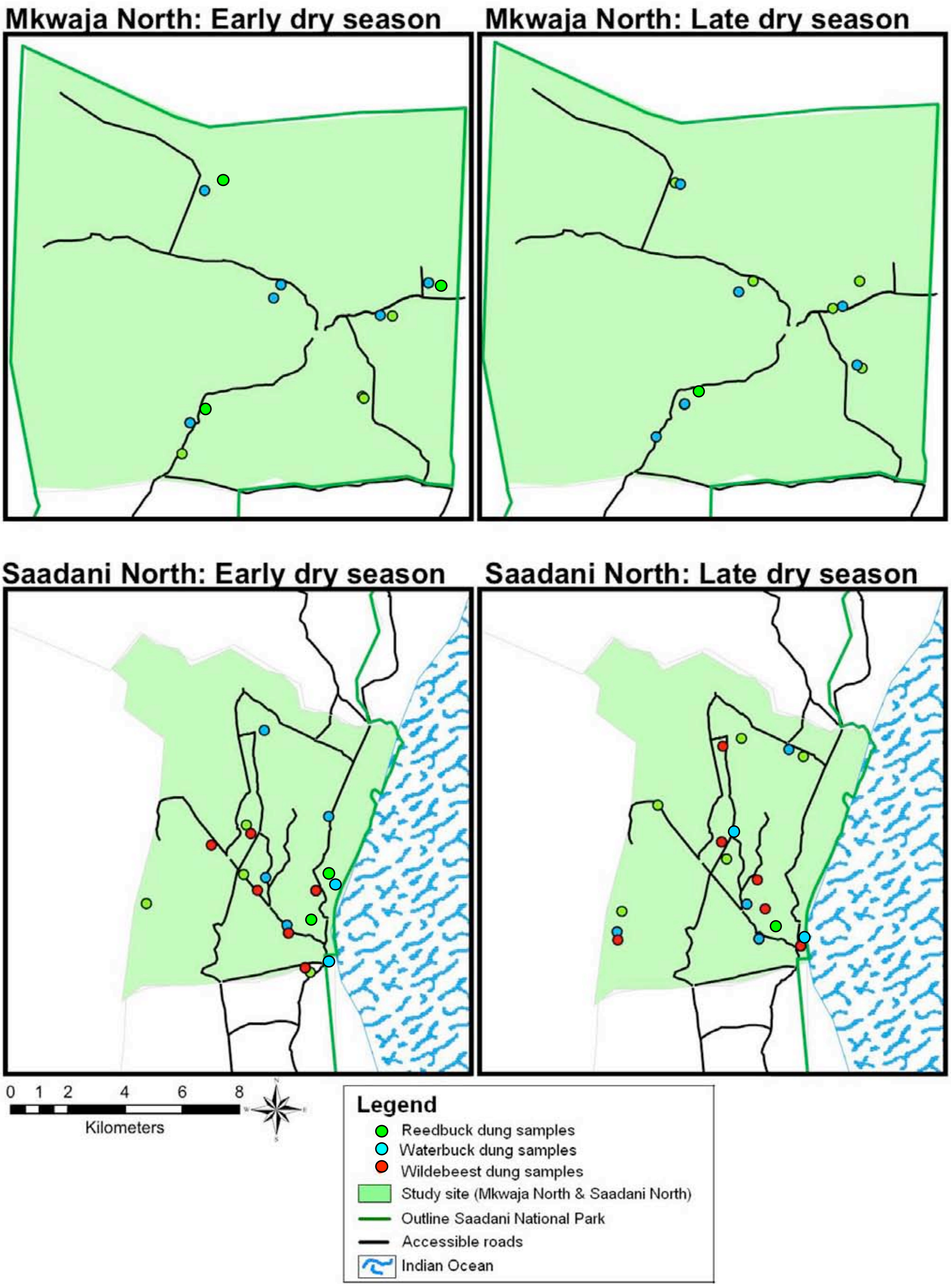
Dung sampling

Faecal samples were collected from each of the study animal species in each season and region during a period of six weeks (16/06/2006 to 01/08/2006) in the early dry season (by Gutbrodt and Halsdorf) and five weeks (12/01/2006 to 14/02/2006) in the late dry season (by Halsdorf). The location of the dung samples was fixed using GPS [Garmin 12 XL]. Species affiliation and freshness of each sample was determined by an experienced ranger of the Saadani National Park in each region according to the method of Stuart (1994). Shape and size of dung is species-specific and errors of identification are very unlikely. Freshness can be determined according to texture (moisture, gloss) and state of decay, as coprophagous insects are highly active especially during the wet season (Edwards 1991, Leuenberger 2004). Dung samples were sun-dried and transported to ETH (Swiss Federal Institute of Technology, Zurich, Switzerland) for microhistological analysis.

For each study animal species and for each region and season 6 samples were chosen according to following criteria: 1. Wide distribution of samples over study area (at least 500 m apart); 2. Freshest sample available; 3. Random selection (Figure 4). No distinction was made between sex and age of animals, but dung of juvenile individuals was not included in the set of analyses.

Faecal analysis

In this study a microhistological technique, as first described by Stewart (1967), was used to assess the dietary composition of the study animals. This method is based on the fact that fragments of epidermis and cuticula of plants ingested by animals remain intact as they pass through the digestive system and can be identified in the dung (Stewart 1967). Based on the shape and distribution of epidermal cell forms, the plant fragments found in the dung can be identified to species or plant group level. Information on these species-specific traits is obtained from reference slides of fresh plant material (Barthlott & Martens 1979). Reference slides were prepared from fresh, fully expanded leaves of all important grass species occurring in the study area (Table 4). The epidermis of the upper and lower sides of the leaf from each plant species was retrieved using a scraping technique, by which the leaf was grated using a razor blade until only the colourless epidermis remained. This was then fixed with glycerine and photographed (see Appendix A: Identification key).



Mkwaja North: Early dry season

Mkwaja North: Late dry season

Saadani North: Early dry season

Saadani North: Late dry season

Figure 4: Distribution of the dung samples in the study area for the two seasons.

Table 4: Plant species collected in the study area and prepared for reference with habitat where plant species occurs, and % coverage. Data is based on vegetation surveys from the early dry season. For abbreviations of habitat types, see Table 1. FP= Forage preference of plant species for zebus cattle according to Kozak (1983).

	Mkwaja North	Saadani North	FP
Grass species			
Andropogon gayanus	Tall (-80%)	Tall (-15%)	**
Aristidia adscensionis	xxx	xxx	ne
Bothriochloa bladii	PM (-1%), Tall (< 1%)	GL (-20%), BC (-15%)	xxx
Bothriochloa insculptum	PM (-5%)	GL (-1%)	ne
Brachiaria leucacrantha	xxx	xxx	***
Chloris mosambicensis	Aca (< 1%)	Aca (-20%), GL (-20%)	**
Cymbopogon caesius	Tall (-10%)	Tall (-40%), BC (-20%)	**
Cynodon dactylon	PC (-100%)	–	***
Dactylothenium aegyptiacum	Tall (-6%), PM (-2%)	–	ne
Dactylothenium geminatum	xxx	xxx	xxx
Digitaria milanjiana	PM (-15%), Tall (-5%), Aca (-3%)	GL (-60%), Tall (-10%)	***
Diheteropogon amplectens	Tall (-35%)	GL (-80%), Tall (-20%)	**
Echinochloa haploclada	PC (< 1%), PM (< 1%)	BC (-15%), GL (< 1%)	ne
Enteropogon sechellensis	Aca (-3%)	–	**
Eragrostis superba	PM (-30%), Aca (-5%)	Tall (-10%), Aca (-5%)	**
Heteropogon contortus	PM (-80%), Aca (-35%), Tall (-10%)	BC (-15%), Tall (-10%), Aca (-5%)	**
Hyperthelia dissoluta	Tall (-60%)	Tall (-45%)	*
Hyparrhenia rufa	PM (-15%)	–	*
Panicum infestum	PM (-85%), Aca (-70%), PC (-5%), Tall (< 1%)	BC (-75%), Aca (-60%), GL (-30%), Tall (-10%)	***
Panicum maximum	PC (< 1%)	–	***
Paspalum dilatatum	PC (< 1%)	–	**
Setaria incrassata	Aca (-5%), Tall (-5%)	BC (-70%)	*
Sporobolus pyramidalis	Aca (-50%)	BC (-60%), Aca (-50%), GL (-20%)	ne
Themeda triandra	Aca (-30%)	–	**
Sedge species			
Fimbristylis triflora	Aca (-40%), PM (-30%), Tall (-10%)	Aca (-20%), GL (-2%)	xxx

xxx	No data available
–	Plant species not observed in region
***	High preference, very often eaten
**	Preference, often eaten
*	Low preference, rarely eaten
ne	Not preferred, not eaten

Preparation and analysis of dung samples was carried out according to Suter et al. (2004), modified from the method of De Jong et al. (1995). Dung samples were filled into 50 ml tubes and soaked with distilled water and then autoclaved at 121°C (Barthlott & Martens 1979, De Jong et al. 2004). The samples were then crushed and ground in a mortar. About 5 gram of moist dung was weighed into a household blender and processed for one minute, while more distilled water was added. This solution was rinsed through a 0.1 mm sieve first using tap water and then washed and transferred into 70 % ethanol in a glass container. In contrast to De Jong et al. (1995, 2004), no bleach was added because the presence of natural colours helps to identify the epidermal fragments. For analysis the samples were transferred into a Petri dish and allowed to settle. Using a Pasteur pipette, 10 random grab samples consisting of 2-3 drops each were put on a glass slide and covered with a 2.4 cm cover slip and viewed at 200x magnification.

On each slide I determined ten fragments in at least two transects, using the identification key and photographs of the epidermis of the reference slides (Appendix A). The area of each fragment was estimated using a reticule in the microscope ocular. Only fragments recognized as epidermal tissue and consisting of at least four plant cells, or with visible stomata, were recorded. In total 100 fragments were determined for each sample, including unidentified (monocot or dicot) and undetermined monocot fragments. These are presented in Figures 5 and 6, but for further analysis the unidentified fragments and undetermined monocots were excluded and, where possible, the proportion of the plant species in the diet was not recalculated.

The two species of the genera *Bothriochloa* and *Dactylothenium* were pooled for diet composition evaluation. The epidermal structure of *Andropogon gayanus* and *Themeda triandra* look very much alike and therefore could often not be distinguished. However, based on my observations I assume that the respective fragments are *Andropogon gayanus*, as it is much more common in the study area and was found to be grazed in many sites. *Themeda triandra* on the other hand is rare (Halsdorf, personal observation). Furthermore, I have distinguished between *Panicum infestum*, *Panicum maximum* and *Panicum "undetermined"*. For *Panicum "undetermined"* the characteristic micro hair was not visible (Appendix A), but it was most likely *Panicum infestum* based on the similarity of overall epidermal structure and pattern. In the further analyses of the diet composition, *Panicum infestum* and *Panicum "undetermined"* were lumped together. The same identification problem and procedure applied for *Heteropogon contortus* and *Heteropogon "undetermined"*.

The microhistological method may return biased results, as certain plant species are better digestible than others and are therefore underestimated in their actual proportion in the animal's diet (Fitzgerald & Waddington 1979, Putman 1984). This problem grows with increasing travel time through the gut and therefore is of different magnitude for different animal species (Putman 1984). As a consequence, the evaluation of the diet composition based on fragment size favours plant species that are less easily digested. The evaluation based on fragment count can equally cause bias and may represent the diet composition poorly, as some plant species are better recognizable than others (Marti 1982, Putman 1984). In this study I report the diet compositions as proportions derived from both fragment count and fragment area (Appendix B). The proportions obtained by the two methods correlated very closely (Spearman Roh = 0.9752, $p < 0.0001$), and for further analysis the proportions of plant species in the diet were evaluated using the data based on the fragment area.

To evaluate the breadth of plant species included in the diet of each animal species, Levin's measure of niche breadth (B) was calculated for every individual animal studied, based on the following formula (Krebs 1999, Prins et al. 2006):

$$B = \frac{1}{\sum^{n}_{i=1} P^2_i}$$

P_i = % of total sample belonging to species i (i=1,2,..n),
n= total number of species in all samples for one region

For this index, the proportions of the plant species in the dung were recalculated, as the elimination of the unidentified and undetermined monocot fragments produced large disruptions in the pattern. The value for B increases with increasing number of species in the diet. A low value indicates that a species is selective for a few specific forage plant species.

In order to estimate the diet overlap between animal species, the Simplified Morisita's index (C_H) according to Horn (1966) was calculated as follows:

$$C_H = \frac{2\sum P_{ij} P_{ik}}{\sum P^2_{ij} + \sum P^2_{ik}}$$

P_{ij}, P_{ik} = proportion of resource in the total resources used by the two species j and k

To calculate the diet overlap between animal species, seasons and regions, I used the proportion of each consumed plant species derived from the total percentage based on the fragment area of the replicate dung samples.

Nutrient analysis and dry matter digestibility

To determine the nitrogen and phosphorus concentrations, and dry matter digestibility of grass species available as forage, all occurring grass species as well as the sedge species *Fimbristylis triflora* were sampled in each region. Data on the nutrient concentrations of plants from the late dry season are preliminary results of Halsdorf.

For each of the four habitat types existing in the two regions (Mkwaja North and Saadani North), five locations were selected in order to represent the study area. The locations were marked using a GPS [Garmin 12 XL] and were visited during a period of three weeks (16/06/2006 – 04/07/2006) in the early dry season (by Gutbrodt and Halsdorf) and five weeks (10/01/2006 to 20/02/2006) in the late dry season (by Halsdorf). At each location, 10-20 of the youngest, fully expanded leaves of at least five individuals of every occurring species were sampled and a vegetation survey was carried out for an area of 10 m^2. Leaf samples were sun-dried and transported to ETH Zurich (Switzerland) for further analysis.

Nutrient concentrations and dry matter digestibility of plants vary not only between species but also considerably between plant parts. Young leaves are nutrient richer and have a higher digestibility than mature leaves and stems (Mowat et al. 1965, Minson 1990). Therefore, in this study only young fresh leaves were analysed for information on diet quality and I focused on the variation of quality only between plant species.

Nitrogen and phosphorus concentrations were analysed for all replicate samples after Kjeldahl digestion. Plant material was ground and incubated at 420°C for one hour with 5 ml of concentrated sulphuric acid (H_2SO_4) and a Kjeldahl tablet. The digested solution was then transferred into a 100 ml Erlenmeyer flask and filled up with distilled water. This solution was neutralised and the total nitrogen and phosphorus concentrations were measured by means of the "Flow Injection Analysis" (Bradstreet 1965).

Crude protein content was calculated as 6.25 times the nitrogen concentration, as proteins on average consist of 16 % nitrogen (Robbins 1993, Watson & Owen-Smith 2000). Additionally the N/P-ratio of each sample was calculated.

Table 5: Analysed plant species according to observed frequency in dung of all study animals in the early dry season for the two regions.

	Mkwaja North	**Saadani North**
Very often found > 20 %	*Panicum infestum*	*Panicum infestum*
Often found Up to 15 %	*Andropogon gayanus* *Eragrostis superba*	*Andropogon gayanus* *Eragrostis superba*
Few found Up to 2 %	*Cymbopogon caesius* *Cynodon dactylon*	*Cymbopogon caesius*
Rarely found < 1 %	*Digitaria milanjiana* *Diheteropogon amplectens* *Sporobolus pyramidalis*	*Digitaria milanjiana* *Diheteropogon amplectens* *Sporobolus pyramidalis*

Dry matter digestibility of the sampled leaves was only assessed for the early dry season and a selection of grass species. Grass species were classified into species often found, rarely found and never found in dung samples of the early dry season. From each category a selection of plant species was chosen for analysis (Table 5).

The dry matter digestibility of the chosen species was analysed for 3 replicate samples per species and region by the method adapted from Jones and Hayward (1975). Since *Panicum infestum* was found to a great extent in the dung samples of all animal species and occurs in all habitat types, this grass was chosen to give an overview on the variation of dry matter digestibility among habitat types. Therefore, 29 replicate samples of *Panicum infestum* (MN 11, SN 18) from different habitats were analysed according to the method of Jones and Hayward (1975). The dry matter *in vitro* digestibility method determines the percentage of digestible dry plant material, using pepsin enzymes retrieved from the stomach lining of a pig and fungal cellullase enzymes.

For each sample 200 mg plant material (oven-dried for 24 h at 70°C and ground to 1 mm) was incubated with 20 ml of 0.1 N HCl containing 0.2% pepsin (0.7 FIP–U/mg, Merck) in 100 ml screw-cap tubes for 24 h at 40°C. This solution was filtered (Filter Nr LS 14, diameter 4.5 cm, Schleicher & Schüll) and the supernatant retrieved into a new 100 ml screw-cap tube. The filter was rinsed with a cellulase solution (70 mg *Trichoderma Viride* [BDH Ltd, Poole, Dorset] in phosphate citrate buffer pH 4.6 [10.65 ml 0.1 M citric acid und 9.35 ml 0.2 M Na_2PO_4]) and the volume filled up to approx. 20 ml. The sample was returned to the oven and incubated for 48 h at 40°C, shaking by inversion three times daily. The solution was filtered using oven-dried (for 24 h at 70°C) and weighed filters (Filter Nr LS 14, diameter 4.5 cm, Schleicher & Schüll). The indigestible residues on the filters were oven-dried for 24 h at 70°C. The amount of digested material was calculated as a percentage of the original dry matter:

$$\text{Digestibility (\%)} = \frac{100*(\text{weight plant material} - \text{weight residue})}{\text{weight plant material}}$$

Statistical analysis

Data on the diet composition of the three study animals were evaluated by a correspondence analysis (CA) using *CANOCO*, because data was not normally distributed. The proportions of the plant species in the diet were recalculated, as elimination of unidentified and undetermined monocots produced great disruption in the pattern of the data set. Percentages of plant species in the diet were transformed using a square root transformation to weaken the impact of plant species with low proportions in the diet. To test for differences between seasons, regions and animal species, a canonical correspondence analysis (CCA) was performed for the entire data set as well as for each animal species.

I used one-way ANOVAs, followed by Tukey's multiple comparison tests ($p < 0.05$), to test for significant differences between animal species in the number of plant species found in the diet, and diet breadth, as well as between grass species in leaf nitrogen concentrations, leaf phosphorus concentrations, leaf N/P-ratio and dry matter digestibility of selected grass species. Transformations of variables were carried out if residuals were not normally distributed. Mean number of plant species and N/P-ratio were transformed using a square root transformation. Nitrogen and phosphorus concentrations were $\log_{10}$-tranformed.

I used two-way and three-way ANOVAs to test for significant effects of species, seasons and regions, and their interactions. As some plant species were not found in either region or season, the following species were excluded from the three-way ANOVA testing for differences in leaf nutrient concentrations: *Brachiaria leucacrantha*, *Chloris mosambicensis*, *Cynodon dactylon*, *Dactylothenium* sp., *Paspalum dilatatum*, *Setaria incrassata* and *Themeda triandra*.

Various correlations between nutrients (i.e. nitrogen concentrations, phosphorus concentrations), dry matter digestibility and frequency of plant species found in the dung of study animals were calculated by means of Spearman correlations.

Unless otherwise indicated, all statistical analyses were carried out with JMP v6.

Results

Diet composition

The diet composition of all three study animals in both regions and seasons consisted of only a few plant species contributing large proportions to the diet. Within animal species there was a considerable variation in diet composition among individuals (Figure 5,6). The diet compositions of the studied animal species were significantly different ($p < 0.001$; data not shown). The diet of reedbuck consisted mainly of *Panicum infestum* and dicots, the diet of waterbuck and wildebeest of *Panicum infestum* and *Heteropogon contortus*. *Panicum infestum* was one of the species highly preferred by cattle when Mkwaja ranch was still in use, whereas *Heteropogon contortus* was less preferred but still eaten.

There were significant seasonal differences in the diet compositions of all three animal species (Table 6, Figures 7,8). In the early dry season the study animals clearly favoured *Panicum infestum* as the major component of their diet in both regions. Dicots also played a major role in the average diet composition of reedbuck although this was caused by one individual in each region (Appendix B). In the late dry season the diet of reedbuck consisted mainly of dicots. Waterbuck and wildebeest showed a similar shift in diet composition; *Panicum infestum* decreased in the late dry season and was replaced by *Heteropogon contortus*.

The diet composition of reedbuck was not significantly different between the regions Mkwaja North and Saadani North, but a tendency could be detected (Table 6). The pattern of reedbuck feeding on dicots in the late dry season was observed in both regions, but was stronger in Mkwaja North, where five of six individuals consumed dicots. The proportion of *Panicum infestum* was significantly higher in the diet composition of waterbuck in Saadani North compared to Mkwaja North during the late dry season (Table 6, Figures 7,8).

Table 6: Proportion of explained variance (%) by variables (season, region and interaction) and total explained variance. P-values indicate significance (Canonical correspondence analysis).

	Reedbuck	Waterbuck	Wildebeest
Season	10.0 ($p< 0.001$)	16.7 ($p< 0.001$)	24.9 ($p< 0.01$)
Region	6.9 ($p= 0.07$)	9.7 ($p< 0.001$)	
Season*Region	7.6	7.3	
Total explained	24.5	33.8	24.9

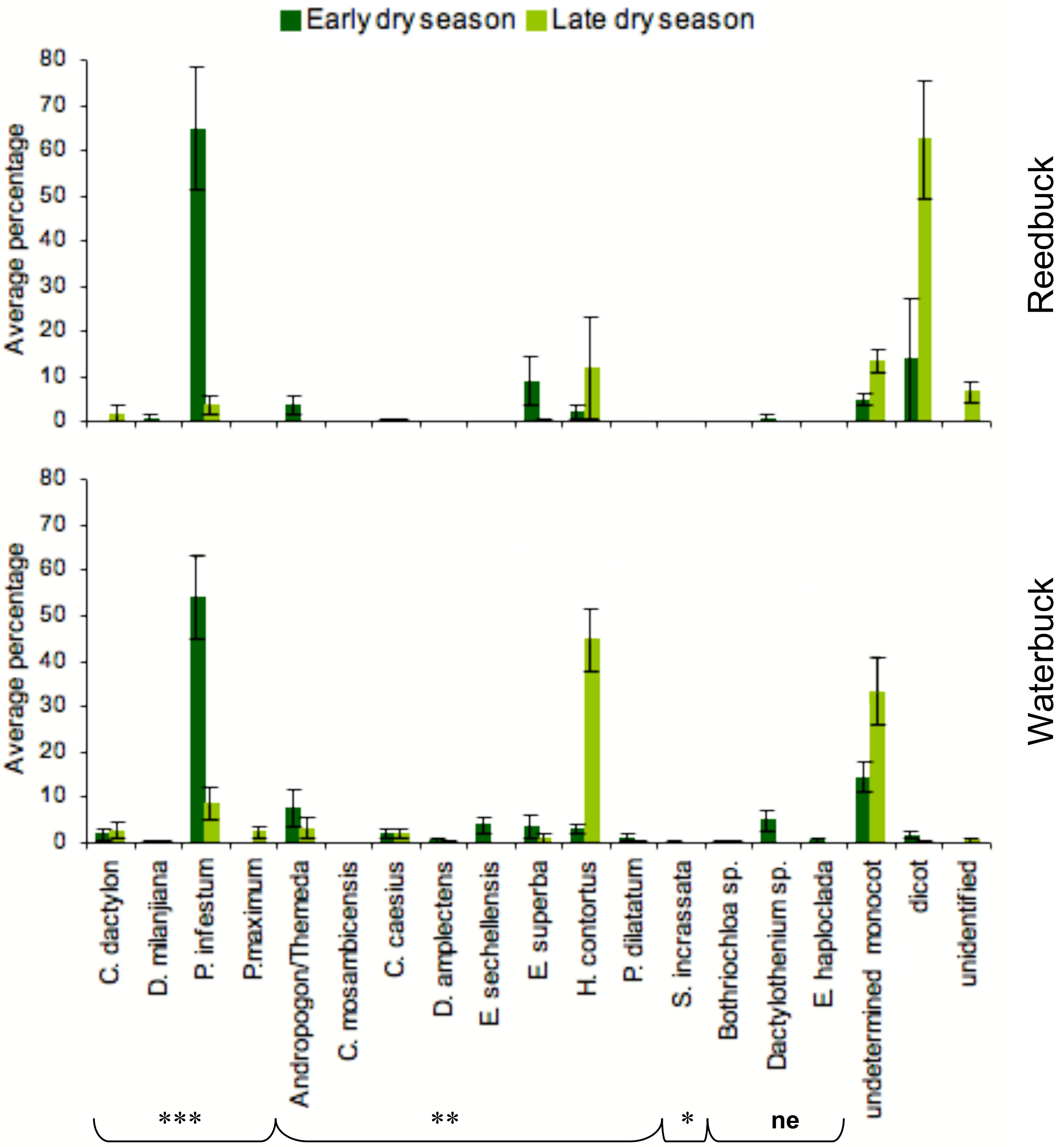


Figure 5: Average percentages of plant species in dung of reedbuck and waterbuck in Mkwaja North for two seasons. Error bars represent the SE. Plant species are sorted according to preference of plant species observed by cattle in Mkwaja North (Kozak 1983): * = high preference, ** = preference, * = low preference, ne = not eaten.**

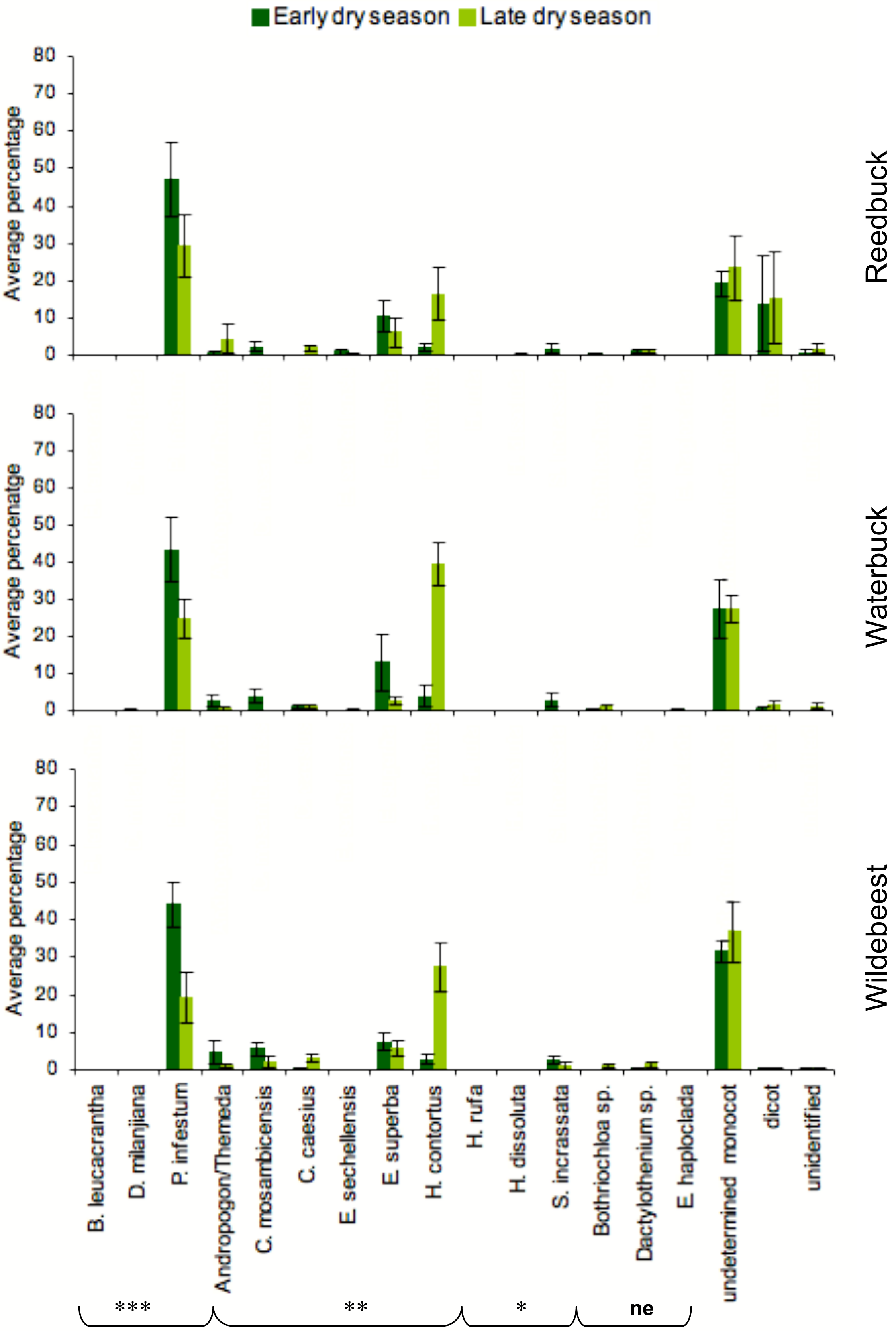


Figure 6: Average percentages of plant species in dung of reedbuck, waterbuck and wildebeest in Saadani North for two seasons. Error bars represent SE. Plant species are sorted according to preference of plant species observed by cattle in Mkwaja North (Kozak 1983): * = high preference, ** = preference, * = low preference, ne = not eaten.**

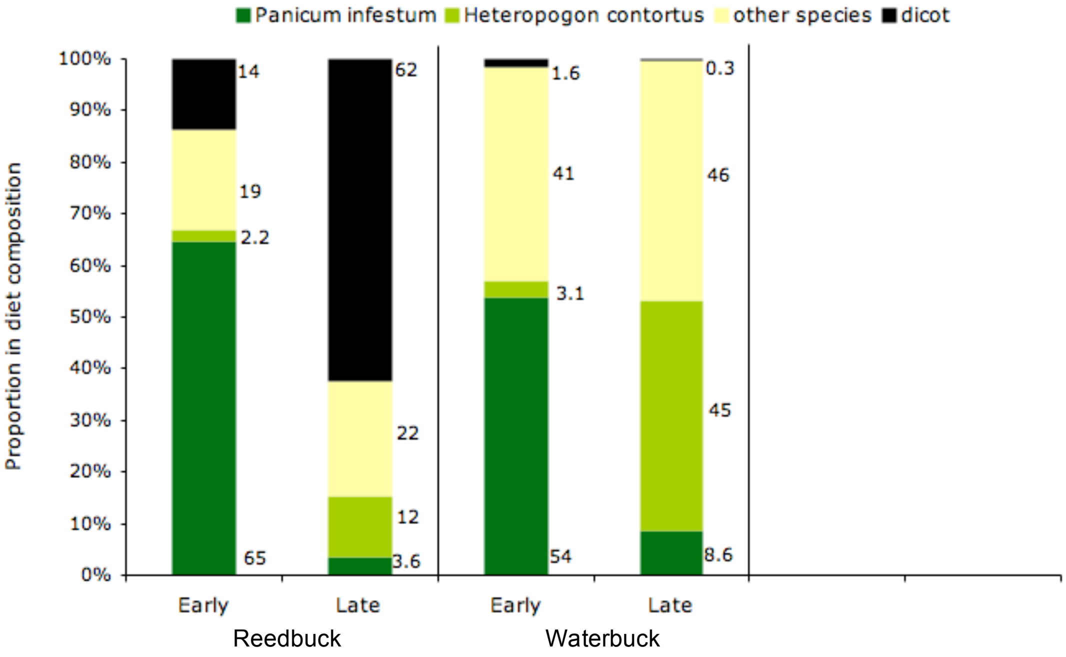


Figure 7: Seasonal shift in proportion of major dietary components for reedbuck and waterbuck in Mkwaja North. Note that "other species" was largely made up of undetermined monocots.

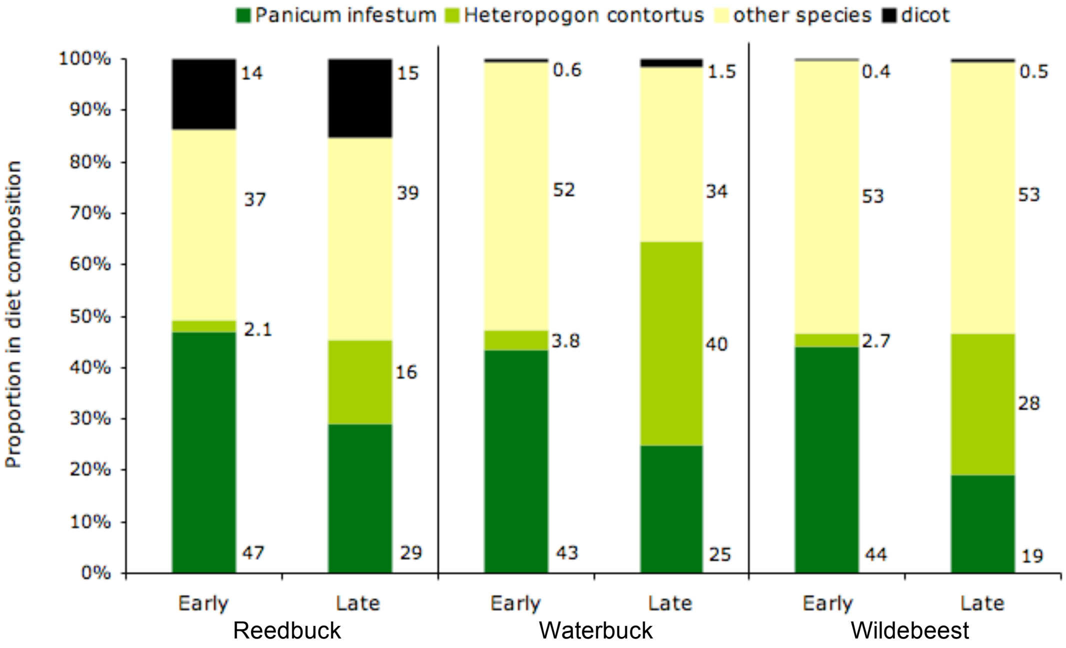


Figure 8: Seasonal shift in proportion of major dietary components for reedbuck, waterbuck and wildebeest in Saadani North. Note that "other species" was largely made up of undetermined monocots.

The total number of plant species eaten was very low for all three study animals in both regions and seasons. Especially reedbuck in Mkwaja North included a very low number of plant species during the late dry season (Table 7). The highest number of plant species included in the diet was found for waterbuck in Mkwaja North during the early dry season. In Saadani North no large differences were observed between animal species or seasons (Table 7).

In Mkwaja North the average number of plant species in the diet between reedbuck and waterbuck were significantly different (2-way ANOVA; Table 8). The variation within species was too large to demonstrate this by means of a one-way ANOVA (Figure 9). In Saadani North the number of plant species included in the diet did not significantly differ between animal species or seasons (Table 8).

Diet breadth, i.e. diet diversity, showed a similar pattern with the lowest values recorded for reedbuck in Mkwaja North in both seasons (Figure 10). Differences in diet breadth were significant between regions and seasons for reedbuck and waterbuck (Table 9). In Mkwaja North the diet breadth of reedbuck was significantly lower than that of waterbuck. Diet breath did not differ significantly between seasons or between animal species in Saadani North (Figure 10, Table 9).

Table 7: Total number of plant species in diet of the three study animals based on faecal analysis.

Region	**Mkwaja North**		**Saadani North**	
Season	Early dry	Late dry	Early dry	Late dry
Reedbuck	6	10	12	13
Waterbuck	13	15	10	12
Wildebeest			11	10

Table 8: ANOVA table for number of plant species included in the diet of the three study animals (reedbuck, waterbuck and wildebeest). Wildebeest was not included in three-way analysis. Table shows degrees of freedom (Df), F-value and p-value. MN= Mkwaja North, SN= Saadani North.

	Df	F-value	Significance
3-way ANOVA			
Animal species	1	9.5	0.004
Region	1	0.3	0.595
Season	1	3.7	0.062
Animal species*Region	1	9.6	0.004
Animal species*Season	1	0.1	0.811
Region*Season	1	0.6	0.426
Animal species*Region*Season	1	0.5	0.487
2-way ANOVA MN			
Animal species	1	32.9	< 0.001
Season	1	6.4	0.020
Animal species*Season	1	0.2	0.674
2-way ANOVA SN			
Animal species	2	0.6	0.579
Season	1	0.1	0.769
Animal species*Season	2	0.6	0.542

Table 9: ANOVA table for diet breadth of the three study animals (reedbuck, waterbuck and wildebeest). Wildebeest was not included in three-way analysis. Table shows degrees of freedom (Df), F-value and p-value. MN= Mkwaja North, SN= Saadani North.

	Df	F-value	Significance
3-way ANOVA			
Animal species	1	6.3	0.016
Region	1	3.4	0.073
Season	1	0.4	0.512
Animal species*Region	1	5.3	0.026
Animal species*Season	1	0.5	0.503
Region*Season	1	1.2	0.289
Animal species*Region*Season	1	0.6	0.460
2-way ANOVA MN			
Animal species	1	12.4	0.002
Season	1	0.1	0.766
Animal species*Season	1	1.1	0.309
2-way ANOVA SN			
Animal species	2	0.6	0.550
Season	1	0.9	0.335
Animal species*Season	2	0.2	0.829

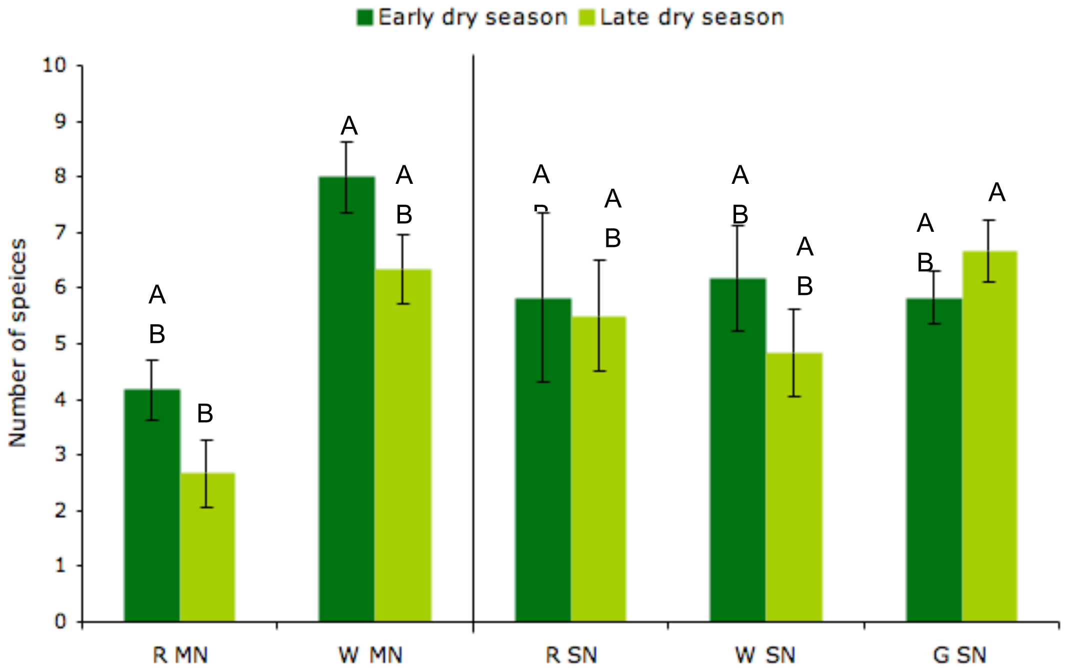


Figure 9: Average number of plant species in dung of three herbivores from two savanna regions in Tanzania. Error bars represent SE. R= reedbuck, W= waterbuck, G= wildebeest, MN= Mkwaja North, SN= Saadani North. Levels not sharing the same letter are significantly different (one-way ANOVA, Tukey-Kramer Test, p < 0.05, n= 6).

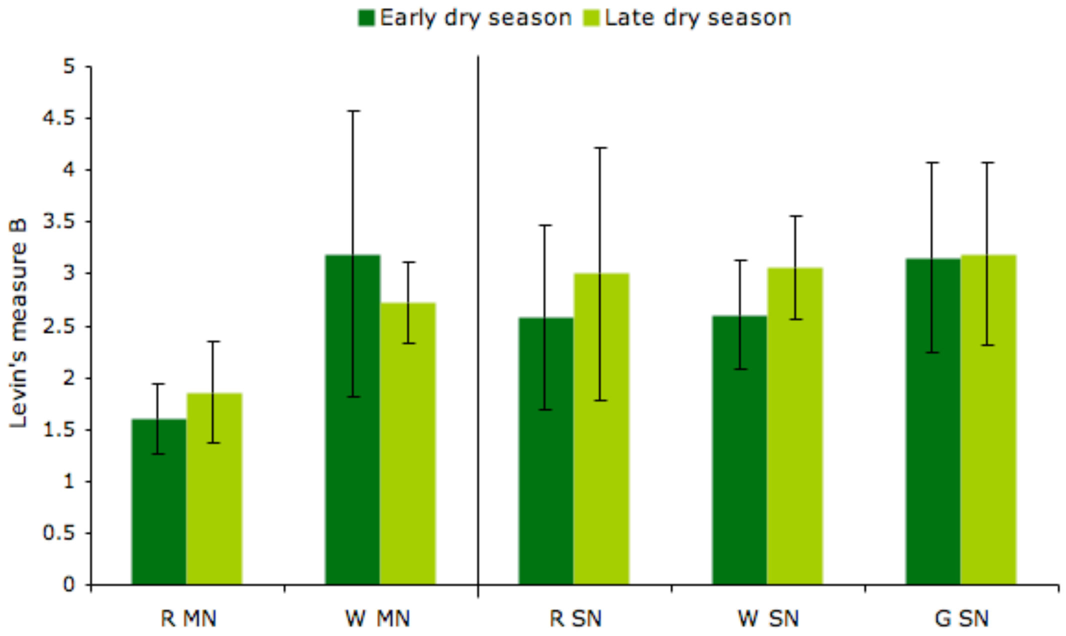


Figure 10: Mean values for diet breadth of the three study animals. Error bars represent SE. R= reedbuck, W= waterbuck, G= wildebeest, MN= Mkwaja North, SN= Saadani North. Diet breadth was not significantly different among values shown (one-way ANOVA, Tukey-Kramer Test, p < 0.05, n= 6).

Table 10: Diet overlap (Simplified Morisita Index) between study animals and between seasons for each region, as well as diet overlap between the two regions for reedbuck and waterbuck.

Diet overlap between animal species (%)

	Mkwaja North		**Saadani North**	
	Early	Late	Early	Late
Reedbuck-Waterbuck	95	23	96	78
Reedbuck-Wildebeest			97	80
Waterbuck-Wildebeest			99	93

Diet overlap between seasons (%)

	Mkwaja North	**Saadani North**
Reedbuck Early-Late	25	82
Waterbuck Early-Late	24	59
Wildebeest Early-Late		57

Diet overlap between regions (%)

	Reedbuck		**Waterbuck**	
	Early	Late	Early	Late
Mkwaja North-Saadani North	96	53	94	89

Diet overlaps between animals were very high (> 95 %) in the early dry season in both regions, underlining the preference for the same plant species (Table 10). In the late dry season diet overlap between the animal species remained high in Saadani North, but was very low in Mkwaja North. The diet overlap of waterbuck and wildebeest is remarkably high also in the late dry season (Table 10). Differences in the diet composition between seasons were larger than between animal species, with particularly low overlap in Mkwaja North. Between regions the diet composition was more similar in the early dry than in the late dry season for both reedbuck and waterbuck (Table 10).

Leaf nutrient concentrations

Leaf nitrogen and phosphorus concentrations and the N/P-ratio were significantly different between plant species, seasons and regions (Table 11).
The grasses mainly eaten by the animals in this study, *Panicum infestum* and *Heteropogon contortus*, did not have higher nutrient concentrations than other species in both regions (Figures 11,12).

In Mkwaja North, the highest nitrogen and phosphorus concentrations were found in both seasons in the paddock centre species: *Cynodon dactylon* and *Paspalum dilatatum* (Figure 11,12). The N/P-ratio of these species was very low (Appendix B).

Two further important patterns were observed. Nitrogen and phosphorus concentrations were significantly higher in the late dry season compared to values of the early dry season (Table 12). Nitrogen concentrations were significantly higher in plant species in Mkwaja North compared to Saadani North, whereas phosphorus content was significantly higher in plant species in Saadani North (Table 12).

Table 11: Three-way ANOVA table for nitrogen and phosphorus concentrations and N/P-ratio in fresh leaves of plant species from study area. Season = early dry and late dry; region = Mkwaja North and Saadani North.

Nitrogen	**DF**	**F-value**	**Significance**
Plant species	11	11.2	< 0.001
Season	1	8.7	0.003
Region	1	4.3	0.038
Plant species*Season	11	1.7	0.081
Plant species*Region	11	1.2	0.292
Region*Season	1	6.1	0.014
Plant species*Region*Season	11	0.3	0.988
Phosphorus	**DF**	**F-value**	**Significance**
Plant species	11	10.5	< 0.001
Season	1	30.9	< 0.001
Region	1	8.9	0.003
Plant species*Season	11	1.9	0.036
Plant species*Region	11	2.3	0.011
Region*Season	1	0.4	0.539
Plant species*Region*Season	11	1.5	0.131
N/P-ratio	**DF**	**F-value**	**Significance**
Plant species	11	2.0	0.038
Season	1	5.5	0.019
Region	1	15.7	< 0.001
Plant species*Season	11	1.3	0.228
Plant species*Region	11	0.8	0.641
Region*Season	1	6.3	0.013
Plant species*Region*Season	11	0.7	0.772

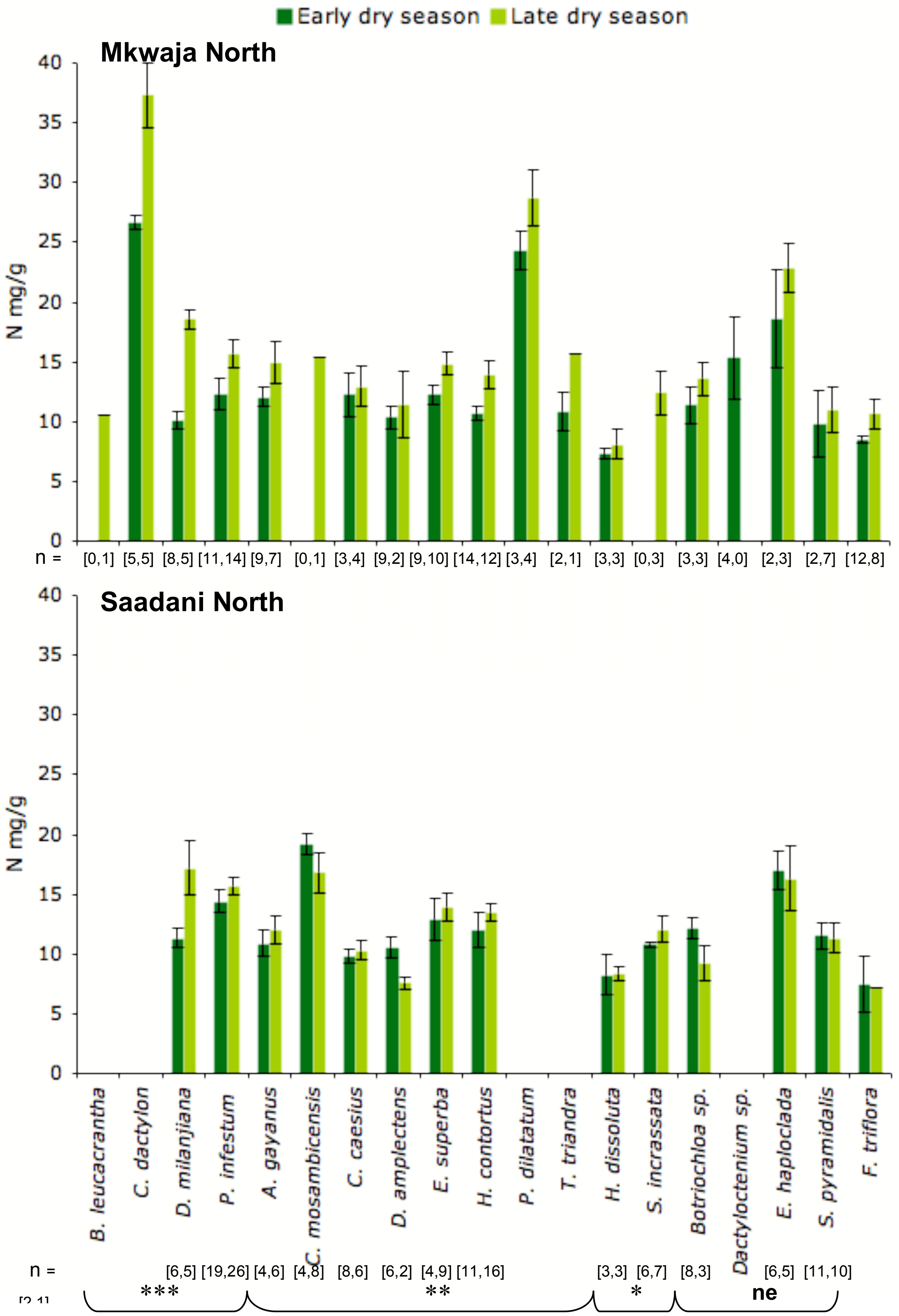


Figure 11: Mean nitrogen concentrations in youngest leaves of plant species for early dry and late dry season. Figure shows regional differences between Mkwaja North and Saadani North. Error bars represent SE. [n] is number of replicates. Data from late dry season are preliminary results from Halsdorf.

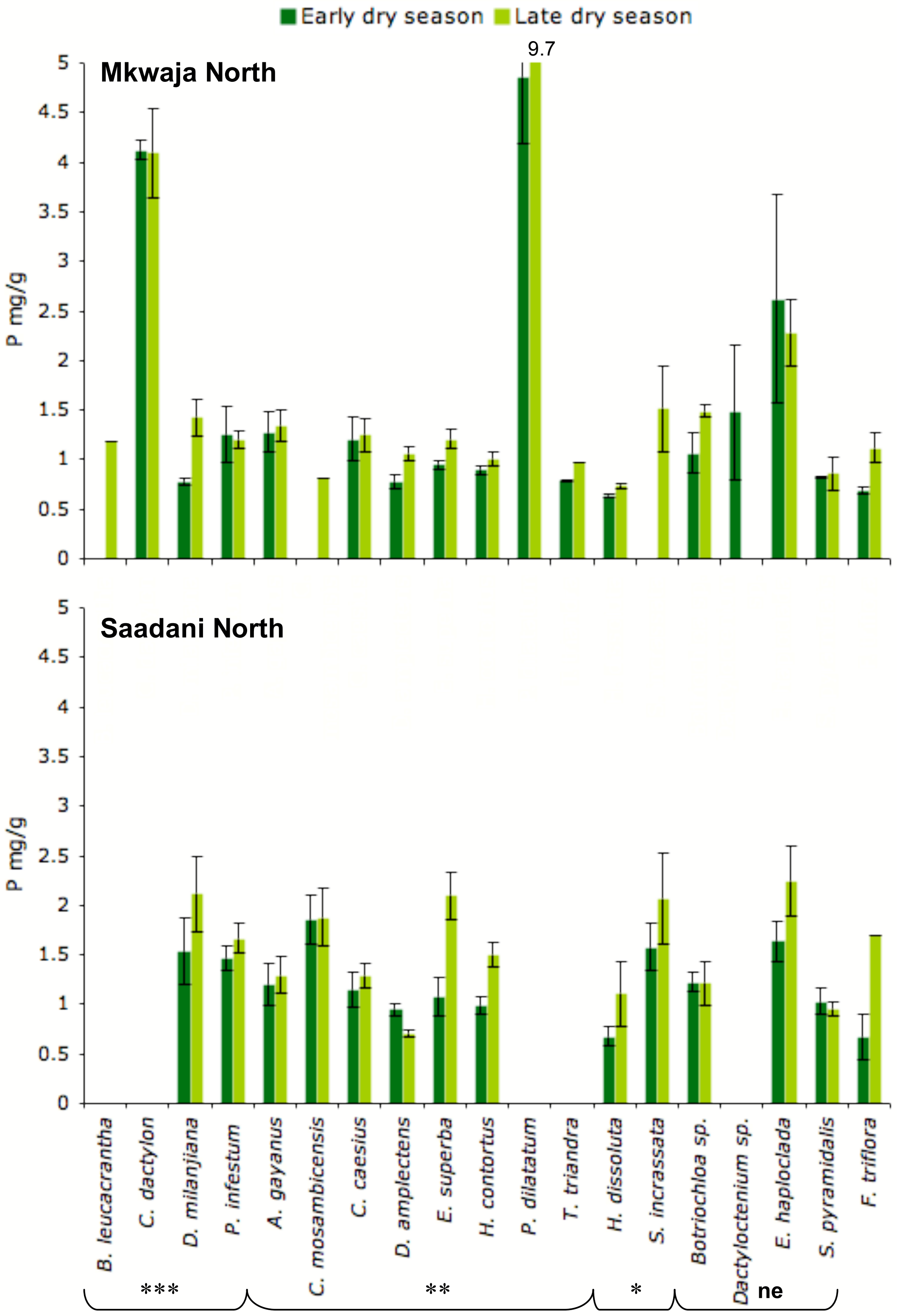


Figure 12: Phosphorus concentrations in leaves of plant species in early dry and late dry season in Mkwaja North and Saadani North (means with standard errors). Data from late dry season are preliminary results from Halsdorf.

Table 12: Two-way ANOVA table for nitrogen and phosphorus concentrations and N/P-ratio in youngest leaves of the plant species in the study area. Season = early dry and late dry.

Mkwaja North			
Nitrogen	**DF**	**F-value**	**Significance**
Plant species	14	18.6	< 0.001
Season	1	20.9	< 0.001
Plant species*Season	14	0.8	0.679
Phosphorus	**DF**	**F-value**	**Significance**
Plant species	14	52.7	< 0.001
Season	1	23.2	< 0.001
Plant species*Season	14	1.7	0.066
N/P-ratio	**DF**	**F-value**	**Significance**
Plant species	14	6.8	< 0.001
Season	1	0.2	0.665
Plant species*Season	14	0.8	0.632
Saadani North			
Nitrogen	**DF**	**F-value**	**Significance**
Plant species	13	7.8	< 0.001
Season	1	0.04	0.844
Plant species*Season	13	1.1	0.327
Phosphorus	**DF**	**F-value**	**Significance**
Plant species	13	6.4	< 0.001
Season	1	14.2	< 0.001
Plant species*Season	13	1.8	0.051
N/P-ratio	**DF**	**F-value**	**Significance**
Plant species	13	1.8	0.047
Season	1	9.9	0.002
Plant species*Season	13	1.0	0.459

Digestibility

Sporobolus pyramidalis was the least digestible plant species analysed. *Panicum infestum*, *Eragrostis superba* and *Andropogon gayanus* also showed low levels of digestibility (Figure 13). Digestibility of plant species did not differ significantly between the two regions Mkwaja North and Saadani North (Figure 13). The dry matter digestibility of *Panicum infestum* from seven different habitat types did not differ significantly (Figure 14).

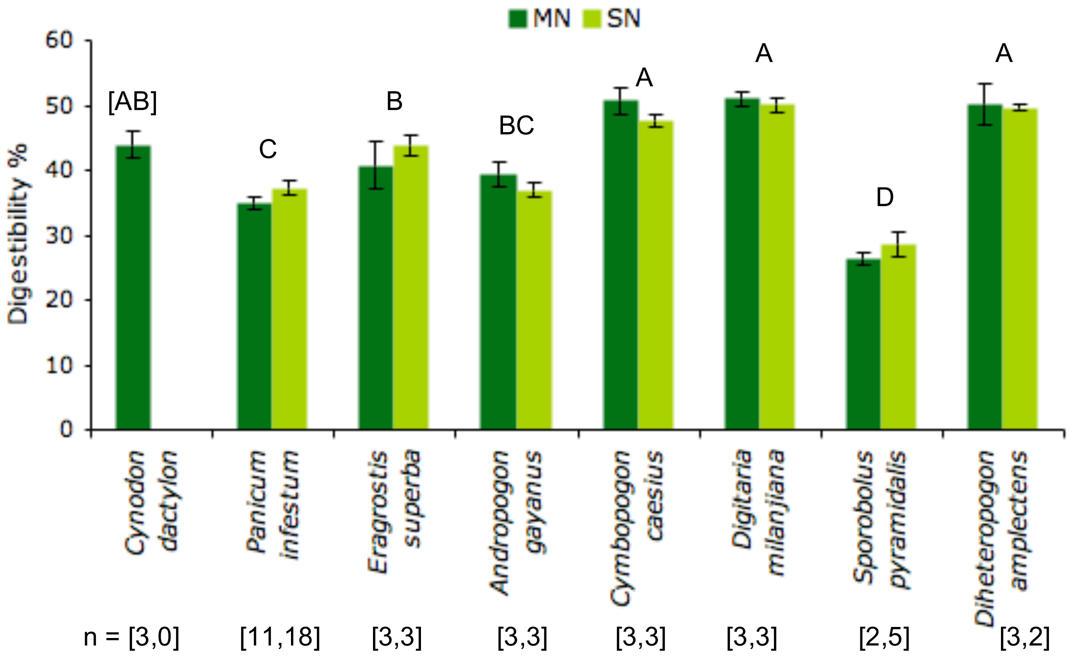


Figure 13: Dry matter digestibility (mean and SE) of selected grass species from Mkwaja North (MN) and Saadani North (SN) in the early dry season. [n] is the number of replicates. Species not sharing same letter are significantly different, species did not differ significantly between regions (ANOVA, Tukey-Kramer Test, p< 0.05).

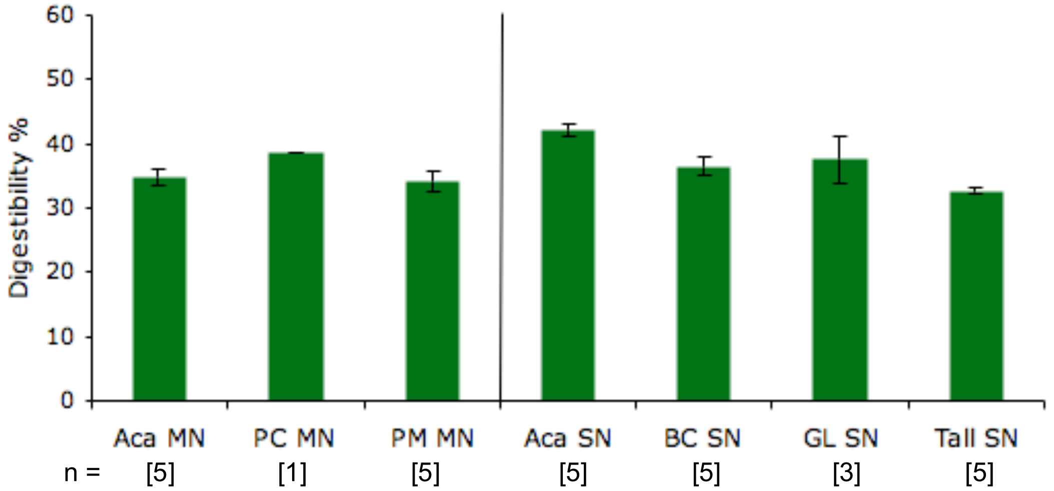


Figure 14: Dry matter digestibility (mean and SE) of *Panicum infestum* in the early dry season, for three respectively four habitat types of the regions Mkwaja North (MN) and Saadani North (SN). [n] is the number of replicates. Aca= acacia forest, PC= paddock centre, PM= paddock margin, BC= black cotton soil, GL= grazing lawn, Tall= tall grass. No significant differences were found between regions or habitat types (ANOVA, Tukey-Kramer Test, p < 0.05).

Correlations between food quality and food preference

Leaf nitrogen and phosphorus concentrations were significantly correlated with each other, but not with digestibility, in both regions and seasons (Table 13). Furthermore, the proportion of plant species found in the dung of study animals was not significantly correlated with nitrogen, phosphorus, N/P-ratio or dry matter digestibility of these plant species (Table 14).

Table 13: Correlation of food quality variables in plants. N= nitrogen concentration, P= phosphorus concentration, N/P= nitrogen to phosphorus ratio, DMD= dry matter digestibility, S-value= Spearman correlation coefficient, Sign= significance.

Mkwaja North		**Early dry season**		**Late dry season**	
Variable	**By variable**	**S-value**	**Sign.**	**S-value**	**Sign.**
N	P	0.91	< 0.001	0.75	0.005
N	N/P	-0.60	0.039	0.08	0.812
P	N/P	-0.71	< 0.001	-0.38	0.217
N	DMD	0.07	0.866		
P	DMD	-0.28	0.509		
N/P	DMD	0.16	0.713		

Saadani North		**Early dry season**		**Late dry season**	
Variable	**By variable**	**S-value**	**Sign.**	**S-value**	**Sign.**
N	P	0.72	0.005	0.91	< 0.001
N	N/P	0.63	0.021	0.53	0.062
P	N/P	0.04	0.886	0.25	0.409
N	DMD	0.00	1.000		
P	DMD	0.22	0.606		
N/P	DMD	-0.01	0.977		

Table 14: Correlation of plant species preference by study animals with food quality variables. N= nitrogen content, P= phosphorous concentration, N/P= nitrogen to phosphorous ratio, DMD= dry matter digestibility, S-value= Spearman correlation coefficient, Sign= significance.

Mkwaja North		**Early dry season**		**Late dry season**	
Variable	**By variable**	**S-value**	**Sign.**	**S-value**	**Sign.**
Reedbuck	N	-0.23	0.481	0.19	0.542
Reedbuck	P	-0.26	0.422	-0.35	0.475
Reedbuck	N/P	0.45	0.144	0.47	0.122
Reedbuck	DMD	-0.19	0.643		
Waterbuck	N	0.12	0.745	0.23	0.475
Waterbuck	P	0.01	0.982	-0.19	0.552
Waterbuck	N/P	0.18	0.566	0.54	0.068
Waterbuck	DMD	-0.26	0.531		

Saadani North		**Early dry season**		**Late dry season**	
Variable	**By variable**	**S-value**	**Sign.**	**S-value**	**Sign.**
Reedbuck	N	0.48	0.100	-0.04	0.885
Reedbuck	P	0.13	0.677	-0.12	0.690
Reedbuck	N/P	0.33	0.276	0.42	0.156
Reedbuck	DMD	0.02	0.955		
Waterbuck	N	0.68	0.011	-0.02	0.951
Waterbuck	P	0.28	0.362	-0.08	0.782
Waterbuck	N/P	0.54	0.059	0.26	0.393
Waterbuck	DMD	0.12	0.774		
Wildebeest	N	0.42	0.151	0.13	0.665
Wildebeest	P	0.17	0.589	0.03	0.929
Wildebeest	N/P	0.33	0.276	0.34	0.251
Wildebeest	DMD	0.12	0.774		

Discussion

All the three study animals had a narrow diet because of the strong preference for *Panicum infestum*, *Heteropogon contortus* or dicots. For reedbuck a narrow diet was expected because of its low body weight (45 kg) and its selective feeding strategy. The hypothesis that reedbuck would feed on less plant species than the other herbivores was only supported by evidence found in Mkwaja North (Table 8). The diets of waterbuck and wildebeest did not imply a bulk feeding strategy although their body weight (200 kg and 260 kg respectively) is clearly above the threshold of 90 kg (c.f. Van Soest 1996). Similarly, Ego et al. (2003) found that wildebeest, hartebeest (185 kg) and cattle (350 kg) mainly consumed three grass species on a ranch in a semi-arid savanna in Kenya. Macandza et al. (2004) observed that the feeding behaviour of buffalo (500 kg) in South Africa consisted of more than 10 plant species contributing major proportions to the diet. Hence, it seems that among all the mentioned herbivores only the very heavy buffalo was feeding on the kind of broad diet expected of a bulk feeder. Animals with a body weight of over 90 kg, such as waterbuck and wildebeest, also seem to be able to feed selectively on only a few plant species.

A clear seasonal pattern was found in this study. *Panicum infestum* was clearly the most preferred fodder species for all three animals in the early dry season. However, later in the dry season *Panicum infestum* decreased or disappeared entirely from the diet of the three animals. Reedbuck increased feeding on dicots, while waterbuck and wildebeest included large proportions of *Heteropogon contortus* in their diet. Hence diet compositions between the three study animals were very similar in the early dry season, but showed a decreasing diet overlap in the late dry season. This result supported my first hypothesis that the diet overlap between the study animals decreases in the dry season. The pattern agrees with findings by Prins et al. (2006), who observed a decrease in diet overlap in the dry season between red duiker, common duiker and suni (three browsers) in a moist savanna ecosystem in Mozambique.

While diet composition was similar between regions in the early dry season, regional differences in the feeding strategies in the late dry season were apparent for reedbuck and waterbuck. The shift from *Panicum infestum* to alternative fodder species (i.e. *Heteropogon contortus* and dicots) was stronger in Mkwaja North than in Saadani North, where *Panicum infestum* still contributed to the diet. A possible explanation is that in Mkwaja North *Panicum infestum* is the only forage species available in both sufficient quantity and quality. It may be simply all eaten up in the late dry season, which may be related to the land-use history of the area. Since the cattle ranch was closed down, Mkwaja North has been a defaunated savanna. The lack of large grazers enhanced the occurrence of nutrient-poor tall grasses, where *Panicum infestum* is either rare or is not found by animals (Tobler et al. 2003, Treydte 2004, Van de Koppel et al., unpublished manuscript).

Only three main components were found in the diet of the study animals (i.e. *Panicum infestum*, *Heteropogon contortus* and dicots). This raises the question of how, and to what extent, food quality accounts for this preference of forage.

Both *Panicum infestum* and *Heteropogon contortus* are highly abundant in the study area, occurring in dense patches in all habitat types, with perhaps the exception of *Panicum infestum* in the late dry season (see above) (Halsdorf 2002). In other study areas where *Panicum* species and *Heteropogon contortus* were abundant, they also represented large proportions in the diet of waterbuck, wildebeest, buffalo and zebra (Tomlinson 1980, Ben-Shahar 1991, Bodenstein et al. 2000, Macandza et al. 2004). Previous studies on the feeding behaviour in Mkwaja North showed *Panicum infestum* to be a highly preferred forage species for cattle, whereas *Heteropogon contortus* was less preferred but still often eaten (Kozak 1983). My results showed that leaf crude protein levels (nitrogen concentration multiplied by 6.25) of both grass species were above the critical level of 4% as defined by Sinclair (1975). The nutrient concentrations were much higher than levels observed by Bodenstein et al. (2000) in plant species that wildebeest included in their diet in a semi-arid savanna in South Africa. Ben-Shahar & Coe (1992) observed leaf nitrogen and phosphorus concentrations in forage species of wildebeest in South Africa that are similar to my results. However, I found that plant species, which were not included in the diets, had even higher nutrient levels (Figures 11,12). Also the dry matter digestibility of *Panicum infestum* leaves was rather low compared to that of other plant species in this study, as well as compared to values observed in forage species of wildebeest in other studies (Berry & Louw 1982, Bodenstein et al. 2000). The dry matter digestibility of *Heteropogon contortus* could not be determined in this study (not enough samples of plant material available), but it seems that its digestibility is even lower than that of *Panicum infestum* in the Saadani National Park (Halsdorf 2002). Hence, nitrogen and phosphorus concentrations as well as digestibility are not sufficient in explaining the preference for these two grass species. Perhaps other food quality factors (e.g. Ca, Cu, Na, Zn) are important in determining why certain plant species are preferred as forage (McNaughton 1990). In addition, factors altering food quality or its spatial distribution such as fire may attract herbivores to specific areas, plant communities or species (Wilsey 1996).

According to Kozak (1983), vegetation types characterized by *Heteropogon contortus* in Mkwaja North show high levels of crude protein in early growth stages compared to other vegetation types. Early growth stages in the late dry season are often the result of burning. Green flushes after fire incidents offer not only high quality forage but also feeding sites with short grass (Dörgeloh 1999). This might be specifically important for wildebeest, as they generally depend on sites with short and dense grass (Wilmshurst et al. 1999, Traill 2004). Murray & Illius (2000) observed that wildebeest can graze down the vegetation sward to a height below that accessible to narrow-mouthed selective feeders. This could explain why much less *Heteropogon contortus* was found in the diet of reedbuck. Moreover, burned areas that provide regrowth of high quality are variable in time and space, making this a rather unreliable source of forage (Stephens & Krebs 1986). Reedbuck, which need to feed on high quality food all the time, may therefore have adapted to selecting more reliable plant species, such as dicots in the late dry season. They may be feeding on *Heteropogon contortus* only if directly confronted with a recently burned area (Hanley 1982, Van Soest 1996, Stephens & Krebs 1986). Further explanations could be found in the different behavioural constraints of the animals. As territorial behaviour by reedbuck is strong, it possibly limits their mobility towards burned areas. The territories of waterbuck and wildebeest are larger. They tolerate other individuals to some degree and are more mobile (Estes 1991). Furthermore, to limit predation risk reedbuck require a certain amount of cover and therefore shun burned areas (Estes 1991).

The diet of reedbuck contained large amounts of dicots, particularly in the late dry season. Legumes, and dicots in general, have higher leaf nitrogen (or crude protein) and phosphorus concentrations, as well as a higher digestibility than grasses (Minson 1990, Owen-Smith 1997). Preliminary data of nitrogen concentrations of grasses, legumes and other herbs in the Mkwaja area confirm this pattern (Cech, unpublished). Dicots are a high quality food source, hence a large proportion of dicots in the diet supports my hypothesis that reedbuck feed on forage of better quality than waterbuck and wildebeest. I did expect to observe an overall increase of dicots in the diet of all three study animals during the late dry season, especially in the small, selective reedbuck. However, these large quantities were unexpected and contradict information from literature (Table 3). Further determination of the dicots and their allocation to a distinct species or taxonomic group was not possible in this study. I assume that they mainly consist of herbs (legumes and others) rather than leaves from woody plants, but this needs to be confirmed by further studies. Besides high nutrient levels, dicots have higher levels of tannins and other allelochemicals than grasses, which grazers often cannot cope with (Owen-Smith 1997, Sorensen & Dearing 2003). Reedbuck may be more resistant to these allelochemicals in dicots than waterbuck and wildebeest due to adaptive detoxification mechanisms (Sorensen & Dearing 2003). This remains speculative and further studies on why especially waterbuck in Mkwaja North do not feed on dicots need to be carried out.

According to Senft et al. (1987), selectivity can occur on different hierarchical levels. Differences between the feeding strategies of animals may occur on different spatial scales, ranging from specific plant parts (plant scale) or specific plant species (community scale) to specific plant communities (landscape scale) or landscapes (regional scale) (Senft et al. 1987). In the following, I suggest that reedbuck, waterbuck and wildebeest may be pursuing different feeding strategies although they all feed on the same grass species in the early dry season (i.e. *Panicum infestum*).

Reedbuck may be feeding selectively on specific plant parts or maturity stages, actively searching young and nutritious parts of *Panicum infestum*. They may further be selecting *Panicum infestum* of higher quality than waterbuck and wildebeest by feeding exclusively in specific habitat types or at specific sites (e.g. termite mounds) (Melton 1987, Mobaek et al. 2005).

Waterbuck may have an intermediate feeding strategy, as proposed by East (1984). They may feed selectively but on less widely dispersed forage items than reedbuck. Waterbuck is reported to be selective in habitats and moves from one habitat to the next if the food quality (i.e. crude protein content) requires this (Tomlinson 1980, Melton 1987, Traill 2004). Therefore, waterbuck may be selecting the most abundant plant species, actively searching for feeding sites (e.g. termite mounds) or habitats with high quality specimens of such plant species (Mobaek et al. 2005). Depending on season or region, shifts from bulk to selective feeding may possibly occur.

Wildebeest may be feeding selectively on a landscape scale, visiting the same preferred patches every season (Melton 1987, Ben-Shahar & Coe 1992, Wilmshurt et al. 1999, Fryxell et al. 2005). A main restriction for wildebeest may be the sward height, as Saadani National Park has few large open areas with short grazing lawns (cf. Fryxell 1991, Tobler et al. 2003, Traill 2004). This reduces available forage quantity for wildebeest to a great extent. Besides limiting predation risk, herding behaviour also allows the bulk feeders to engineer and secure their food source (Fryxell 1991). By heavily grazing on the same patches, they encourage regrowth and at the same time return nutrients to the soil through their excrement. On these so-called "grazing lawns", wildebeest actively regulate biogeochemical processes, nutritional properties, growth form, sward height and plant species composition of the vegetation (Georgiadis & McNaughton 1990, Augustine & McNaughton 1998, Murray & Illius 2000, Anderson et al. 2006). By grazing on the same patches over time, wildebeest can maintain and secure their food resource (Fryxell 1991). The role of *Panicum infestum* with regard to the preference and maintenance of these patches needs to be analysed in further studies.

Nitrogen and phosphorus concentrations, or digestibility of green leaves, do not sufficiently explain the feeding preferences, particularly those of waterbuck and wildebeest in the Saadani region. Plant characteristics such as growth form, spatial distribution and herbage density possibly all influence foraging choices in studied animals, maximizing the amount of good quality biomass per bite. In addition, habitat requirements and spatial behavioural constraints of the animal species have to be considered. This may be an important factor particularly in Mkwaja North, because there habitat variability is much higher than in other savanna ecosystems such as Serengeti (Tobler et al. 2003).

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Female reedbuck (*Redunca redunca*); photograph by Jean-David Gerber.

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Appendix A: Microhistological Dung Analysis

Contents

Introduction

The epidermises of plants are coated with a thin wax layer, the cuticula, rendering them highly robust. During ingestion of plant material by herbivores, the epidermis is generally resistant to digestion, passes the digestion tract intact and can therefore be detected in the dung. As the cell structure of the epidermis is specific in each plant taxon, already small fragments are sufficient to determine the plant species. Therefore, the analysis of dung can make precise statements on the qualitative and quantitative composition of the ingested diet (Barthlott & Martens 1979).

Botanical-taxonomical aspects

Monocotyledon plants (e.g. grasses and sedges) are easily distinguishable from dicotyledons (e.g. trees, shrubs and herbs). Epidermal cells of dicotyledons show a random distribution, mostly circular alignment (Figure 15), while monocotyledons show a clear parallel cell alignment (Barthlott & Martens 1979, Mühlenberg 1993). The family of grasses (e.g. gramineae) show the largest taxon-specific diversity in epidermal structures of all plant families. Consequently, in most cases the determination of even closely related species of the same genus is possible. The most differentiated epidermal structures are found on the abaxial (bottom) side of the grass leaves. The outer basal part and the immediate tip of the lamina can show certain divergence of the cell structure and should therefore not be considered for preparing references. The epidermis can be separated and isolated by mechanical abrasion of the overlaying plant tissue. Usually, colouring of the epidermis is unnecessary (Barthlott & Martens 1979).

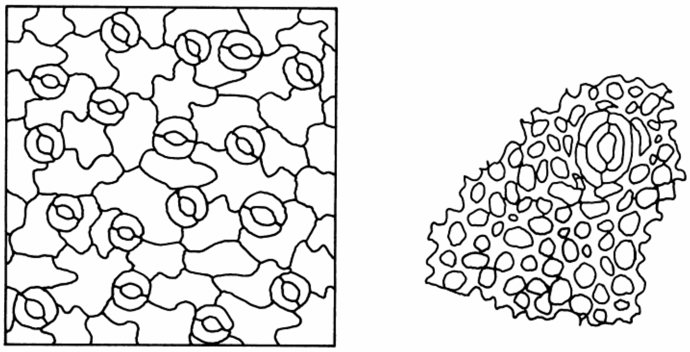

Figure 15: Epidermis of dicotyledonous leave (left) and fruit (right), (Mühlenberg 1993).

Plant micromorphology

The most striking feature of grass leaves is their parallel venation. The cell stripes above the leave nerve is called costal, the cell tissue between nerves intercostal. Grass species are identified according to characteristic features of epidermal cells or specific patterns of these cell forms (Figure 16).

Epidermal cell forms

Long cells are not differentiated, cell walls generally interlocked in wavy pattern, sometimes with round papilles: either small and appearing in groups in each long cell, or big and appearing singly in long cells and between stomata.

Short cells are significantly smaller than long cells and generally in pairs in between long cells in the intercostal or in long row of pairs in the costal. The short cells are commonly shaped like a dumb-bell, and are important features of recognition.

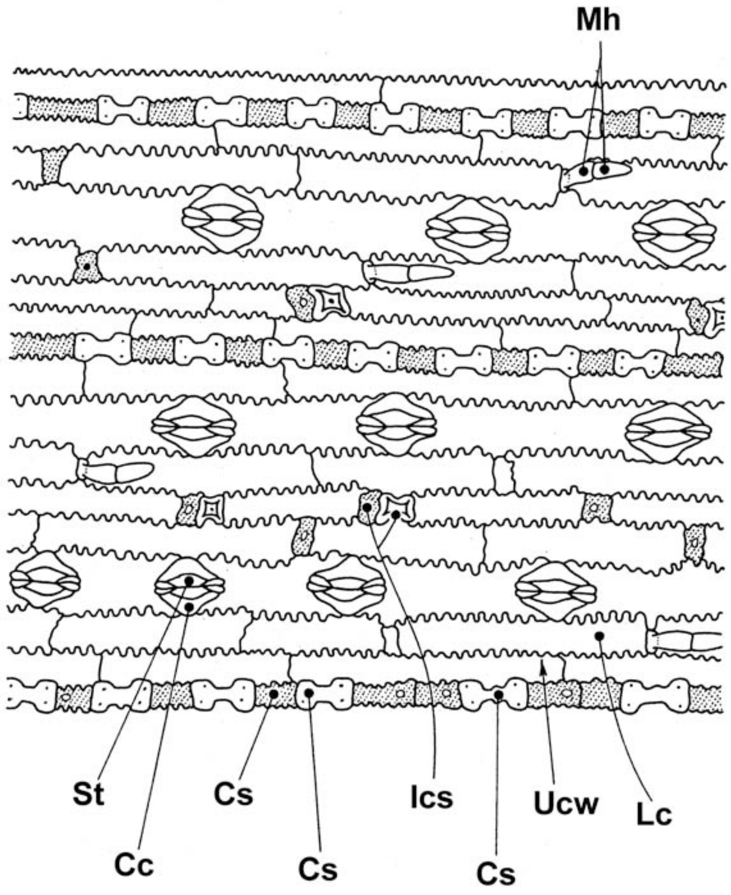

Figure 16: Epidermis of grass with characteristic cell forms: St – Stomata, Cc – Concomitant cell (triangle shaped), Cs – Costal short cell, Ics – Intercostal short cell, Ucw – Undulating cell wall, Lc – Long cell, Mh – Micro hair (Barthlott & Martens 1979).

Trichoma are three distinguishable types of hair (micro hair, prickle hair, macro hair).

Micro hair consist of two cells and are very common. The shape and proportion of both cells to each other and to other epidermal cell forms are important features of recognition. The second cell making up the micro hair tip is generally poorly visible, and in this paper declarations on micro hair length are referring to only the first cell.

Prickle hair consist of one cell and have a thick cell wall. They appear in the intercostal and costal. Hook hair are a specific kind of prickle hair. They appear only in the intercostal and have a circular round base and short curved tip. Large prickle hairs are sometimes present in the costal and most species show a row of large prickle hair in the basal costal.

Macro hair are long single cellular spiky hairs. Their base is surrounded by a group of pillow like thick-walled epidermis cells. The relationship between length of hair and width of basis is an important feature and distinguishes macro hair from prickle hair.

Stomata consist of one pair of lips, porus and two concomitant cells; these are either round or triangle shaped.

Epidermal cell patterns

Patterns of epidermal cells can also be an important feature of recognition. Such patterns are breadth (number of cell rows) of intercostal and costal fields or the distribution of trichoma, short cells, stomata and homogenous structure of long cells.

Distinguishing features of analysed plant species

Description and photographs of the abaxial side

Andropogon gayanus

Long cells with many small papilles (> 4) and undulating cell walls. Many papilles present in between stomata. Short cells reniform and shapeless in long rows in the costal. Many large prickle hair present in the costal. Stomata are broad and triangle shaped (Figure 17).

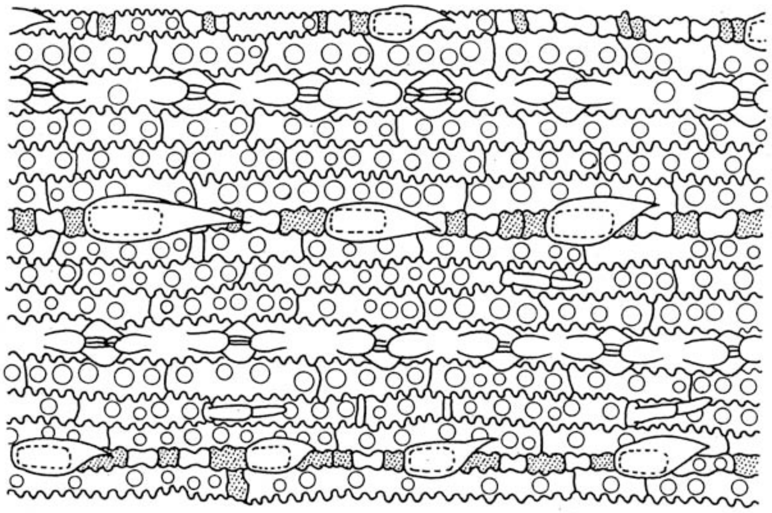

Figure 17: ***Andropogon gayanus*****, abaxial side (Barthlott & Martens 1979).**

Figure 18: ***Aristidia adscensionis,*** **abaxial side.**

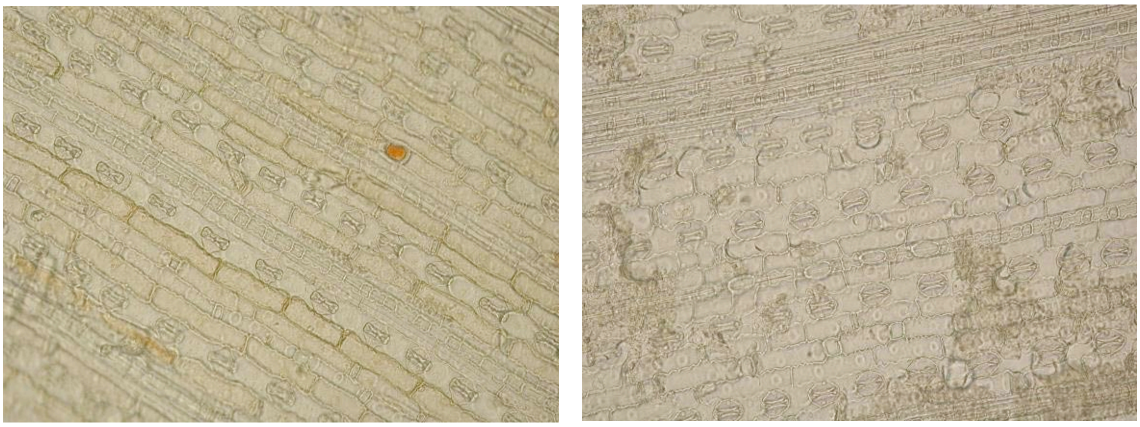

Figure 19: ***Bothrochloa bladhii*** **(left) and** ***Bothriochloa insculptum*** **(right), abaxial side.**

Aristidia adscensionis

Long cells with no papilles and undulating cell walls. Short cells dumb-bell shaped and larger than stomata. Many large prickle hairs in the costal. Stomata flat and triangle shaped (Figure 18).

Bothriochloa bladii

Long cells with many papilles (2-4) and weak undulating cell walls. Large single papille in between stomata. Short cells are dumb-bell and square shaped in long rows in costal. Single rectangular short cells present in intercostal. Stomata are broad and triangle shaped. Micro hairs are slightly longer than stomata.

Note: Papilles are only poorly visible and fill out the entire width of the long cells, therefore being larger than papilles observed by *Andropogon gayanus* and *Themeda triandra* (Figure 19).

Bothriochloa insculptum

Long cells with many papilles (2-3) and weak undulating cell walls. Large single papille in between stomata. Short cells are dumb-bell and square shaped in long rows in costal. Single rectangular short cells present in intercostal. Few hook hairs present in intercostal and micro hairs are shorter than stomata. Stomata are broad and round.

Note: Papilles are only poorly visible and fill out the entire width of the long cells, therefore being larger than papilles observed by *A. gayanus* and *T. triandra* (Figure 19).

Brachiaria leucacrantha

Long cells with no papilles and undulating cell walls. Short cells are reniform and stick shaped. Single stick shaped short cells present in intercostal. Micro hair longer than stomata, macro hair frequent. Stomata are flat slightly triangle shaped (Figure 20).

Chloris mosambicensis

Long cells with no papilles and strong undulating thick cell walls. Short cells shapeless or caterpillar shaped with big round cells followed by strong undulating short cells similar to long cells. Single stick shaped short cells present in intercostal. Large prickle hair sparsely present in costal. Stomata are round (Figure 20).

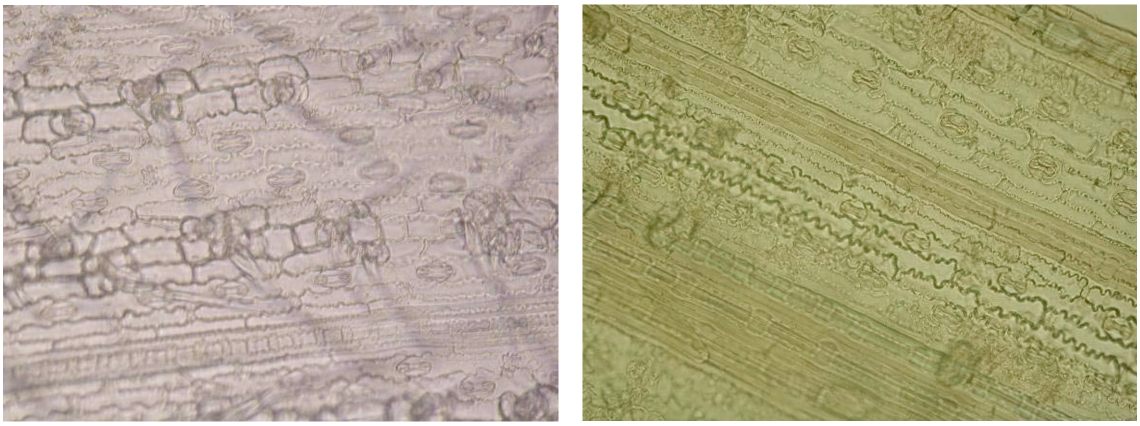

Figure 20: ***Brachiaria leucacrantha*** **(left) and** ***Chloris mosambicensis*** **(right), abaxial side.**

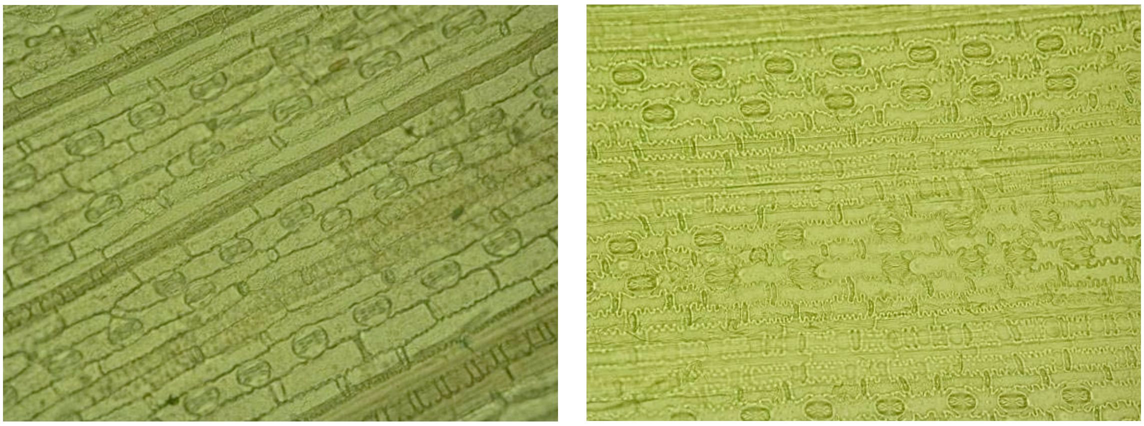

Figure 21: ***Cymbopogon caesius*** **(left) and** ***Cynodon dactylon*** **(right), abaxial side.**

Cymbopogon caesius

Long cells with no papilles and weak undulating, almost linear cell walls. Short cells are dumb-bell shaped and stick shaped. Single stick shaped short cells frequently present in intercostal. Few hook hair present. Stomata are broad and round (Figure 21).

Cynodon dactylon

Long cells with single papille in the far end and strong undulating cell walls. Short cells are caterpillar shaped with big round cells followed by strong undulating short cells similar to long cells. Single or pairwise stick shaped short cells present in intercostal between each cell, and frequently in costal. Stomata are broad and round.
Note: Papille is often not visible in every long cell (Figure 21).

Dactylothenium aegyptiacum

Long cells oval shaped, with very large single papille and weak undulating, almost linear cell walls. Characteristically, the long cells are not rectangular as they bulge out in the middle to fit the large papille, often bigger than the stomata. Large papilles also present between stomata. Short cells reniform or shapeless. Stomata are round (Figure 22).

Dactylothenium geminatum
Long cells oval shaped with single papille and linear cell walls. Large papilles also present between stomata. Short cells are shapeless. Few large prickle hair present in costal. Micro hairs are as long as stomata. Stomata are flat and round.
Note: Papilles are only poorly visible and smaller than in *D. aegyptiacum* (Figure 22).

Digitaria milanjiana
Long cells with no papilles and undulating cell walls. Short cells are reniform or shapeless. Thorne shaped hook hair frequent in intercostal and at costal-intercostal boarder. Macro hairs are frequent and micro hairs are as long as stomata. Stomata are broad and round (Figure 23).

Diheteropogon amplectens
Long cells oval shaped with no papilles and linear cell walls. Short cells are dumb-bell shaped and square shaped. Few short cells present in the intercostal in pairs with one dumb-bell shaped and one square shaped cell. Micro hairs are shorter than stomata. Stomata are flat (Figure 23).

Echinochloa haploclada
Long cells with large single papille in the centre and weak undulating cell walls. Short cells variably shaped. Macro hair present and micro hairs shorter than stomata. Sparsely large prickle hair present in costal. Stomata are more or less round (Figure 24).

Enteropogon sechellensis
Long cells with single papille in the far end and undulating cell walls. Short cells shapeless or caterpillar shaped. Many large prickle hairs in the costal. Stomata are small in relation to papilles. Short cells are broad and round (Figure 24).

Eragrostis superba
Long cells with no papilles and strong undulating cell walls. Costal consists of rows of many pairs of round and stick shaped short cells in between long cells. Single or pairwise stick shaped short cells present in intercostal between each cell. Stomata are broad and round (Figure 25).
Note: Short cells in intercostal generally shorter than breadth of long cells.

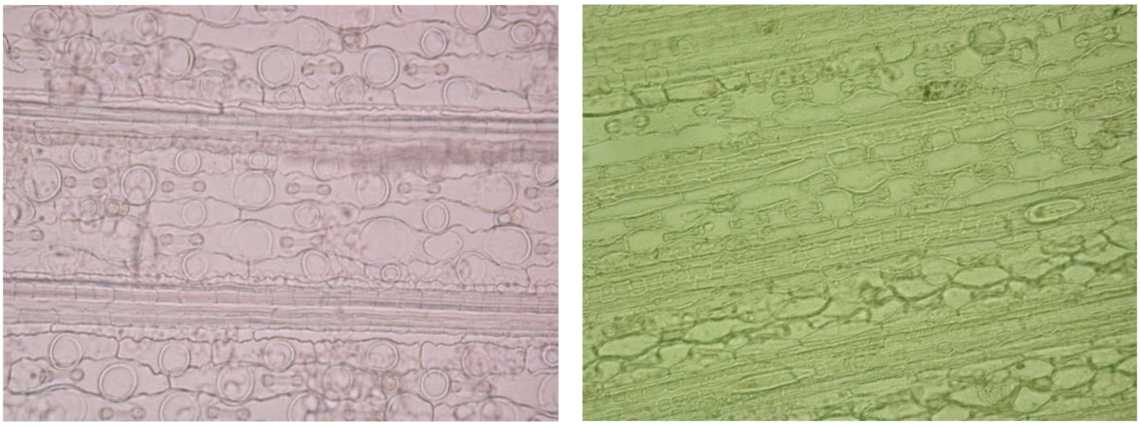

Figure 22: ***Dactylothenium aegyptiacum*** **(left) and** ***Dactylothenium geminatum*** **(right), abaxial side.**

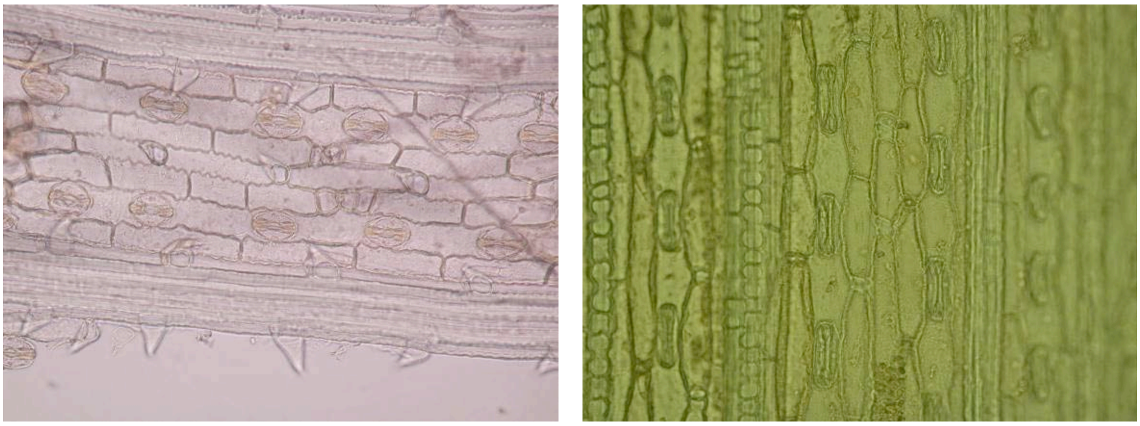

Figure 23: ***Digitaria milanjiana*** **(left) and** ***Diheteropogon amplectens*** **(right), abaxial side.**

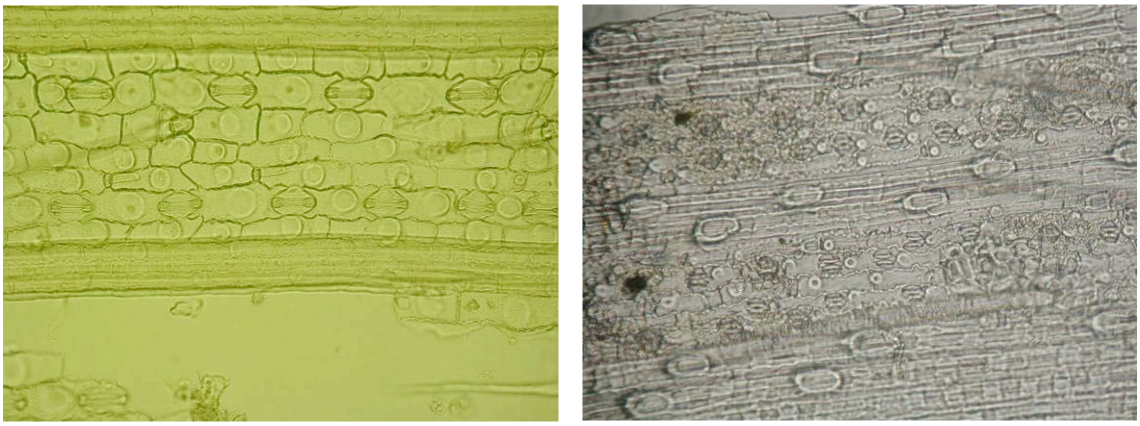

Figure 24: ***Echinochloa haploclada*** **(left) and** ***Enteropogon sechellensis*** **(right), abaxial side.**

Heteropogon contortus

Long cells with single papille in the far end and undulating cell walls. Short cells are dumb-bell shaped and square shaped. Small drop shaped hook hair present in intercostal, and micro hairs are as long as stomata. Stomata are broad and triangle shaped (Figure 25).

Hyparrhenia rufa

Long cells with no papilles and undulating cell walls. Large papilles present in between stomata. Short cells are dumb-bell and stick shaped. Dumb-bell shaped short cells in costal are as wide as stomata. Many stick shaped short cells present in the intercostal and sparsely short cells in pairs with one dumb-bell shaped and one stick shaped cell. Prickle hair as large as stomata present in costal and drop shaped hook hair present in intercostal. Micro hairs are as long as stomata. Stomata are broad and more or less triangle shaped (Figure 26).

Hyperthelia dissoluta

Long cells with no papilles and undulating cell walls. Large papilles present in between stomata. Short cells are dumb-bell and square shaped. Small drop shaped hook hair present in intercostal and micro hair longer than stomata. Stomata are flat and more or less round (Figure 26).

Panicum infestum

Long cells with no papilles and undulating cell walls. Short cells are dumb-bell shaped (often with knot in the middle) and shapeless. Drop shaped hook hair frequently present in intercostal and micro hair longer than stomata. Macro hairs are present. Stomata are broad and triangle shaped (Figure 27).

Panicum maximum

Long cells with no papilles and undulating cell walls. Short cells are dumb-bell shaped (often with knot in the middle) and shapeless. Drop shaped hook hair larger than stomata frequently present in intercostal and micro hair longer than stomata. Macro hairs are present. Stomata are broad and triangle shaped (Figure 27).

Paspalum dilatatum

Long cells with no papilles and undulating cell walls. Short cells are dumb-bell shaped and shapeless. Small drop shaped hook hair frequently present in intercostal and micro hair shorter than stomata. Stomata are more or less round and broad (Figure 28).

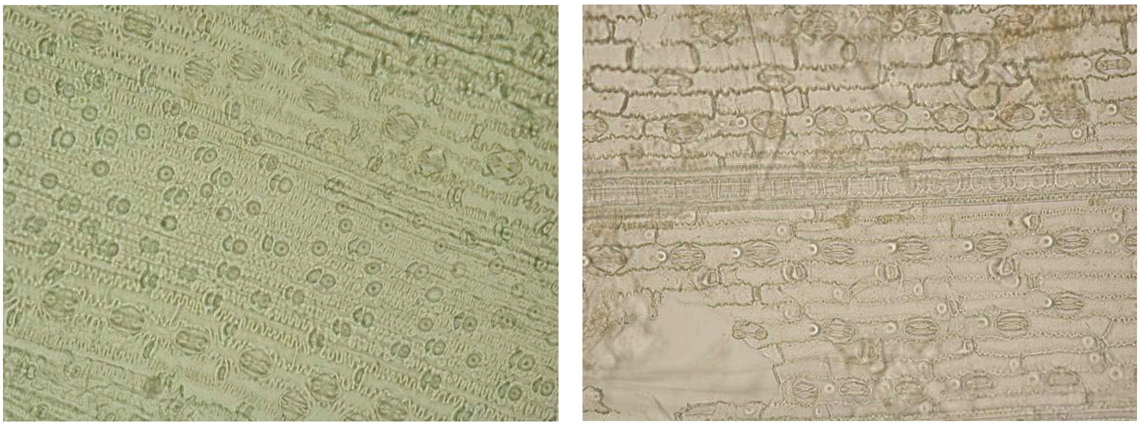

Figure 25: ***Eragrostis superba*** **(left) and** ***Heteropogon contortus*****, abaxial side.**

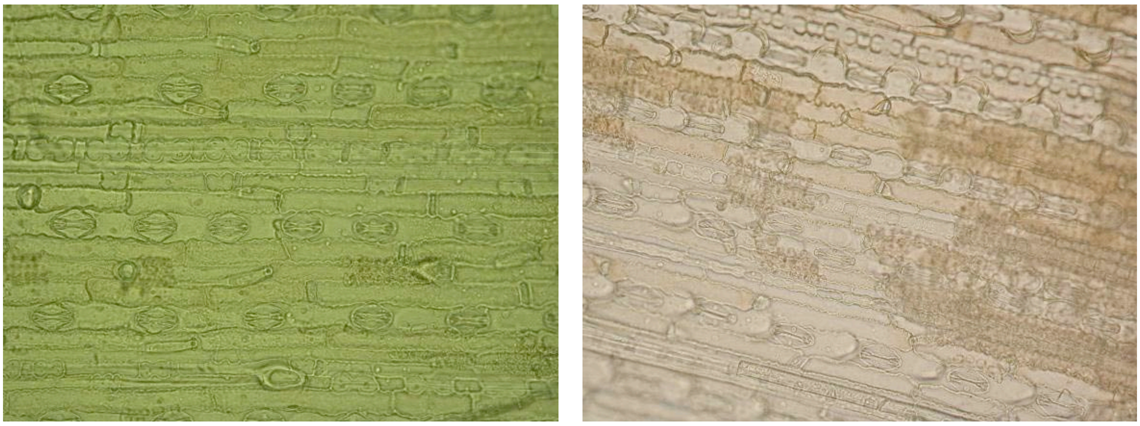

Figure 26: ***Hyparrhenia rufa*** **(left) and** ***Hyperthelia dissoluta*** **(right), abaxial side.**

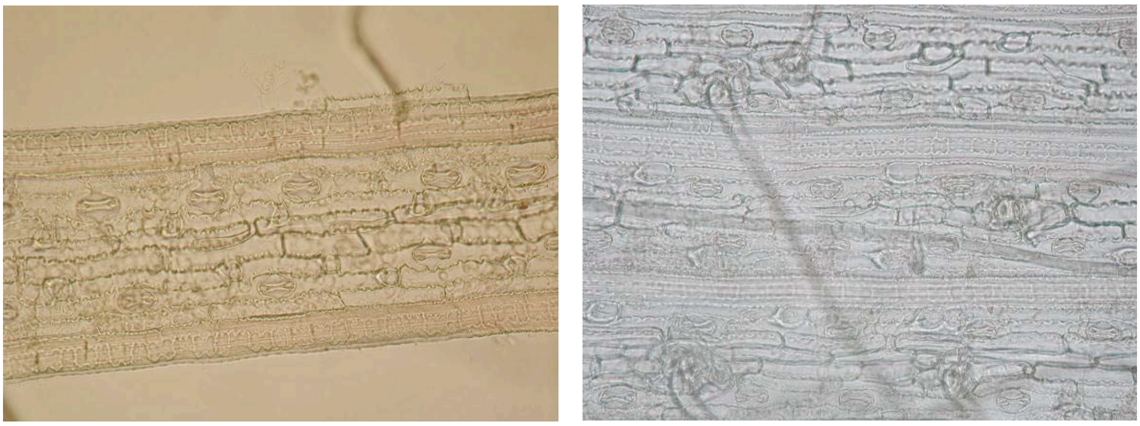

Figure 27: ***Panicum infestum*** **(left) and** ***Panicum maximum*** **(right), abaxial side.**

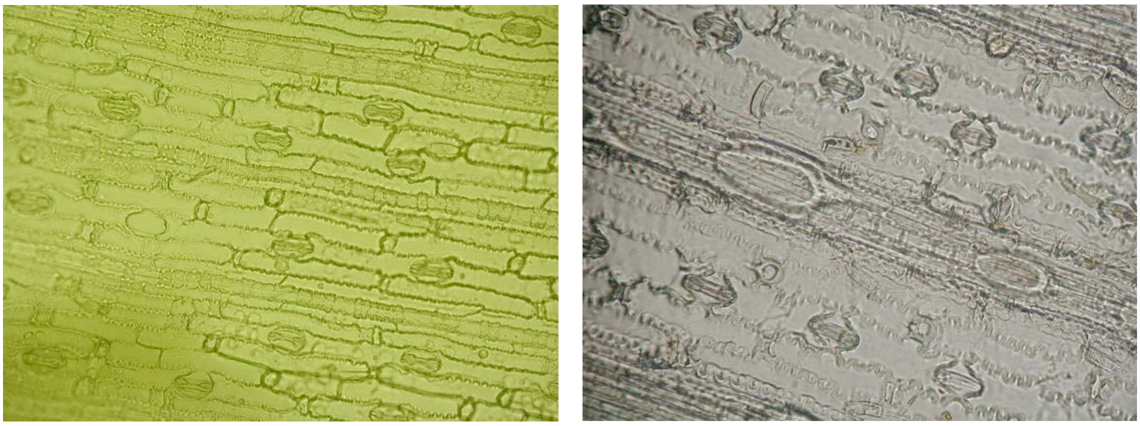

Figure 28: *Paspalum dilatatum* (left) and *Seatria incrassata* (right), abaxial side.

Setaria incrassata

Long cells with no papilles and undulating cell walls. Short cells are reniform and stick shaped. Drop shaped hook hair frequently present in intercostal and large prickle hair frequently present in costal. Micro hairs are shorter than stomata. Stomata are triangle shaped (Figure 28).

Sporobolus pyramidalis

Long cells with no papilles and linear cell walls. Costal consists of rows of many pairs of square shaped short cells in between long cells. Pairs of square shaped short cells present in intercostal. Hook hair larger than stomata present in intercostal and large prickle hair in costal. Micro hairs are shorter than stomata and poorly visible. Stomata are round (Figure 29).

Themeda triandra

Long cells with many small papilles (> 4) and undulating cell walls. Single large, or often 2-4 small papilles in between stomata. Short cells dumb-bell shaped. Drop shaped hook hair frequent in intercostal and prickle hair present in costal. Micro hairs are longer than stomata. Stomata are broad and triangle shaped (Figure 29).

Fimbristylis triflora

Long cells with no papille and undulating cell walls. No short cells or trichoma present in entire epidermis. Stomata are broad and round (Figure 30).

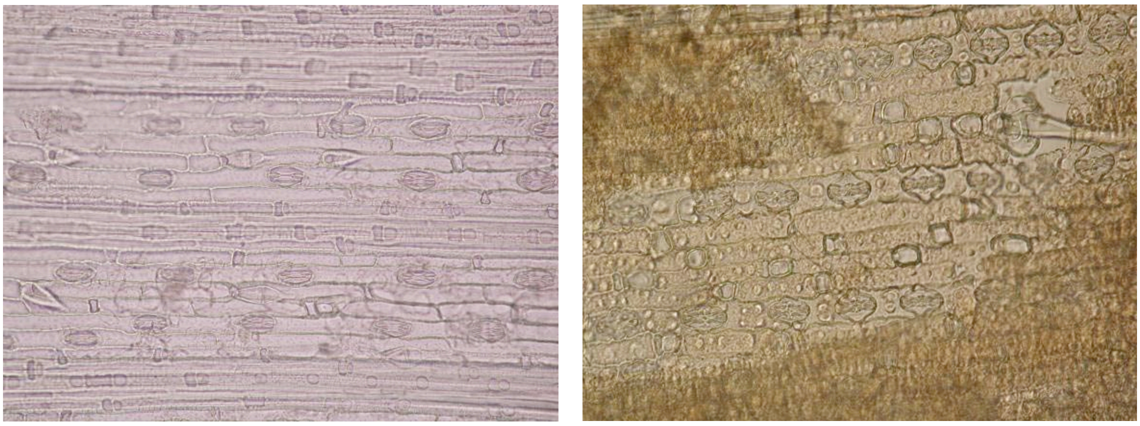

Figure 29: ***Sporobolus pyramidalis*** **(left) and** ***Themeda triandra*** **(right), abaxial side.**

Figure 30: ***Fimbristylis triflora*****, abaxial side.**

Key of determination

1. Costal short cells in long rows……………………………………………………...…**2**
– Costal short cells in small groups……………………………….***Eragrostis superba***
– or not distinguishable…………………………………………….***Fimbristylis triflora***
– Short cells often in pairs or groups, long cells not undulating ……………………….
…………………………………………………………...…***Sporobolus pyramidalis***

2. Papilles present………………………………………………………………...**3**
– Papilles not present……………………………………………………………...**14**

3. Multiple papilles in each long cell…………………………………………….……**4**
– Single papille present in each long cell………………………………...……..........**7**

Multiple papilles

4. 2-4 papilles as broad as long cell, single rectangular short cells present in intercostal ……………………………………………………………………………..**5**
– Many small papilles (> 4) in each long cell, costal prickle hair common.................**6**

5. Stomata are broad and triangle shaped. Micro hairs are slightly longer than stomata…………………......……………......................................***Bothriochloa bladhii***
–Few hook hairs present in intercostal and micro hairs are shorter than stomata. Stomata are broad and round………………………………..***Bothriochloa insculptum***

6. No intercostal hook hair……………………...……………***Andropogon gayanus***
Micro hair and intercostal hook hair present.....……………………***Themeda triandra***

Single papille

7. Single large papille only between stomata……………………………………….…**8**
– Single papille in each long cell……………………………………….…………..**9**

8. Short cells dumb-bell and stick shaped. Many stick shaped short cells in intercostal. Costal prickle hairs present, as large as stomata. Micro hairs as long as stomata, stomata triangle shaped and broad………………………………….***Hyparrhenia rufa***
– Short cells dumb-bell and square shaped. Micro hair longer than stomata, stomata round and flat……………………………………..….***Hyperthelia dissoluta***

9. Long cells oval…………………………………………...…………………..**10**

– Long cells rectangular…………………………………………………………….……..**11**

10. Very large papille, bigger than stomata, stomata round ……………………………
……………………………………….………………...….***Dactylothenium aegyptiacum***
– Papille smaller, costal prickle hair, stomata flat and round ………………………….
…………………………………………………………***Dactylothenium geminatum***

11. Stick shaped short cells very regular in between long cells, often in pairs ………...
…………………………………………………………………....***Cynodon dactylon***
– Intercostal short cells not present or not frequent……………………….……...**12**

12. Papille in centre of each long cell……………………….…***Echinochloa haploclada***
– Papille in far end of each long cell……………………………………….…………..**13**

13. Short cells dumb-bell shaped and square shaped. Hook hair present in intercostal, micro hairs as long as stomata. Stomata broad and triangle shaped …………………...
……………………………………………………………***Heteropogon contortus***
– Short cells shapeless or caterpillar shaped. Many large prickle hairs in the costal. Stomata small in relation to papilles and short cells, broad and round …..……………..
…………………………………………………………***Enteropogon sechellensis***

No papilles
14. Long cells oval, stomata flat…….….…………………***Diheteropogon amplectens***
– Long cells rectangular………………………………………………………...**15**

15. Hook hair in intercostal……………………………….…………………….....**16**
– No hook hair in intercostal…………………………………..……….………**19**

No papilles, with hook hair
16. Stomata triangle shaped……………………………………..………………...**17**
– Stomata round, micro hair shorter than stomata…………………………..…….**18**

17. Micro hair shorter than stomata. Short cells butterfly shaped, large prickle hair in costal…………………………………………………….……..***Setaria incrassata***
– Micro hair longer than stomata, hook hair broad and smaller than stomata. Short cells dumb-bell shaped……………..…………………………….…***Panicum infestum***
– Micro hair longer than stomata, hook hair broad with short tip and larger than stomata…………………………………………………….***Panicum maximum***

18. Thorne shaped hook hair, row of hook hair at costal-intercostal boarder ………….
…………………………………………………………..…..***Digitaria milanjiana***
– Drop shaped hook hair, stomata less broad...…..……………..…***Paspalum dilatatum***
– Hook hair sparse, many short cells in intercostal, long cell walls almost linear ……..
………..…………………………………………………………***Cymbopogon caesius***

No papilles, no hook hair
19. Short cells caterpillar shaped, long cells with thick cell walls, square shaped short cells in intercostal…………………………………………...***Chloris mosambicensis***
– Short cells dumb-bell shaped or reniform……………..……………………….…..**20**

20. Short cells dumb-bell shaped, longer than stomata. Many large prickle hair in costal……………………………………….…………….…...***Aristidia adscensionis***
Short cells reniform, single stick shaped short cells present in intercostal. Micro hair longer than stomata………………………………………***Brachiaria leucacrantha***

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Appendix B: Data

Contents

Table 15: Overview of the diet composition of reedbuck in Mkwaja North in both seasons.

Legend (Table 15 – Table 19)

Sample % fragment area	Percent value of each plant species for each sample (Smpl1-Smpl6) based on the epidermal fragment area
Mean, Error	Average of plant species found in dung of all samples (Smpl1-Smpl6), with standard error
fragment area sum	Sum of all fragment areas of one plant species found in dung of all samples (mm^2)
fragment area %	Percent value of plant species based on the sum of fragment areas found in all dung samples combined
Total no.	Total number of fragments of plant species found in dung, sum of all dung samples
% no. fragm.	Percent value of plant species based on the sum of number of fragments found in all dung samples

Reedbuck MN

EARLY DRY SEASON

Sample % fragment area

	Smpl1	Smpl2	Smpl3	Smpl4	Smpl5	Smpl6	Mean	Error	fragment area sum	fragment area %	Total no.	% no. fragm.
Andropogon/Themeda	0	2	0	9	11	1	3.7	2.0	10	4	33	6
Chloris mosambicensis	0	0	0	0	0	0.6	0.1	0.1	0.3	0.1	1	0.2
Cymbopogon caesius	0	0	1	0	0	0	0.2	0.2	0.6	0.2	2	0.3
Dactylothenium sp.	0	0	4	0	0	0	0.7	0.7	2	0.7	6	1
Digitaria milanjiana	0	0	0	4	0	0	0.7	0.7	2	0.7	1	0.2
Echinochloa haploclada	0	0	0	0.5	0	0	0.1	0.1	0.3	0.1	1	0.2
Eragrostis superba	19	2	1	0	0	32	9.0	5.5	24	9	62	10
Heteropogon contortus	10	1	0	1	0	2	2.2	1.6	7	2	18	3
Heteropogon undetermined	0	0	0	0	0	0	0	0	0	0	0	0
Panicum infestum	60	72	0	62	65	47	51	11	138	52	258	43
Panicum undetermined	9	22	2	20	17	12	14	3.0	37	14	103	17
undetermined monocot	2	1	9	5	7	5	4.8	1.3	12	5	43	7
dicot	0	1	82	0	0	0	14	14	36	13	72	12
unidentified	0	0	0	0	0	0	0	0	0	0	0	0

EARLY DRY SEASON

Sample % fragment area

	Smpl1	Smpl2	Smpl3	Smpl4	Smpl5	Smpl6	Mean	Error	fragment area sum	fragment area %	Total no.	% no. fragm.
Cymbopogon caesius	0.5	0	0.9	0	0	0	0.2	0.2	1	0.3	2	0.3
Cynodon dactylon	0	0	11	0	0	0	1.8	1.8	9	3	11	2
Eragrostis superba	0	2	0	0	0	0	0.3	0.3	0.8	0.2	2	0.3
Heteropogon contortus	0.8	1	58	0	0	0	10	9.7	50	15	55	9
Heteropogon undetermined	0	1	9	0	0	0	1.7	1.5	8	2	14	2
Panicum infestum	2	2	0.9	0	4	0	1.3	0.6	4	1	5	0.8
Panicum undetermined	0	10	0	0	3	0	2.3	1.7	6	2	8	1
undetermined monocot	22	14	20	8	9	8	14	2.6	47	14	80	13
dicot	72	56	0	82	75	89	62	13	195	58	383	64
unidentified	3	15	0	10	8	3	6.5	2.2	18	5	40	7

Table 16: Overview of the diet composition of waterbuck in Mkwaja North in both seasons.

Waterbuck MN

EARLY DRY SEASON

	Sample % fragment area											
	Smpl1	Smpl2	Smpl3	Smpl4	Smpl5	Smpl6	Mean	Error	fragment area sum	fragment area %	Total no.	% no. fragm.
Andropogon/Themeda	4	6	28	0	7	2	7.7	4.2	22	8	52	9
Bothriochloa sp.	0	0	0	0	2	0	0.3	0.3	0.8	0.3	1	0.2
Cymbopogon caesius	0	4	1	6	1	0	2.1	1.1	6	2	11	2
Cynodon dactylon	7	0	4	0	0	0	1.8	1.2	5	2	14	2
Dactylothenium sp.	11	7	11	0	0	0	4.9	2.2	14	5	13	2
Digitaria milanjiana	0	0	0	0.8	0	0	0.1	0.1	0.4	0.1	1	0.2
Diheteropogon amplectens	0	0.9	0	0	0	3	0.6	0.4	2	0.6	2	0.3
Echinochloa haploclada	0.5	0	0	3	0	0	0.6	0.5	2	0.5	4	0.7
Enteropogon sechellensis	8	12	2	2	0	0	3.9	2.0	10	4	22	4
Eragrostis superba	15	1	3	0.6	0	0.5	3.5	2.4	10	4	18	3
Heteropogon contortus	0	3	2	7	1	5	2.8	1.0	8	3	14	2
Heteropogon undetermined	0	0.6	0	0.6	0.5	0	0.3	0.1	0.8	0.3	3	0.5
Panicum infestum	21	35	24	42	64	64	42	7.8	118	42	213	36
Panicum undetermined	6	11	8	16	15	16	12	1.7	34	12	99	17
Paspalum dilatatum	0	0	0	2	2	3	1.2	0.6	4	1	5	0.8
Setaria incrassata	0	0	2	0	0	0	0.3	0.3	0.8	0.3	2	0.3
dicot	0	4	2	3	1	0	1.6	0.7	4	2	11	2
undetermined monocot	28	15	13	16	7	7	14	3.2	41	14	115	19
unidentified	0	0	0	0	0	0	0	0	0	0	0	0

LATE DRY SEASON

	Sample % fragment area											
	Smpl1	Smpl2	Smpl3	Smpl4	Smpl5	Smpl6	Mean	Error	fragment area sum	fragment area %	Total no.	% no. fragm.
Andropogon/Themeda	0.7	1	15	0.9	0	2	3.2	2.3	12	3	17	3
Bothriochloa sp.	0.7	0	1	0	0.4	0	0.4	0.2	2	0.4	4	0.7
Cymbopogon caesius	0	4	0	0	6	2	1.9	1.0	8	2	7	1
Cynodon dactylon	0	0	0	2	11	3	2.7	1.7	14	3	13	2
Digitaria milanjiana	0	0	0	1	1	0	0.4	0.2	2	0.5	3	0.5
Diheteropogon amplectens	0	0	0	0	2	0	0.3	0.3	2	0.4	1	0.2
Eragrostis superba	0	0	0	6	0	0	1.1	1.1	5	1	5	0.8
Heteropogon contortus	34	63	38	36	13	43	38	6.6	144	35	237	40
Heteropogon undetermined	6	3	19	6	3	5	7.0	2.5	28	7	52	9
Panicum infestum	10	16	2	2	6	1	6.2	2.4	23	6	20	3
Panicum maximum	9	0	0	0.4	5	0	2.3	1.5	11	3	12	2
Panicum undetermined	0	9	5	0	0	0	2.3	1.6	7	2	11	2
Paspalum dilatatum	0.9	0	0	0	0	1	0.3	0.2	1	0.3	2	0.3
Setaria incrassata	0.3	0	0	0	0	0	0.1	0.1	0.3	0.1	1	0.2
dicot	0	0	1	0	0	0.6	0.3	0.2	1	0.3	3	0.5
undetermined monocot	39	5	17	45	53	43	33	7.6	154	37	207	35
unidentified	0.1	0	2	0	1	0	0.5	0.3	2	0.6	5	0.8

Table 17: Overview of the diet composition of reedbuck in Saadani North in both seasons.

Reedbuck SN

EARLY DRY SEASON

	Sample % fragment area											
	Smpl1	Smpl2	Smpl3	Smpl4	Smpl5	Smpl6	Mean	Error	fragment area sum	fragment area %	Total no.	% no. fragm.
Andropogon/Themeda	2	0	2	0	0	0	0.6	0.4	2	0.9	6	1
Bothriochloa sp.	0	0.5	0.6	0	0	0.5	0.3	0.1	0.8	0.3	3	0.5
Chloris mosambicensis	0	0.5	8	0	0	5	2.3	1.4	6	2	13	2
Cymbopogon caesius	0	0	0	0	0	0.5	0.1	0.1	0.3	0.1	1	0.2
Dactylothenium sp.	0	4	0	0	0	2	1.0	0.7	3	1	4	0.7
Digitaria milanjiana	0	0	0	0	0	0.8	0.1	0.1	0.4	0.1	1	0.2
Enteropogon sechellensis	0	0	0.6	0	0	4	0.8	0.7	2	0.9	7	1
Eragrostis superba	1	25	15	0	16	6	10	4.0	29	10	54	9
Heteropogon contortus	0	0	2	0	6	3	1.9	1.0	5	2	14	2
Heteropogon undetermined	0	0.5	1	0	0	0	0.2	0.2	0.6	0.2	3	0.5
Panicum infestum	38	23	19	6	53	28	28	6.6	80	29	130	22
Panicum undetermined	35	22	19	0	20	18	19	4.6	55	20	123	21
Setaria incrassata	1	3	0	0	0	7	1.8	1.1	5	2	7	1
undetermined monocot	24	21	29	13	6	24	19	3.5	53	19	143	24
dicot	0	0	3	78	0	2	14	13	33	12	85	14
unidentified	0	0	0.6	4	0	0	0.7	0.6	2	0.6	6	1

LATE DRY SEASON

	Sample % fragment area											
	Smpl1	Smpl2	Smpl3	Smpl4	Smpl5	Smpl6	Mean	Error	fragment area sum	fragment area %	Total no.	% no. fragm.
Andropogon/Themeda	0	0	1	0	0.7	25	4.4	4.1	9	4	30	5
Bothriochloa sp.	0	0	0.5	0	0	0	0.1	0.1	0.3	0.1	1	0.2
Chloris mosambicensis	0	0	0	0	0.7	0	0.1	0.1	0.3	0.1	1	0.2
Cymbopogon caesius	4	5	2	0	0.7	1	1.9	0.7	5	2	12	2
Dactylothenium sp.	4	0	1	0	0	0.8	1.0	0.6	2	0.9	6	1
Enteropogon sechellensis	0	1	0	0	0.7	0	0.2	0.1	0.5	0.2	2	0.3
Eragrostis superba	0	3	9	0	24	0	6.1	3.9	14	6	35	6
Heteropogon contortus	3	40	30	0	21	0	15	7.0	40	16	99	17
Heteropogon undetermined	1.0	0.6	2	0	0.7	0.8	0.9	0.3	2	0.9	7	1
Hyperthelia dissoluta	0	0	0	0	1	0	0.2	0.2	0.5	0.2	1	0.2
Panicum infestum	6	37	18	0	14	43	20	7.0	46	19	89	15
Panicum undetermined	19	7	6	1	8	16	9.6	2.7	22	9	63	11
Setaria incrassata	0.6	0	0	0	0	0	0.1	0.1	0.3	0.1	1	0.2
undetermined monocot	63	6	30	16	13	13	23	8.6	57	23	141	24
dicot	0	2	0	75	16	0	15	12	42	17	99	17
unidentified	0.3	0.6	0.5	8	0	0	1.6	1.4	5	2	13	2

Table 18: Overview of the diet composition of waterbuck in Saadani North in both seasons.

Waterbuck SN

EARLY DRY SEASON

	Sample % fragment area											
	Smpl1	Smpl2	Smpl3	Smpl4	Smpl5	Smpl6	Mean	Error	fragment area sum	fragment area %	Total no.	% no. fragm.
Andropogon/Themeda	0.5	10	0.6	5	0	0	2.7	1.7	7	3	24	4
Bothriochloa sp.	2	0	0	1	0	0	0.5	0.3	1	0.5	3	0.5
Chloris mosambicensis	7	4	0	11	2	0	3.9	1.7	10	4	21	4
Cymbopogon caesius	0	0	0	3	2	0	0.9	0.6	2	0.8	8	1
Digitaria milanjiana	0	0.5	0	0	0.7	0	0.2	0.1	0.5	0.2	2	0.3
Echinochloa haploclada	0	0	0	0	0	2	0.3	0.3	0.8	0.3	2	0.3
Eragrostis superba	6	9	51	7	6	0	13	7.6	34	13	84	14
Heteropogon contortus	13	0	0.6	1	2	0	2.8	2.1	8	3	16	3
Heteropogon undetermined	5	0	0	0.9	0	0.6	1.1	0.8	3	1.11	11	2
Hyparrhenia rufa	0.5	0	0	0	0	0	0.1	0.1	0.3	0.1	1	0.2
Panicum infestum	4	8	37	36	43	56	31	8.3	78	30	155	26
Panicum undetermined	14	9	8	12	18	14	13	1.5	33	13	87	15
Setaria incrassata	2	0	0	0	4	12	2.9	1.9	7	3	9	2
undetermined monocot	45	55	3	22	23	16	28	7.8	73	28	172	29
dicot	0.5	3	0	0.6	0	0	0.6	0.4	2	0.7	4	0.7
unidentified	0	0.5	0	0	0	0	0.1	0.1	0.3	0.1	1	0.2

LATE DRY SEASON

	Sample % fragment area											
	Smpl1	Smpl2	Smpl3	Smpl4	Smpl5	Smpl6	Mean	Error	fragment area sum	fragment area %	Total no.	% no. fragm.
Andropogon/Themeda	0	0.3	2	0.6	0	0	0.5	0.4	2	0.5	6	1
Bothriochloa sp.	5	0.7	0	0	0	0	0.9	0.8	3	0.9	5	0.8
Brachiaria leucacrantha	0	0	0	0	0	0.7	0.1	0.1	0.5	0.2	1	0.2
Cymbopogon caesius	0.5	0	2	4	0	0	1.0	0.6	3	0.8	5	0.8
Enteropogon sechellensis	0	1	0	0	0	0	0.2	0.2	1	0.3	1	0.2
Eragrostis superba	6	0	4	6	0	0	2.6	1.2	7	3	12	3
Heteropogon contortus	35	20	23	51	19	38	31	5.1	97	30	198	33
Heteropogon undetermined	15	3	12	3	4	14	8.4	2.4	27	8	61	10
Panicum infestum	13	22	5	12	22	7	13	3.0	45	14	49	8
Panicum undetermined	6	17	7	11	21	7	11	2.6	38	12	66	11
undetermined monocot	20	35	31	14	32	33	27	3.5	92	29	176	29
dicot	0	1	8	0	0	0	1.5	1.3	4	1	12	2
unidentified	1	0	5	0	0.7	0	1.2	0.9	3	1	8	1

Table 19: Overview of the diet composition of wildebeest in Saadani North in both seasons.

Wildebeest SN

EARLY DRY SEASON

	Sample % fragment area											
	Smpl1	Smpl2	Smpl3	Smpl4	Smpl5	Smpl6	Mean	Error	fragment area sum	fragment area %	Total no.	% no. fragm.
Andropogon/Themeda	9	0	18	2	0	0	4.8	3.0	11	4	42	7
Chloris mosambicensis	10	0	9	9	6	0	5.6	1.9	14	5	28	5
Cymbopogon caesius	0	0	2	0	0.5	0	0.3	0.3	0.8	0.3	3	0.5
Dactylothenium sp.	0	2	0	0	0.8	0	0.4	0.3	1	0.4	3	0.5
Digitaria milanjiana	0	0	0	0	0	0.5	0.1	0.1	0.3	0.1	1	0.2
Eragrostis superba	10	13	3	1.0	2	15	7.4	2.5	21	8	38	6
Heteropogon contortus	0.6	1	9	0.5	2	0	2.2	1.4	5	2	14	2
Heteropogon undetermined	0.6	0.8	0.8	1.0	0	0	0.5	0.2	1	0.5	5	0.8
Panicum infestum	20	26	8	22	30	25	22	3.2	63	23	87	15
Panicum undetermined	12	36	16	22	28	19	22	3.5	62	23	122	20
Setaria incrassata	0	0	5	4	4	2	2.6	0.9	7	2	15	3
undetermined monocot	37	21	30	38	27	36	31	2.7	87	32	235	39
dicot	1	0	0	0	0	1	0.4	0.3	1	0.5	5	0.8
unidentified	0	0.5	0	0	0	0.5	0.2	0.1	0.5	0.2	2	0.3

LATE DRY SEASON

	Sample % fragment area											
	Smpl1	Smpl2	Smpl3	Smpl4	Smpl5	Smpl6	Mean	Error	fragment area sum	fragment area %	Total no.	% no. fragm.
Andropogon/Themeda	0	0	3	3	0	0	1.0	0.6	4	1.0	4	0.7
Bothriochloa sp.	1	0	1	0	0	3	0.9	0.4	4	1	5	0.8
Chloris mosambicensis	0	0.8	9	2	0.9	0	2.1	1.4	9	2	16	3
Cymbopogon caesius	5	3	0	8	3	0.4	3.2	1.2	11	3	10	2
Dactylothenium sp.	1	5	0	2	0	0.7	1.5	0.8	5	1	6	1
Eragrostis superba	3	11	0	14	3	5	5.8	2.2	18	5	38	6
Heteropogon contortus	10	52	18	23	11	31	24	6.4	84	23	167	28
Heteropogon undetermined	5	3	3	1	1	6	3.4	0.8	13	4	28	5
Hyperthelia dissoluta	0.6	0	0	0	0	0	0.1	0.1	0.5	0.1	1	0.2
Panicum infestum	9	12	0	6	30	8	11	4.2	36	10	39	7
Panicum undetermined	6	5	0	9	20	12	8.6	2.7	29	8	55	9
Setaria incrassata	6	0	0	0	0.9	0	1.2	1.0	5	1	5	0.8
undetermined monocot	54	9	66	31	29	32	37	8.2	148	40	217	36
dicot	0	0.3	0	0	1	1	0.5	0.3	2	0.4	5	0.8
unidentified	0	0	0.6	0.6	0	0.6	0.3	0.1	1	0.3	4	0.7

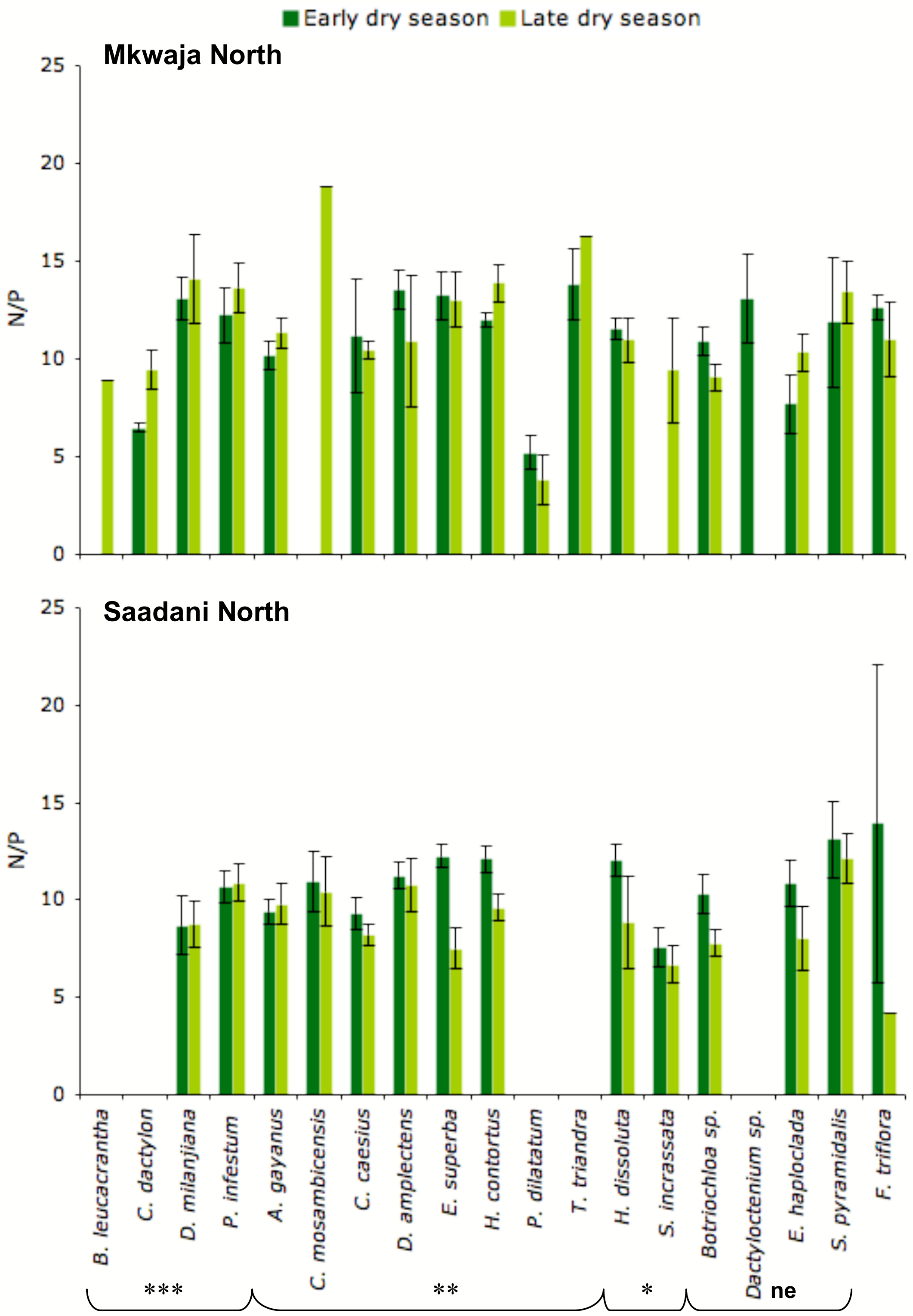

Figure 31: The N/P-ratio in young leaves of plant species in Mkwaja North and Saadani North. Values presented for early dry and late dry season, with standard error. Data from late dry season are preliminary results from Halsdorf. Plant species are sorted according to preference for plant species observed by cattle in Mkwaja North (Kozak 1983): *** = high preference, ** = preference, * = low preference, ne = not eaten.