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Diet selection of Nguni goats in relation to season, chemistry and physical properties of browse in sub-humid subtropical savanna

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A B S T R A C T

This study was conducted to determine the influence of plant chemical, physical and phenology properties on diet selection of Nguni goats during the dry, early wet and late wet seasons in savanna in South Africa. Diet composition was estimated by direct observation of two different adult Nguni goats randomly selected from a herd each day for 7–8 days in each season. Observations were made during active foraging periods for 2 h in the morning and 1.5 h in the afternoon. The duration of each feeding bout and the species of woody plant from which bites were cropped at each feeding station were recorded. Diet selection was determined from the relative duration of feeding. Diet preference of each species was expressed as an index calculated using the selection and relative abundance of woody species. Browse species consumed by goats were sampled and analysed to determine crude protein, neutral detergent fibre, acid detergent fibre, acid detergent lignin, condensed tannins, cellulose and hemicellulose. Diet selection varied among the three seasons. The five species most selected (utilised) by goats were *Scutia myrtina*, *Acacia nilotica*, *Dichrostachys cinerea*, *Acacia natalitia* and *Chromolaena odorata*. *S. myrtina* was the most selected species during the dry season while *D. cinerea* was the most selected in the wet seasons. *S. myrtina* was the most preferred (highest utilisation relative to availability) in the dry and early wet seasons while *A. nilotica* was most preferred in the late wet season. Spinescent species were generally selected more than non-spinescent species in all seasons, while fine-leaf and deciduous species were selected more than broad-leaf and evergreen ones in the wet seasons. However, preference for broad-leaf and evergreen species increased in the early wet season. Although plant chemistry varied across seasons, it did not explain the preference of goats for various plant species in this study. Instead, effects of chemistry were species-specific. In conclusion, this study demonstrates the importance of evergreen browse species as a source of fodder when deciduous species are unavailable.

1. Introduction

Savannas occupy 65% of the total area of Africa, 60% of sub-Sahara Africa (Scholes and Archer, 1997) and 54% of KwaZulu-Natal province in South Africa (Breebaart et al., 2002). Savanna browse adds significantly to the total forage of livestock and wildlife in Africa (Bergström, 1992). Therefore, the savanna is important to support human populations in Africa through supporting livestock production (Scholes and Archer, 1997). A key to improving the management of savannas is the development of sound understanding of diet selection. Diet selection describes the decisions animals make with regard to the plant

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material (plant parts, plant species and patches) they choose (Newman et al., 1995; Morrison et al., 2002). However, the patterns of diet selection are not regular in space or time, which may be due to changes in forage availability (Edenius et al., 2002). Additionally, differences in chemical and physical defence influence the diet selection by herbivores (Illius et al., 1999; Dziba et al., 2003).

Chemicals such as tannins are assumed to function as defences against herbivores (Bergström, 1992). Besides changing the taste of feed, the negative feedback of tannins causes rumen microbial inhibition and decreased digestibility and animal performance (Silanikove et al., 2001; Min et al., 2003), but is advantageous in goats in dealing with tannin diet and that tolerate them without exhibiting toxic syndrome (Silanikove et al., 1996; Landau et al., 2000; Silanikove, 2000). However, tannins are not totally avoided by goats but are tolerated at a certain minimum level (Jansen et al., 2007). It has been suggested that the minimum level of tannin for ruminants to tolerate in forages is 55 g/kg DM (Min et al., 2003), but if this amount is exceeded and free tannins reach the rumen, tannins can form indigestible complexes with bacterial enzymes (Priolo et al., 2000), or cellulose and hemicelluloses (Haslam, 1989). Thus, tannins can protect plant cell walls against rumen organisms and reduce animal performance (Jachman, 1989; Priolo et al., 2000). In spite of negative effects, tannins may have positive effects on ruminants, such as increased nitrogen retention when protein–tannin complexes dissociate in the post-rumen (Nsahlai et al., 1998). This may provide additional amino acids and prevent excessive degradation of high-quality leaf protein in the rumen (Mehansho et al., 1987; Min et al., 2003).

Ruminants need sufficient dietary fibre for standard rumen functions by maintaining enough saliva and optimal pH (Church, 1988). Fibre has a significant role in goats because it limits intake and maintains normal fermentation in the rumen (Lu et al., 2005; Ndlovu and Nherera, 1997). Minimizing acid detergent fibre is a way to explain preferences in the case of *Acacia* species (Jansen et al., 2007), while lignin reduces the digestibility of browse (Moore and Jung, 2001).

In addition to plant fibre, diet selection in mammalian herbivores can be influenced by physical plant factors. Spines, thorns and other physical traits may limit leaf accessibility and intake rates resulting in lower preference of species that have these traits (Shipley et al., 1998; Dziba et al., 2003; Wilson and Kerley, 2003b).

Because savannas are seasonal environments, the challenge is to understand the relationships between chemical or physical factors and diet selection by goats at different time of the year. The objectives of this study were (i) to explore the diet selection of goats foraging in different seasons in a sub-humid subtropical savanna, and (ii) to investigate the possible relationships between diet selection and various physical, chemical and phenological features, such as condensed tannins, crude protein, fibre fractions, spinescence, leaf type and deciduousness. To achieve these objectives, we tested the following hypotheses. Firstly, seasonal variations in availability and quality of forage in sub-humid subtropical savanna may alter diet selection (Abate, 1996). Second, inherent differences in leaf chemistry among different plant species could affect diet selection (Scogings et al., 2004). Thirdly, variations of different plant species in leaf morphology (Shipley et al., 1998; Dziba et al., 2003; Wilson and Kerley, 2003a), spinescence (Cooper and Owen-Smith, 1986) and leaf phenology (Shipley et al., 1998; Watson and Owen-Smith, 2002) might influence diet selection.

2. Materials and methods

2.1. Study area

The study was conducted at the Owen Sitole College of Agriculture (OSCA) in northern KwaZulu-Natal, South Africa. OSCA is placed within the Zululand Coastal Thornveld (Mucina and Rutherford, 2006) and is located at 28°57′45″–28°57′22″S latitude and 31°55′31″–31°57′22″E longitude (Van der Linden et al., 2005). The mean annual rainfall of OSCA is 995 mm, with 75% of it falling in the wet season (October–April). The experimental paddocks (2–2.5 ha each) were fenced and a pen was erected in one corner of each paddock to keep the animals at night. Confining livestock in enclosures at night is commonly practiced in the area to prevent theft and predation. Ad lib water was provided in a trough. Fieldwork was carried out during the dry season (late June/early July, 2008), early wet season (late November/early December, 2008) and late wet season (late February/early March, 2009).

2.2. The relative abundance of woody species

For estimating the relative abundance of woody species, the vegetation was recorded by means of 2-m wide belt transects oriented north–south. Each transect started and ended 10 m from the edges of the paddocks. Impenetrable thickets of *Chromolaena odorata* were avoided. Because each paddock was not quadrangular, transect lengths varied between 20 and 120 m, but ultimately 5% of each paddock area was sampled. In each transect, the height (cm) of each woody plant was measured and identified to species level (according to Coates Palgrave, 2002). When there was no foliage below 1.5 m the plant was recorded as unbrowseable. The data from all transects in a paddock were used to calculate the relative abundance of each species, which was calculated as the total number of browseable plants of each species divided by the total number of browseable plants of all species.

2.3. Species samples and chemicals analysis

Browse species and grass which were accepted by goats were sampled. Species that were avoided by goats were not sampled because the study focused only on species utilized by goats during the three seasons of the study. Browse samples were taken from three unbrowsed trees (below 1.5 m above ground) per species and grasses were cut from three different ungrazed areas. Plant samples were collected in the last 2 days of each period, kept in paper bags and air dried prior to oven drying at 60 °C for 48 h. Samples were ground through 1 mm mesh and analysed for chemical composition on a dry matter basis. Crude protein (CP) was calculated using nitrogen concentration which was determined by AOAC method 990.03 (AOAC, 1997) using a LECO, FP2000, nitrogen analyzer. Nitrogen was converted to CP using 6.25 as a conversion factor. Neutral detergent fibre (NDF), acid detergent fibre (ADF) and acid detergent lignin (ADL) were determined according to Van Soest et al. (1991) using the ANKOM Technology Technique. Cellulose was calculated as the difference between ADF and ADL, while hemicellulose was derived from the difference between NDF and ADF. The acid-butanol proanthocyanidin assay (Porter et al., 1986) was used to determine condensed tannins (CT) (Makkar, 1995).

2.4. Diet selection and selection index

Previous browsing influence on chemical traits (protein and tannin) for the main species (*Scutia myrtina*, *Acacia nilotica*, *Dichrostachys cinerea*, *Acacia natalitia*) was tested because one paddock was used twice. Samples from ten trees per species per area were sampled and analysed for protein and condensed tannin. Control samples were taken from an area that was not previously browsed. Previous browsing did not influence the protein (t = 0.46, df = 118, P = 0.32) and tannin contents (t = −1.34, df = 118, P = 0.092) compared to unbrowsed species. Diet selection was estimated over seven or eight consecutive days during each season by direct observation of goats while feeding. Observations were made between 08:30 and 10:30 and from 12:00 onwards until observations had been collected for at least 1.5 h. Each day, two different goats were randomly selected from a herd of 22–24 castrated males that were 3 years old and weighed 45.8 kg (SEM: 0.78). The two selected goats were allowed to forage with the others and each goat was continuously observed from a distance of about 5 m by two people, with minimal disturbance. The flock was herded to a new, randomly selected part of the paddock at the start of each day so that depletion of forage would not be a factor in diet selection. The size of the paddock was big enough to allow us to do this. Feeding bouts were defined as any event 5 s long or longer that the animal spent biting material from a plant. Events of biting that were less than 5 s were ignored. The duration of each feeding bout and the species of woody plant from which bites were cropped were recorded. Grazing bouts were simply recorded as grazing (without identifying grass species). When a focal animal was lost from view for 5 s or more, the period of time for which it was not visible was recorded. The diet selection index (SI) of each species which was eaten by goats was calculated. Species on which goats spent very little time were summed together as "other browse" species (OB). Diet selection was estimated according to relative duration (total time spent on a species/total time spent on all species) rather than frequencies of bouts due to large variation among bout durations. Selection index was calculated according to Ivlev's forage ratio (E_i) using the relative abundance of the species in the diet divided by the relative abundance of the species in the available vegetation, because this method is simple, yet does not produce results different to more complex methods (Tanentzap et al., 2009). Selection index values above 1.0 indicate preference while values less than 1.0 indicate avoidance. Potential seasonal variations in feed availability were assumed to be negligible because of the humid climate of the study area.

2.5. Statistical analysis

Analysis of variance was used to test effects of season and plant species on diet selection and selection index, and separation of means was done using the probability of difference (SAS, 2002). Correlation was used to test the relationships between selection index and chemical variables. The effects of spinescence (spines vs. no spines), leaf type (broad vs. fine), or phenology (evergreen vs. deciduous), or combinations thereof on selection index, were analysed using t-tests. Goats were regarded as replicates. Significant effects were stated at the probability level of P < 0.05.

3. Results

3.1. Diet selection

Goats spent 28%, 38% and 22% of their time grazing during the dry, early wet and late wet seasons, respectively. Goats selected the following species in the three seasons: *S. myrtina*, *A. nilotica*, *D. cinerea*, *A. natalitia* and *C. odorata* (Table 1). The selection of plant species depended on the season of observation ($F_{17, 396}$ = 7.11, P < 0.001). In the dry season, *S. myrtina* was the most selected, followed by *C. odorata*, *A. natalitia*, *D. cinerea* and *A. nilotica*. During the early wet season *D. cinerea* was most selected, followed by *A. natalitia*, *S. myrtina*, *C. odorata* and *A. nilotica*, while in the late wet season, *D. cinerea* was most selected followed by *A. nilotica*, *S. myrtina*, *A. natalitia* and *C. odorata*.

The species included in the diet covered a range of physical traits or phenology (Table 2). Spinescent species were selected more than spineless species (t = −9.20, df = 271, P < 0.001), while fine-leaf species were selected more than broad-leaf species (t = −4.66, df = 301, P < 0.001) (Fig. 1). Furthermore, deciduous species were selected more than evergreen species (t = 3.79, df = 294, P < 0.001) (Fig. 1). When

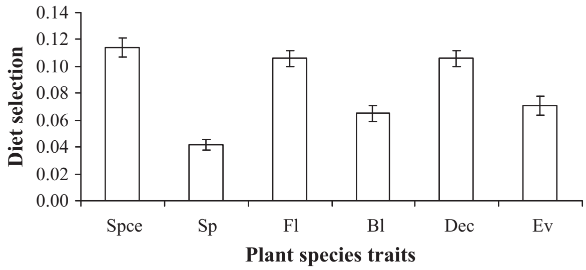

Fig. 1. The effect of physical traits and phenology of plant species on diet selection (proportion) across the seasons (the data across 22 days, 44 goats and 3 seasons). Error bars represent the standard errors. Spce = spinescent, Sp = spineless, Fl = fine leaves, Bl = broad leaves, Dec = deciduous and Ev = evergreen.

the data were analysed within seasons, the proportion of spinescent species in each season was significantly higher than that of spineless species (Table 3). Goats included a larger amount of fine-leaf species than broad-leaf species during the early and late wet season (Table 3). Likewise, deciduous species comprised a larger proportion of the diet than evergreen species during the early and late wet seasons (Table 3).

3.2. Selection index

The most abundant species were also the most preferred in the three seasons, which were *S. myrtina*, *A. nilotica*, *D. cinerea*, *A. natalitia* and *C. ordata* (Tables 4 and 5). Selection index of species depended on season of observation ($F_{13, 324}$ = 4.48, P < 0.001). *S. myrtina* had the greatest selection index in the dry season, followed by *Rhus pentheri*, *Lantana camara* and *A. nilotica*. In the early wet season, *S. myrtina* had the highest index, followed by *Jasminum multipartitum*, *D. cinerea* and *A. nilotica*, while in the late wet season *A. nilotica*, *L. camara*, *S. myrtina* and *D. cinerea* were most preferred.

When the data set was pooled according to physical traits or phenology within seasons, fine-leaf species had a higher mean selection index than broad-leaf species in the dry season (t = 1.16, df = 129, P < 0.029), while in the early wet season the opposite was observed (t = 3.28, df = 83, P < 0.001) (Table 6). Goats preferred spinescent species more than spineless species in the dry and early wet seasons (t = −4.65, df = 102, P < 0.001 and t = −3.91, df = 78, P < 0.001, respectively) (Table 6). Only in the early wet season, evergreen species had a significantly higher selection index than deciduous (t = −3.28, df = 253, P = 0.002) (Table 6). However, when the data were pooled across the seasons, only selection index of spinescent species was significantly higher than those of spineless species (2.06 ± 0.153 vs. 1.26 ± 0.144, t = −3.78, df = 316, P < 0.001).

When the data were sorted and pooled according to browse species across the seasons, the relationships between the browse species selection index and their chemical traits were obtained (Table 7, Fig. 2). Selection index for *A. nilotica* was positively correlated to ADF (r = 0.32, n = 44, P = 0.035), ADL (r = 0.32, n = 44, P = 0.035) and cellulose (r = 0.31, n = 44, P = 0.04). For *D. cinerea* NDF (r = 0.36, n = 44, P = 0.018), ADF (r = 0.29, n = 44, P = 0.059),

Table 1
The effect of season and plant species on diet compositions for goats.

Species	Season		
	Dry	Early wet	Late wet
Acacia natalitia	0.089 ± 0.013	0.101 ± 0.011	0.098 ± 0.013
Acacia nilotica	0.061 ± 0.015	0.050 ± 0.008	0.124 ± 0.019
Chromolaena odorata	0.119 ± 0.015	0.051 ± 0.013	0.084 ± 0.011
Dichrostachys cinerea	0.069 ± 0.010	0.142 ± 0.016	0.205 ± 0.024
Scutia myrtina	0.223 ± 0.040	0.083 ± 0.020	0.118 ± 0.026
Lantana camara	0.021 ± 0.004	–	0.015 ± 0.005
Other browse	0.089 ± 0.014	0.151 ± 0.026	0.088 ± 0.012
Psidium guajava	0.006 ± 0.002	–	–
Pavetta lanceolata	0.029 ± 0.007	–	–
Rhus pentheri	0.022 ± 0.007	–	–
Jasminum multipartitum	–	0.040 ± 0.006	0.039 ± 0.010
Coddia rudis	–	–	0.015 ± 0.005

Table 2
Life form, leaf morphology, spinescence and phenology of major plant species frequently browsed by goats in Zululand Coastal Thornveld.

Plant species	Life form	Leaf morphology	Spine	Phenology
Acacia natalitia[a]	Tree	Fine	√	Deciduous
Acacia nilotica	Tree	Fine	√	Deciduous
Chromolaena odorata[b]	Climber	Broad	×	Evergreen
Dichrostachys cinerea	Tree	Fine	√	Deciduous
Scutia myrtina	Shrub	Broad	√	Evergreen
Coddia rudis	Shrub	Broad	×	Evergreen
Lantana camara[b]	Shrub	Broad	×	Evergreen
Psidium guajava[b]	Tree	Broad	×	Evergreen
Pavetta lanceolata	Shrub	Broad	×	Evergreen
Rhus pentheri	Shrub	Broad	×	Evergreen
Jasminum multipartitum	Climber	Broad	×	Evergreen

[a] Formerly part of *Acacia karroo* (Coates Palgrave, 2002).
[b] Invasive non-native species.

ADL ($r = 0.31$, $n = 44$, $P = 0.042$) and CP ($r = 0.53$, $n = 44$, $P < 0.001$) were positively related to selection index, while for *S. myrtina* the selection index was negatively related to NDF ($r = 0.46$, $n = 43$, $P = 0.002$), CP ($r = 0.46$, $n = 43$, $P = 0.002$) and CT ($r = 0.47$, $n = 43$, $P = 0.002$). Selection index for *C. odorata* was positively correlated to NDF ($r = 0.46$, $n = 44$, $P = 0.002$), ADF ($r = 0.34$, $n = 44$, $P = 0.001$) and cellulose ($r = 0.43$, $n = 44$, $P = 0.004$), while no significant relationship was noticed between the chemicals and selection index of *A. natalitia*, *Coddia rudis*, *J. multipartitum*, *L. camara*, *Psidium guajava*, *Pavetta lanceolata* and *R. pentheri*. However, there were no significant relationships between selection index and chemistry of plant leaves when the data were pooled according to the seasons, except CP in early wet season, which was negatively related to selection index ($r = -0.22$, $n = 94$, $P = 0.030$).

Table 3
The statistical variables of diet selection (proportion) of physical traits and/or phenology of plant species within seasons.

Season	Species traits	Mean ± SE	*t*-Test	*df*	*P*
Dry	Spinescent	0.110 ± 0.011	−4.30	79	<0.001
	Spineless	0.043 ± 0.007			
	Fine leaves	0.073 ± 0.007	0.23	111	0.821
	Broad leaves	0.076 ± 0.012			
	Deciduous	0.073 ± 0.023	−0.82	91	0.414
	Evergreen	0.086 ± 0.014			
Early wet	Spinescent	0.093 ± 0.008	−4.62	80	<0.001
	Spineless	0.043 ± 0.007			
	Fine leaves	0.097 ± 0.009	−3.41	82	0.001
	Broad leaves	0.055 ± 0.008			
	Deciduous	0.097 ± 0.009	3.41	82	0.001
	Evergreen	0.055 ± 0.007			
Late wet	Spinescent	0.136 ± 0.011	−7.39	91	<0.001
	Spineless	0.042 ± 0.006			
	Fine leaves	0.142 ± 0.013	−5.60	83	<0.001
	Broad leaves	0.058 ± 0.008			
	Deciduous	0.142 ± 0.013	4.93	88	<0.001
	Evergreen	0.066 ± 0.009			

SE = standard error; DF = degree of freedom; P = significance level.

Table 4
The proportion of relative abundance of browse species (using number of browseable plants) of two paddocks in Zululand Thornveld used in three seasons (one paddock was used twice, in the dry season and early wet season).

Species	Dry	Early wet	Late wet
A. natalitia	0.1937	0.1937	0.1692
A. nilotica	0.0303	0.0303	0.0438
C. odorata	0.2814	0.2814	0.2387
D. cinerea	0.0827	0.0827	0.0952
S. myrtina	0.0352	0.0352	0.0430
C. rudis	–	–	0.0176
L. camara	0.0079	0.0079	0.0039
Other browse[a]	0.0754 (14 sp)[b]	0.1352 (15 sp)	0.1418 (16 sp)[b]
P. guajava	0.0247	0.0247	–
P. lanceolata	0.0492	0.0492	–
R. pentheri	0.0056	0.0056	–
J. multipartitum	0.0185	0.0185	0.0292
Not-selected[c]	0.2140 (15 sp)	0.1356 (13 sp)	0.2132 (18 sp)

[a] Species selected by goat but occurring in small proportions (less than 15 times found in the field or the diet), including *Acokanthera rotundata*, *Apodytes dimidiata*, *Canthium inerme*, *Carissa bispinosa*, *Diospyros simii*, *Euclea daphnoides*, *Gymnosporia heterophylla*, *Gymnosporia maranguensis*, *Hippobromus pauciflorus*, *Lippia javanica*, *Phyllanthus reticulata*, *Rhus dentata*, *Rhus rehmanniana*, *Schinus terebinthifolius*, *Sideroxylon inerme* and *Ziziphus mucronata*.
[b] Includes *J. multipartitum* in the dry season and unknown species in the late wet season.
[c] Species not in the diet, including *Azima tetracantha*, *Cordia caffra*, *Cussonia spicata*, *Diospyros lycioides*, *Ehretia rigida*, *Grewia occidentalis*, *Gymnosporia harveyana*, *Gymnosporia glaucophylla*, *Phoenix reclinata*, *Putterlickia verrucosa*, *Rhoicissus tridentate*, *Schotia brachypetala*, *Scolopia zeyheri*, *Senna bicapsulata*, *Sesbania sesban*, and *Trichilia emetica*.

Table 5
The effect of season and plant species on selection index by goats.

Species	Season		
	Dry	Early wet	Late wet
Acacia natalitia	0.483 ± 0.065	0.552 ± 0.058	0.633 ± 0.083
Acacia nilotica	2.173 ± 0.507	1.802 ± 0.290	3.094 ± 0.477
Chromolaena odorata	0.478 ± 0.083	0.191 ± 0.047	0.381 ± 0.047
Dichrostachys cinerea	0.888 ± 0.117	1.887 ± 0.253	2.345 ± 0.295
Scutia myrtina	6.783 ± 1.164	2.484 ± 0.605	2.880 ± 0.609
Lantana camara	2.935 ± 0.678	–	3.025 ± 0.982
Other browse	1.912 ± 0.475	1.632 ± 0.508	0.868 ± 0.188
Psidium guajava	0.251 ± 0.080	–	–
Pavetta lanceolata	0.632 ± 0.150	–	–
Rhus pentheri	4.055 ± 1.218	–	–
Jasminum multipartitum	–	2.155 ± 0.345	1.477 ± 0.390
Coddia rudis	–	–	0.839 ± 0.231

Table 6
The effect of season, physical traits and phenology of plant species on selection index.

	Season		
Trait	Dry	Early wet	Late wet
Fine leaves	1.962 ± 0.164	1.091 ± 0.246	1.459 ± 0.217
Broad leaves	1.367 ± 0.215	2.466 ± 0.340	1.778 ± 0.314
Deciduous	1.617 ± 0.151	1.091 ± 0.246	1.459 ± 0.217
Evergreen	1.556 ± 0.260	2.466 ± 0.340	0.986 ± 0.237
Spineless	1.024 ± 0.165	0.874 ± 0.200	1.778 ± 0.314
Spinescence	2.370 ± 0.238	2.278 ± 0.298	1.459 ± 0.217

4. Discussion

The goats foraged on 31 out of 44 woody species in the study area. However, this number varied among seasons. The goats were more selectivity in the dry season than the wet season. Some plant species that are avoided during the wet season may be accepted in the dry season because of seasonal variation in availability (Owen-Smith and Cooper, 1988; Abate, 1996). In our study, *S. myrtina* comprised the highest proportion of the diet during the dry season, which may be caused by S. *myrtina* being evergreen. Consequently, the choices of diet are narrow when there is low availability of palatable materials. In the wet season the quality and availability of edible browseable material increases in general (Nyamangara and Ndlovu, 1995). Results from the current study agree partially with observations made in cafeteria style experiments (Dziba et al., 2003; Mkhize, 2008), when it was reported that *S. myrtina* was the most preferred species during the dry season.

In the wet season, *D. cinerea* was the most selected species, while in the dry season its contribution to the diet was lower, which supports previous observations (Yayneshet et al., 2008; Basha et al., 2009). It has been reported that *D. cinerea* comprises a large proportion of

Table 7
Chemical composition (g/kg DM) of selected browse species by goats in Zululand Coastal Thornveld.

Species	Dry season					Early wet season					Late wet season				
	NDF	ADF	ADL	CP	CT	NDF	ADF	ADL	CP	CT	NDF	ADF	ADL	CP	CT
Acokanthera rotundata	434	349	214	59.9	1.7	–	–	–	–	–	–	–	–	–	–
Apodytes dimidiata	–	–	–	–	–	487	322	144	89.0	74.3	–	–	–	–	–
Acacia natalitia	432	294	213	122	118	412	281	197	141	212	534	431	339	133	97.0
Acacia nilotica	242	138	84	116	3.8	263	130	77	136	16.5	281	186	121	138	2.6
Carissa bispinosa	362	224	142	60.1	93.0	420	306	207	76.4	228	–	–	–	–	–
Canthium inerme	517	407	330	94.6	28.7	552	482	361	125	2.3	552	510	373	118	7.2
Chromolaena odorata	386	245	105	186	0.5	233	143	62	216	0.5	354	313	212	226	0.5
Coddia rudis	360	208	130	68.3	5.6	333	213	130	100	4.2	395	318	188	106	2.3
Dichrostachys cinerea	488	356	223	109	45.8	454	259	168	173	59.0	627	548	355	170	33.8
Diospyros simii	450	344	279	84.9	21.0	525	406	262	115	32.0	573	529	351	107	9.2
Euclea daphnoides	552	377	245	69.3	29.9	601	474	339	77.5	52.4	–	–	–	–	–
Gymnosporia heterophylla	392	213	119	88.3	95.9	461	283	175	115	44.6	617	506	275	96.0	13.8
Gymnosporia maranguensis	532	357	219	78.1	56.7	520	379	264	90.6	75.5	585	502	291	76.8	68.2
Hippobromus pauciflorus	444	284	150	101	138	444	292	151	121	169	474	467	219	112	93.6
Jasminum multipartitum	284	182	108	80.4	14.9	336	188	118	127	1.0	507	512	263	136	0.6
Lippia javanica	455	262	130	134	1.3	434	305	145	143	73.3	559	558	293	164	0.2
Lantana camara	342	218	107	116	14.5	362	251	84	150	5.2	429	386	201	156	2.9
Psidium guajava	462	305	167	78.8	24.7	483	332	184	121	106	540	546	327	123	43.5
Pavetta lanceolata	439	327	253	70.6	98.6	582	499	407	122	32.0	625	619	463	107	27.1
Phyllanthus reticulata	–	–	–	–	–	233	133	057	209	4.6	392	162	061	152	7.1
Rhus dentata	514	335	225	96.3	4.4	612	474	365	145	15.8	625	548	404	114	12.3
Rhus pentheri	421	285	213	94.5	104	574	415	287	157	1.8	636	572	399	152	0.5
Rhus rehmanniana	432	269	158	80.7	117	598	451	324	139	22.9	606	573	400	147	6.1
Sideroxylon inerme	412	297	184	96.8	72.0	–	–	–	–	–	–	–	–	–	–
Scutia myrtina	460	313	214	105	32.2	497	273	188	123	208	508	431	293	129	133
Schinus terebinthifolius	402	325	256	96.9	22.7	–	–	–	–	–	481	379	265	117	12.5
Ziziphus mucronata	517	198	111	96.6	26.0	440	192	86	127	23.1	572	446	186	123	15.5

NDF = neutral detergent fibre, ADF = acid detergent fibre, ADL = acid detergent lignin, CP = crude protein and CT = condensed tannin.

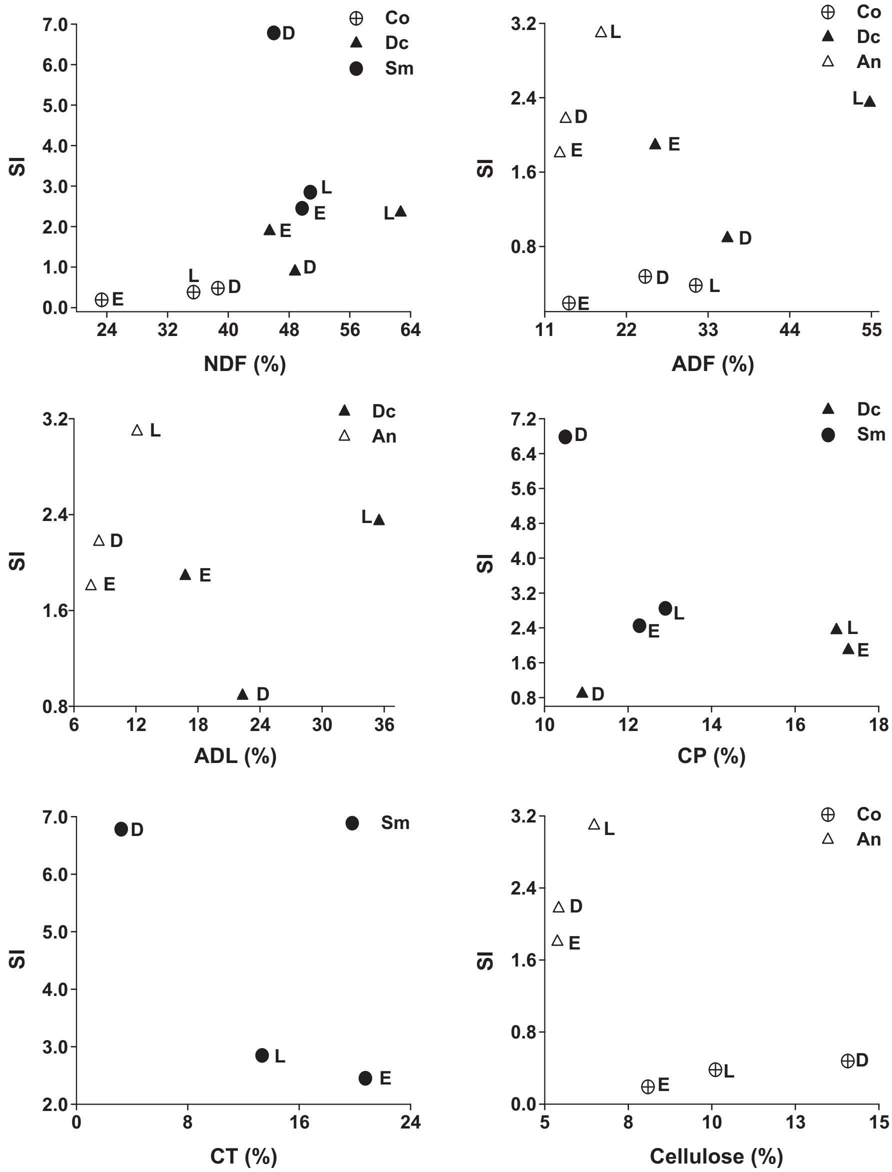

Fig. 2. Relationships between chemical variables of browse species and selection index (SI) of goats in different seasons. An = *Acacia nilotica*, Co = *Chromolaena odorata*, Dc = *Dichrostachys cinerea*, Sm = *Scutia myrtina*, NDF = neutral detergent fibre, ADF = acid detergent fibre, ADL = acid detergent lignin, CP = crude protein, CT = condensed tannin, D = dry season, E = early wet season and L = late wet season.

goat diets (Mlambo et al., 2004), but Sanon et al. (2007) reported avoidance of *D. cinerea* by goats, which could be due to variations in vegetation, climate and soil of the research sites. While it could be inferred that reduced availability in the dry season causes plants that are avoided in the wet season to become accepted in the dry season (Owen-Smith and Cooper, 1988), this was not clearly the case in our study. Many of the deciduous species in the study area are able to retain leaves for most of the dry season because of the humid conditions of the environment. Clearly, factors affecting seasonal variations in diet are more complex than expected and require further research.

The proportion of *A. natalitia* in the diet varied among seasons. Moderate proportions in the dry season might be due to *A. natalitia* having more leaves than other deciduous species at the time (pers. obs.), while the moderate proportion in the early wet season could be attributed to a function of flowering. In this study, goats preferred *A. natalitia* less than other common species, which agrees with previous observations (Basha et al., 2009) but disagrees with observations from studies where choice was limited (Dziba et al., 2003; Mkhize, 2008). During the late wet season *A. nilotica* had the greatest selection index, compared to the dry and early wet seasons. These variations between seasons could be ascribed to more leaves in the late wet season. Inter-annual variations did not seem to be important since the current findings are consistent with the previous part of the study (Basha et al., 2009).

C. odorata is a toxic weed, because of alkaloids that affect feeding (Prasad et al., 2005). In our study, *C. odorata* had the highest biomass throughout all seasons but it was avoided in the wet season and accepted during the dry season. This avoidance could be attributed to chemical traits, but during the dry season the animals may be obligated to feed on *C. odorata* because of low feed availability (Abate, 1996). It is possible that the chemical composition of *C. odorata* changes favourably during the winter, permitting herbivores to consume small amounts.

Physical characteristics of plant species are effective factors that influence diet selection (Wilson and Kerley, 2003a). Preference of spinescent species was significantly higher than that of spineless species within and across the seasons, which supports previous observations (Mkhize, 2008; Basha et al., 2009). Such morphological traits do not deter animals from foraging but reduce bite size and bite rate (Cooper and Owen-Smith, 1986; Woodward and Coppock, 1995). In contrast, Owen-Smith and Cooper (1987) reported that spines negatively influenced selection in the dry season, but this could also be ascribed to leaf size. In the present study goats consumed significantly larger proportions of species with fine leaves across seasons compared to those with broad leaves. However, within seasons, fine-leaved species comprised the larger proportion of the diet only in the wet season, but were more preferred in the dry season than species with broad leaves. High proportion of fine-leaf species in the wet season diet could be ascribed to the increased availability of those species, while higher preference in the dry season might be due to restricted choice of species.

In general, deciduous species comprised a higher proportion of the diet across seasons compared to evergreen species, which supports observations elsewhere (Shipley et al., 1998). Moreover, within the seasons, deciduous species comprised greater proportion of diet during the wet season. However, evergreen species were more preferred during the early wet season compared to deciduous species, while other studies reported that preference was unrelated to phenology (Watson and Owen-Smith, 2002; Dziba et al., 2003; Mkhize, 2008).

We note that the correlation coefficients were low, but nevertheless significant, which suggests other, unmeasured factors are important. However, for chemical traits, the study hypothesized that preference of plant species depends on fibre concentration, which changes with seasons and reduces forage quality through physical toughness and poor digestibility (Watson and Owen-Smith, 2002). Moreover, fibre could influence *in vitro* fermentation (Ndlovu and Nherera, 1997). In this study no significant relationships were found between plant preference and fibre components (NDF, ADF, ADL, cellulose and hemicellulose) in any season, which agrees with other studies (Shipley et al., 1998; Mkhize, 2008). However, between plant species, fibre fractions fluctuated in their relation to feed preference. Preference of *A. nilotica*, *D. cinerea*, and *C. odorata* was positively related to various fibre fractions. Fibre minimizing strategies (Jansen et al., 2007) could not explain preference because these species varied in preference. It has been reported that food selection could be affected negatively by fibre components (Cooper et al., 1988; Basha et al., 2009). Preference for *S. myrtina* among seasons was negatively related to fibre, which supports previous observations.

Studies reported that selection of food depends upon protein levels (Nyamangara and Ndlovu, 1995; Dziba et al., 2003). In the present study a negative relationship was observed between preference and protein in the early wet season. However, among plant species, *D. cinerea* and *S. myrtina* preference was positively and negatively related to protein, respectively. This clearly shows that there is no consistent relationship (i.e., relationships between seasonal variations in chemistry and preference are species-specific). Thus, no evidence was found to support the hypothesis of maximising nutrient intake, which agrees with some studies (Shipley et al., 1998; Jansen et al., 2007), but not others (Dziba et al., 2003). The differences among studies could be ascribed to variations in climate as well as different plant and animal species.

In the present study no relationship was observed between preference and condensed tannin in any season. However, among plant species, seasonal changes in preference of *S. myrtina* were negatively related to condensed tannins suggesting that tannins only have negative effects on preference in some species. In addition, tannins are not avoided completely by goats but they are kept below a certain threshold (Jansen et al., 2007). Also goats could limit the intake when plant species have high concentrations of tannin and lignin (Dziba et al., 2003). However, a varied diet is likely to minimise the effects of tannins. Moreover, an *in vitro* gas production study showed that addition of polyethylene glycol (PEG) to all species in our study emphasized the inhibitory effect of tannins on rumen microbes in tannin-rich feed (unpublished data).

5. Conclusions

The contribution of each plant species to the diet of goats, and the preference of goats for each species, varies among seasons. Factors such as plant spinescence and leaf morphology seem to be having an effect on diet selection with changes within plant species and seasons. However, leaf phenology did not affect the preference. The effect of chemical variables (fibres, protein and condensed tannins) on preference varied among species, indicating that the reasons for preference are species-specific. Therefore, goats forage from a wide range of plant species and this behavior suggests goats can optimize utilisation of the biodiversity of savannas and can be useful for managing woody plants in natural pastures.

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