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ORIGINAL ARTICLE

Preference of goats (*Capra hircus* L.) for tanniniferous browse species available in semi-arid areas in Ethiopia

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Summary

The objectives were to determine browse species preference of goats using dry matter intake (DMI) as a proxy, to compare preference when offered in combination with polyethylene glycol (PEG) and to establish relationships between browse species intake and chemical compositional data. Air-dried leaves of *Acacia etbaica*, *Cadaba farinosa*, *Capparis tomentosa*, *Dichrostachys cinerea*, *Dodonaea angustifolia*, *Euclea racemosa*, *Maerua angolensis*, *Maytenus senegalensis*, *Rhus natalensis* and *Senna singueana* were used. Two cafeteria trials, each lasting 10 days, were conducted using four local mature male goats of 2–2.5 years receiving a daily ration of grass hay (4% of body weight) and 200 g wheat bran. In trial 1, goats were offered 25 g of each browse species for a total of 30 min with intake, time spent on consumption and the number of visits to specific browse species recorded at 10-min intervals. In trial 2, the same procedure was followed except that 25 g of PEG 4000 was added to the daily wheat bran ration. Crude protein and neutral detergent fibre in browse species ranged from 69.0–245.5 to 159.8–560.6 g/kg dry matter (DM) respectively. Total phenols and total tannins contents ranged between 3.7–70.6 and 2.5–68.1 mg tannic acid equivalent/g DM, respectively, and condensed tannins 1.7–18.4 $Abs_{550\ nm}$/g DM. Preference indicators measured in the first 10 min of browse species intake differed significantly among browse species and with PEG ($p < 0.0001$). Principal components explained 69.9% of the total variation in browse species DMI. Despite the high tannin levels, *D. cinerea*, *R. natalensis* and *A. etbaica* were the most preferred species regardless of PEG presence. Tannin levels at the observed browse species DMI did not determine preference, instead, preference appeared to be based on hemicellulose. Determining browse species preference is essential to exploit them to improve nutrient utilization and control parasites in goats.

Keywords browse preference, tannin, phenol, intake behaviour, fibre

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Introduction

Trees and shrubs commonly known as browse significantly contribute to ruminant nutrition in arid and semi-arid areas of the world. Browse species make up a large proportion of goat diets under traditional farming systems in Ethiopia. Average crude protein (CP) and neutral detergent fibre (NDF) content of nine browse species were 145 and 334 g/kg DM, respectively, making them nutritionally superior to five tropical grasses with 76 g/kg DM CP and 754 g/kg DM NDF, both harvested at the vegetative stage from semi-arid Ethiopia (Yayneshet et al., 2009). Browse species are also recognized for possessing plant secondary metabolites (PSM) such as polyphenols which may account for 50% of the organic matter (Reed, 1986). Over the past four decades, condensed tannins have received much attention for their beneficial roles in ruminant nutrition. *In vitro* and *in vivo* anthelmintic properties in sheep (Brunet et al., 2007), *in vitro* (Bezabih et al., 2014) and *in vivo* methane reduction in goats (Puchala et al., 2005) and dairy cows (Huyen et al., 2016a) are the widely reported positive attributes of certain tannin-containing tropical and temperate forages. On the other hand, condensed tannin concentrations of more than 5% DM have been reported to reduce voluntary feed intake, digestibility and lower productivity of grazing ruminants (Min et al., 2003). However, this threshold level was based on temperate forages and did not account for the type of ruminant species nor the dietary niche or experience with tannin-containing forages of the animal.

Tannin concentrations and structural characteristics vary widely among species (Abdulrazak et al., 2000) and tannin sources (Huyen et al., 2016b). The wide variation in characteristics among browse species provides choices for browsing herbivores such as goats. Preference involves the interaction between sensory input (taste, smell, sight) and post-ingestive feedback (Provenza, 1996). The latter is non-cognitive and influenced by early-life experience. Herbivores routinely exposed to tanniniferous diets usually adapt in terms of behaviour and physiology while satisfying their nutrient requirements. A common adaptation to tannin ingestion in domestic and wild herbivores is increased secretion of proline-rich proteins in saliva to form a complex with tannin (Shimada, 2006). Intrinsically, the saliva of goats is high in proline-rich proteins regardless of previous exposure to tannins (Ventura-Cordero et al., 2015). Another mechanism of herbivores is diet diversification, which also explains the trade-off between ingesting nutritious feed and minimizing detrimental effects of PSM ingestion (Alonso-Díaz et al., 2010). Chemical and physical characteristics of feed, physiological stage and previous dietary experience determine preference in goats (Morand-Fehr, 2003). Preference studies can be used as a tool to evaluate tropical tannin-containing forages (Alonso-Díaz et al., 2010), and the use of a tannin binding agent, polyethylene glycol (PEG), enables the investigation of feeding behaviour of goats browsing on tannin-containing woody species (Decandia et al., 2008). Landau et al. (2002) reported an increased intake of lentisk (*Pistacia lentiscus* L.), a tannin-rich forage, by naturally browsing Mediterranean goats having free access to PEG (4000) flakes compared to their control counterparts that did not receive PEG. In another study, supplementation of 50 g/day of PEG (4000) to Sarda goats browsing in lentisk (*P. lentiscus* L.) dominated Mediterranean scrubland increased the proportion of lentisk in the diet compare to the PEG-unsupplemented group (Decandia et al., 2000).

Although the nutritional value of some browse species in the Tigray Region of northern Ethiopia has been studied (Yayneshet et al., 2009; Melaku et al., 2010), information on the preference of these browse species by goats is scarce. Knowledge of the browse species preference of goats is important to develop strategies for effective utilization of browse species growing in sub-Saharan Africa. Accordingly, the objectives of the present study were (i) to determine browse species preference using dry matter intake as a proxy, (ii) to compare preference for the same browse species when PEG is included in the diet and (iii) to establish relationships between browse species intake and browse species components (total tannins, condensed tannins, total phenols and gross nutrient composition).

Materials and methods

Description of study area

Leaves from trees and shrubs were collected from two area exclosures around Abiy Addi town (13°37′23″ N and 39°00′06″ E) in the Tembein district in northern Ethiopia at an altitude range between 1917 and 2275 m above sea level. The exclosures are protected communal areas where natural vegetation is allowed to recover from previous disturbances by humans and animals since the 1990s (Yayneshet et al., 2008; Yayneshet, 2011). The average annual rainfall during 2003–2012 was 485 mm with average minimum and maximum temperature of 13.5 and 30.1 °C respectively (Tigray Regional Meteorological Agency, personal communication). Subsistence mixed crop-livestock farming is commonly practiced with goats and cattle being the most common livestock species.

Browse species and management

Browse species investigated were *Acacia etbaica* (shrub/tree, Fabaceae), *Cadaba farinosa* (shrub, Capparidaceae), *Capparis tomentosa* (shrub, Capparidaceae), *Dichrostachys cinerea* (shrub, Fabaceae), *Dodonaea angustifolia* (tree, Sapindaceae), *Euclea racemosa* (shrub, Ebenaceae), *Maerua angolensis* (tree, Capparidaceae), *Maytenus senegalensis* (shrub/tree, Celasteraceae), *Rhus natalensis* (tree, Anacardiaceae) *and Senna singueana* (tree/shrub, Fabaceae). From each exclosure, leaves (~1 kg per plant) from 15 phenologically similar (vegetative growth stage) mature plants of the respective species were collected by hand-clipping in October 2014, following the long rainy season (July–September) to allow collection of sufficient material. Immediately after collection, a composite sample was made per plant species and leaves were air-dried under shade and stored, pending further treatment.

Experimental animals' management

Four mature male goats of similar age (2–2.5 years) and 14.4 ± 1.07 kg (mean ± SD) live weight of the same local breed were bought from local farmers grazing the goats at the same locality from where browse species were obtained. Transport and handling of goats were according to the federal animal handling guideline of the Ministry of Agriculture and Rural Development, Ethiopia. Goats were assigned randomly to individual pens (1.5 × 1.0 m) located next to each other in closed housing with sufficient ventilation and day light at the small ruminant unit of Mekelle University, Ethiopia. Dry, course wheat straw was used as bedding. Three weeks before commencing the experiment, goats were treated against internal and external parasites using a broad-spectrum anthelmintic, ivermectin injection (Hebei Yuanzheng Pharmaceutical Shijiazhuang, China) and oral administration of albendazole (Ashish life science Pvt., Mumbai, India). Vaccination against anthrax (0.5 ml) and multivitamin injection were given subcutaneously. All dosage rates were applied as specified by the manufacturers. During the 3 weeks before the start of the experiment, each day goats were offered native grass hay *ad libitum* and 200 g wheat bran. Clean water and salt licks were available free of choice before and throughout the experiment.

Treatments and measurement

A cafeteria test was employed using the four goats to study preferences of the 10 browse species. Goats were re-familiarized to all browse species and adapted to eating from 10 identical yellow, removable plastic troughs (38 × 11 × 10 cm) prior to the start of the first trial. The adaptation period lasted for 10 days during which two browse species, each 25 g/day was offered simultaneously for 30 min for two consecutive days. Each browse species was randomly distributed over five of the 10 troughs that were positioned side by side on a diagonal platform (68 cm and 43 cm above ground). The order of browse species offered and randomization was kept the same for all goats during the adaptation period. Each time one observer was positioned on the opposite side of each goat's row of troughs to accustom the goat to the observer's presence. At the end of the 30-min adaptation, all browse species were removed and grass hay was provided from a separate feeder positioned opposite of the row of troughs. Goats were tethered using a rope with a sufficient length (1.3 m) to easily reach all troughs and the feeder. The adaptation period was followed by two trials which lasted 10 days each. In trial 1, grass hay (4% of body weight) and 200 g of wheat bran were divided into two equal portions offered at 8.00 and 15.00 h. During each of the following 10 days, at 10.00 h, the unconsumed grass hay was withdrawn and 25 g of each browse species was provided once for a total of 30 min which was divided into 10-min intervals for intake measurement. The 10-min measurement ensures that browse species selection is based on browse species characteristics and not on availability (Jansen et al., 2007). It also allows goats to express a pattern of choice during the subsequent 10-min intervals. After each 10-min interval, troughs were removed, and browse species were collected and weighed by a digital balance (Voltcraft, CTS-10, Hirschau, Germany) weighing three decimal places, before being returned to their previous position in the row of troughs for the next 10-min preference test. Weighing of the browse species took 15 min. Feed intake was calculated as the difference between the quantities offered and remaining as measured. The location of a particular browse species in a trough was randomly determined each day to avoid conditioned learning (i.e. association between feeder position and browse species) (Alonso-Díaz et al., 2008). During browse species preference measurement periods, two observers positioned in front of the goats recorded the length of time a particular browse species was consumed, with two goats observed alternating each day. Intake per visit was calculated as the ratio of total intake of browse species during the 30 min per total number of visits to specific browse species during this time. Visits were recorded only when there was actual consumption of browse species. Intake rate was calculated as the total amount of specific browse species consumed during 30 min per total time spent eating. The eating time was recorded when goats visited browse species and actual consumption occur. After trial 1, goats were maintained on grass hay (4% of body weight) and wheat bran (200 g) for 10 days whereafter trial 2 was conducted which followed the same procedure except that 12.5 g of PEG 4000 was included in the 100 g wheat bran which was provided twice daily. Over the experimental periods, goats spent only 5–10 min to consume all wheat bran with no difference observed when PEG was included. Samples of browse species, wheat bran and grass hay were collected daily until the end of the two trials, pooled by species/feed type, ground to pass a 1-mm sieve and stored at room temperature awaiting chemical analysis.

Chemical analysis

Feed samples were analysed for dry matter (DM), ash/organic matter (OM) and N following AOAC (1990) protocols with DM determined by oven drying samples (105 °C, 3 h), ash determined by incinerating samples in a muffle furnace (550 °C, 3 h) and N determined by the Kjeldahl method. Crude protein was calculated by multiplying N with a factor of 6.25. Neutral detergent fibre (NDF), acid detergent fibre (ADF) and acid detergent lignin (ADL) were analysed according to Van Soest and Robertson (1985). Hemicellulose was calculated as NDF-ADF and cellulose as ADF-ADL. Total phenols (TP) and total tannins (TT) were determined according to the method of Makkar (2003). Briefly, 100 mg of finely ground browse species sample was weighed in a glass test tube and 5 ml 70% aqueous acetone added to extract phenolics. This was done on ice in an ultrasonic bath for 2 × 5 min whereafter samples were centrifuged, using an Eppendorf centrifuge 5417R, Eppendorf AG, Hamburg, Germany, for 10 min at 5580 *g*. The supernatant was collected into a glass tube and 0.05 ml diluted with 0.45 ml distilled water before 0.25 ml Folin–Ciocalteu reagent, and 1.25 ml sodium carbonate solution was added. After mixing, absorbance of the solution was determined at 725 nm. Tannic acid was used to prepare a standard curve to determine total phenols as tannic acid equivalent (TA eq). Polyvinylpolypyrrolidone (PVPP) was used to bind tannins for total tannins determination. In a test tube, containing 100 mg of PVPP, 1 ml of distilled water and 1 ml of the supernatant, from aqueous acetone extraction mentioned above, was added and kept at 4 °C for 15 min before centrifugation at 5580 *g* for 10 min. The supernatant containing the simple phenolics other than tannins was collected and absorbance read as before and TA eq. The difference between TP and simple phenols was taken to represent TT expressed as TA eq. Condensed tannins (CT) were determined by the method of Grabber et al. (2013). In brief, acetone-HCl-butanol reagent was prepared from 40 mg of ammonium iron (III) sulphate dodecahydrate, 3.3 ml distilled water, 5 ml 12 M HCl, 42 ml n-butanol and 50 ml acetone. Finely ground browse species sample (30 mg) was weighed into a 25-ml thick-walled glass tube with screw cap and 15 ml of the acetone–HCl–iron reagent added. After heating in a water bath (2.5 h, 70 °C) and cooling for 45 min, the reaction mixture was decanted into a 2-ml micro-centrifuge tube which was subsequently centrifuged at 16 825 *g* for 2 min, using a table top centrifuge (Z383, HERMLE, Gosheim, Germany). The supernatant was decanted into quartz cuvettes and absorbance read at 550 nm. Acetone–butanol–iron solution was used as a blank, and as a diluent to keep absorbance reading below 0.6. Condensed tannin values were expressed as absorbance reading per g DM.

Data analysis

Data on dry matter intake (DMI), intake rate and intake per visit were analysed by ANOVA using the PROC MIXED procedure in SAS 9.3 (SAS, 2010) using the model:

$$Y_{ijkl} = \mu + G_i + B_j + P_k + D_l + (B \times P)_{jk} + \varepsilon_{ijkl}$$

where Y_{ijkl} = the dependent variable, μ = the overall mean, G_i = animal effect (i = 1–4), B_j = browse species effect (j = 1–10), P_k = the effect of PEG (k = + or −), D_l = the effect of day (l = 1–10), $(B \times P)_{jk}$ = the interaction between browse species and PEG and ε_{ijkl} = the residual error term. Browse species and PEG intake were fixed variables with animal considered as random factor and day used as the repeated measure. The compound symmetry covariance structure was used which generated the least fit statistics according to the Akaike information criterion (AIC) and Bayesian information criterion (BIC). PROC PLM of SAS was used to separate least square means.

Discrimination of the browse species based on browse species chemical components and the relationships among browse species components were established using principal component analysis (PCA) of SAS. Pearson correlation output from PCA analysis was also used to establish relationships between browse species chemical components and with DMI in the absence and presence of PEG at a statistical significance set at $p < 0.05$.

Multiple regression analysis was performed using PROC REG procedure of SAS with selection of variables based on backward elimination to determine the best predictor of browse species DMI from browse species chemical components. The independent variables were CP, ash, hemicellulose, cellulose, ADL, CT, TT and TP. The criteria for selection of variables were a low Mallow's Cp-criterion and high coefficient of determination (R^2).

Results

All goats remained healthy throughout the experiment. Dry matter intake, intake per visit and intake rate were analysed using data from all goats.

Table 1 shows the chemical composition of browse species, grass hay and wheat bran. Browse species with the exception of *E. racemosa* contained 81.8–245.5 g

Table 1 Chemical composition of browse species, grass hay and wheat bran used in cafeteria experiments

Feed ingredient	DM (g/kg)	Ash	CP	NDF	ADF	ADL	HEMI	CELL	TP*	TT*	CT†
		(g/kg DM)									
Browse species											
Acacia etbaica	918.9	69.4	107.2	315.6	242.4	118.3	73.2	124.1	70.6	68.1	11.2
Cadaba farinosa	909.3	123.0	219.7	255.3	131.0	62.3	124.3	68.7	3.7	2.5	1.7
Capparis tomentosa	923.2	109.2	219.9	270.5	188.9	103.5	81.6	85.4	10.2	8.1	6.8
Dichrostachys cinerea	907.5	72.5	144.8	427.1	303.4	144.2	123.7	159.2	41.3	38.9	9.3
Dodonaea angustifolia	921.7	53.5	107.8	297.6	216.2	81.9	81.4	134.3	66.2	61.1	16.8
Euclea racemosa	908.6	53.1	69.0	560.6	500.6	244.0	60.0	256.6	29.7	28.6	18.4
Maerua angolensis	909.5	139.9	245.5	159.8	106.2	30.5	53.6	75.7	7.2	4.6	3.3
Maytenus senegalensis	891.6	71.0	81.8	467.4	426.3	213.6	41.1	212.7	46.5	32.7	16.9
Rhus natalensis	915.3	76.5	113.4	450.9	303.4	134.5	147.5	168.9	44.9	34.5	17.7
Senna singueana	923.0	71.9	140.6	295.4	231.8	69.7	63.6	162.1	41.6	38.5	6.9
Grass hay	926.3	90.6	73.7	710.5	408.6	62.6	301.9	346.0	–	–	–
Wheat bran	904.6	46.1	160.7	435.0	129.2	38.0	305.8	91.2	–	–	–

DM, Dry matter; CP, crude protein; NDF, neutral detergent fibre; ADF, acid detergent fibre; ADL, acid detergent lignin; HEMI, hemicellulose; CELL, cellulose; NDF-ADF=hemicellulose; ADF-ADL=cellulose; TP, total phenols; TT, total tannins; CT, condensed tannins; –, not determined.
*Calculated as mg tannic acid equivalent/g DM.
†Expressed as $Abs_{550\ nm}$/g DM.

CP/kg DM, which exceeded that of grass hay (73.7 g/kg DM). Neutral detergent fibre content ranged from 159.8 g/kg DM in *M. angolensis* to 560.6 g/kg DM in *E. racemosa* while grass hay had a higher value (710.5 g/kg DM). *Maerua angolensis* had the lowest ADF and ADL values, while higher values were observed for *E. racemosa*. Condensed tannins concentration was highest in *E. racemosa* (18.4 $Abs_{550\ nm}$/g DM) and lowest in *C. farinosa* (1.7 $Abs_{550\ nm}$/g DM), whereas total tannin content was highest in *A. etbaica* (68.1 mg TA eq/g DM) and lowest in *C. farinosa* (2.5 mg TA eq/g DM). Crude protein was negatively correlated with cellulose ($r = -0.873$; $p = 0.001$), ADL ($r = -0.762$; $p = 0.011$), CT ($r = -0.817$; $p = 0.004$), TP ($r = -0.774$; $p = 0.009$) and TT ($r = -0.729$; $p = 0.017$) (data not shown in table). Positive relationships were found between ADL and cellulose ($r = 0.878$; $p = 0.0008$) and ADL with CT ($r = 0.744$; $p = 0.014$) (data not shown in table). Condensed tannins were positively related to TP ($r = 0.650$; $p = 0.042$) and tended to be positively related to TT ($r = 0.575$; $p = 0.082$) (data not shown in table). A strong positive relationship was found for TT and TP ($r = 0.984$; $p < 0.0001$) (data not shown in table).

Browse species DMI during the first 10 min differed ($p < 0.0001$) among browse species and with PEG (Table 2). Comparable and higher intakes were observed for *A. etbaica, D. cinerea* and *R. natalensis*. A significant ($p = 0.008$) interaction was observed between browse species and PEG, but with the exception of *A. etbaica* ($p = 0.012$), inclusion of PEG did not affect browse species intake.

Browse species intake as measured during the three consecutive 10-min periods is shown in Fig. 1. During the first 10 min, goats predominantly consumed *D. cinerea*, *R. natalensis* and *A. etbaica* regardless of PEG presence. Remaining portions of these browse species were eaten during the second 10 min, but also with increasing intake of *M. senegalensis* and *E. racemosa*. In comparison, only negligible quantities of the remaining browse species, predominantly *E. racemosa*, were consumed during the last 10 min.

At the end of the 30 min, significant ($p < 0.0001$) differences in browse species intake were observed (Table 2). Intake was increased by PEG inclusion ($p < 0.0001$) and days ($p < 0.0003$) as shown in Table 2. An interaction existed between browse species and PEG ($p = 0.0001$). Comparable quantities of *A. etbaica*, *D. cinerea*, *M. senegalensis* and *R. natalensis* were consumed irrespective of PEG inclusion. Polyethylene glycol significantly increased ($p \leq 0.036$) the intake of *E. racemosa*, *S. singueana*, *C. tomentosa* and *C. farinosa*. Intake per visit varied significantly among browse species ($p < 0.0001$) and showed a significant browse species and PEG interaction ($p = 0.006$). Intake per visit was highest in *D. cinerea*, *R. natalensis* and *M. senegalensis* in the absence of PEG. However, none of the browse species showed significant differences in intake per visit in the presence and absence of PEG. Intake rate was different ($p \leq 0.027$) among browse species, PEG treatment and day. Similar intake rates were observed among browse species but with lowest rate

Table 2 Mean dry matter intake, intake per visit and intake rate of browse species by goats in the absence (−) and presence (+) of polyethylene glycol (PEG)

	Intake (g DM/10 min)*			Intake (g DM/30 min)†			Intake per visit (g DM/visit)†			Intake rate (g DM/min)†		
	(−)	(+)	p	(−)	(+)	p	(−)	(+)	p	(−)	(+)	p
Browse species												
Dichrostayches cinerea	22.8^{a}	20.3^{a}	0.988	24.3^{a}	24.8^{a}	1.000	9.4^{a}	6.2^{a}	0.522	11.3^{a}	11.0^{ab}	1.000
Rhus natalensis	18.6^{ad}	19.2^{ab}	1.000	24.2^{a}	24.8^{a}	1.000	8.5^{a}	7.8^{a}	1.000	7.8^{a}	9.7^{ab}	1.000
Acacia etbaica	14.5^{ade}	20.6^{a}	0.012	22.4^{a}	24.9^{a}	0.986	8.5^{a}	5.3^{ab}	0.473	8.5^{a}	13.3^{ab}	0.985
Maytenus senegalensis	9.5^{bce}	11.1^{bde}	1.000	22.5^{a}	24.1^{a}	1.000	6.0^{ab}	4.7^{b}	1.000	8.2^{a}	8.7^{ab}	1.000
Capparis tomentosa	9.1^{bce}	12.2^{bd}	0.895	12.4^{bc}	18.3^{bc}	0.014	2.3^{bc}	3.7^{bc}	0.999	8.3^{a}	11.7^{ab}	0.999
Maerua angolensis	8.8^{cde}	13.5^{bc}	0.218	11.8^{bc}	16.5^{cd}	0.173	3.5^{b}	4.4^{b}	1.000	6.5^{a}	7.9^{ab}	1.000
Senna singueana	6.6^{def}	7.3^{de}	1.000	12.5^{bc}	17.9^{bc}	0.036	2.7^{bc}	4.9^{b}	0.961	7.5^{a}	16.0^{a}	0.231
Cadaba farinosa	3.5^{df}	5.7^{d}	0.998	7.5^{cd}	14.0^{d}	0.003	2.5^{bc}	3.3^{bc}	1.000	3.9^{b}	8.5^{ab}	0.987
Euclea racemosa	3.1^{f}	5.9^{d}	0.949	13.9^{b}	21.7^{ab}	<0.0001	3.3^{bc}	5.4^{ab}	0.981	6.5^{a}	5.1^{b}	1.000
Dodonaea angustifolia	2.2^{f}	2.2^{e}	1.000	5.2^{d}	5.0^{e}	1.000	1.9^{bc}	1.5^{c}	1.000	5.3^{b}	7.2^{ab}	1.000

	SEM	p	SEM	p	SEM	p	SEM	p
Browse species	1.186	<0.0001	1.296	<0.0001	0.613	<0.0001	1.778	0.009
PEG	0.965	<0.0001	1.113	<0.0001	0.274	0.722	1.252	0.005
Day	1.186	0.235	1.296	0.0003	0.613	0.041	2.081	0.027
Browse species × PEG	1.414	0.008	1.493	0.0001	0.867	0.006	2.223	0.387

	(−)	(+)	SEM	p
Total browse species (g DM)*	98.5	117.9	3.12	0.0002
Grass hay (g DM/day)	406.3	451.3	12.61	0.006
Wheat bran (g DM/day)	200.0	200.0	–	–

SEM, standard error of the mean; DM, dry matter.
Means within a column with different superscripts differ significantly ($p < 0.05$).
*During the first 10 min.
†During 30 min.

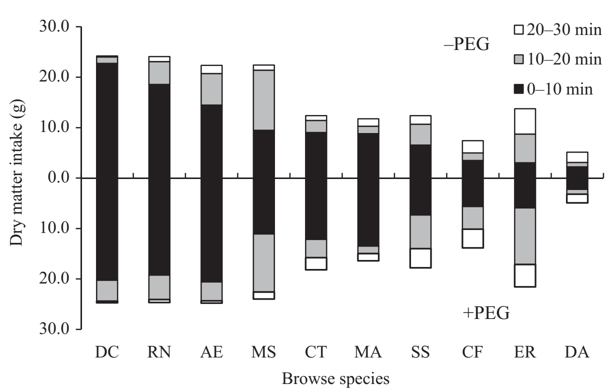

Fig. 1 Mean browse intake of goats during three subsequent 10-min interval in the absence (−) and presence (+) of polyethylene glycol (PEG). DC, *D. cinerea*; RN, *R. natalensis*; AE, *A. etbaica*; MS, *M. senegalensis;* CT, *C. tomentosa;* MA, *M. angolensis*; SS, *S. singueana*; CF, *C. farinosa*; ER, *E. racemosa*; DA, *D. angustifolia*.

of *C. farinosa* and *D. angustifolia* in the absence of PEG. In the presence of PEG, *S. singueana* had the highest and *E. racemosa* the lowest intake rate.

The principal component analysis bi-plot (Fig. 2) shows the relative influence of browse species chemical components and intake on the clustering of browse species. The two principal components explained 69.9% of the total variation, with PC1 explaining 48.8% and PC2 21.1% of the variation. A close association between TT, TP, CT, ADL and cellulose was shown. However, the association between these parameters and intake was less evident. Hemicellulose seemed to be closely related to intake in the presence and absence of PEG. An inverse relationship was observed between CP and CT, TT, TP, ADL and cellulose. Clustering of the browse species showed three distinct groups: the most preferred but with high TT and TP content in group I, fibrous and CT-rich browse species in group II, and browse species with low phenolic components but high CP and ash in group III.

Table 3 shows results of the multiple regression models for the prediction of browse species intake based on chemical composition including phenol and tannin components. From the phenolic groups, TP and TT contributed significantly to browse species

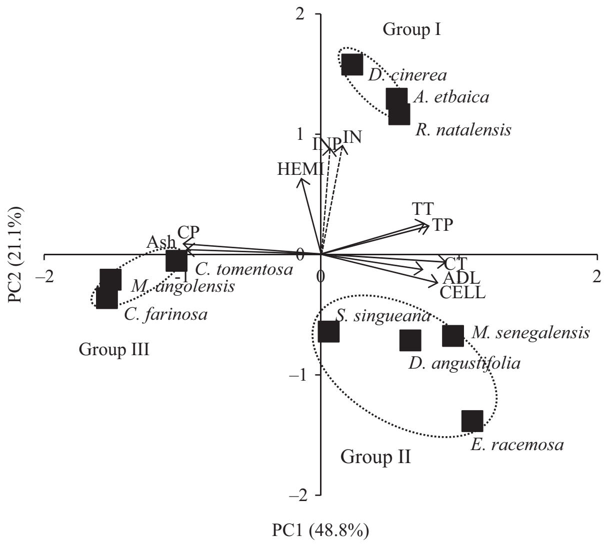

Fig. 2 Principal component analysis (PCA) bi-plot displaying the position of browse species in relation to browse chemical components and intake. ADL, Acid detergent lignin; CELL, cellulose; CP, crude protein; CT, condensed tannins; TP, total phenols; TT, total tannins; HEMI, hemicellulose; IN, browse dry matter intake in the absence of polyethylene glycol (PEG); INP, browse dry matter intake in the presence of PEG.

intake in the absence and presence of PEG respectively. The regression model shows that CP, hemicellulose, cellulose, ADL and TP in the absence of PEG positively contributed to intake. Similarly, in the presence of PEG, the same parameters contributed positively to intake except for the phenolic groups where TT replaces TP.

Discussion

Browse species chemical and phenolic composition

In general, browse species have a superior protein content compared to low quality herbaceous species such as grasses in natural free-range ruminant production systems (Yayneshet et al., 2009). Comparable CP values were reported for most browse species collected from semi-arid areas in Kenya and Ethiopia (Abdulrazak et al., 2000; Yayneshet et al., 2009). *M. angolensis* had the lowest NDF content similar to findings of Osuga et al. (2008). The low fibre content of this species in combination with its high protein content is a desirable characteristic from a nutritional point of view. In comparison, *E. racemosa* and *M. senegalensis* contained higher NDF, ADF and ADL than the other browse species as also reported by Yayneshet et al. (2009), a characteristic which can limit browse species intake or preference. The high fibre contents of these two browse species, however, may in part be due to the presence of insoluble tannin–protein complexes (Reed, 1986) which are not taken into account by currently available fibre analyses (e.g. Van Soest's detergent system). Total phenol content tended to be associated with corresponding levels of total tannins which agrees with previous observations in Acacia species (Abdulrazak et al., 2000). The presence of polyphenolic compounds in plants is widely accepted as a mechanism to deter herbivory and, generally, influences browse species selection by animals. Total tannins accounted for 60–96% of the total phenols and similar percentages of 54–98% were reported for tannin-containing tropical leaves from Kenya (Abdulrazak et al., 2000) and India (Bhatta et al., 2012). The positive correlation between fibre fractions and CT was in line with previous results in tropical browse species (Kaitho et al., 1998; Abdulrazak et al., 2000; Melaku et al., 2010) but disagrees with reports on Spanish shrubs (Frutos et al., 2002). Differences in tannin concentration among species (Abdulrazak et al., 2000; Osuga et al., 2008) or forage maturity stage (Koupai-Abyazani et al., 1993) may explain this discrepancy. Crude protein and fibre content of the grass hay in the present study was comparable to values reported for grasses harvested from rangelands during the vegetative growth stage in a similar climatic area (Yayneshet et al., 2009).

Table 3 Multiple linear regression equation for the relationship between goats' browse species intake and browse species chemical components measured during the first 10 min in the absence (−) and presence (+) of polyethylene glycol (PEG)

	Intercept	CP	Ash	HEMI	CELL	ADL	TP	TT	p
(−)	−169.508	0.425	0.300	0.143	0.253	0.120	0.874		<0.0001
SE	25.95	0.08	0.11	0.03	0.06	0.03	0.13		
p	<0.0001	<0.0001	0.0098	<0.0001	<0.0001	0.0004	<0.0001		
(+)	−153.926	0.231	0.645	0.120	0.211	0.119		0.875	0.001
SE	36.49	0.09	0.18	0.04	0.08	0.04		0.18	
p	0.0002	0.027	0.0008	0.002	0.011	0.007		<0.0001	

SE, standard error; CP, crude protein; HEMI, hemicellulose; CELL, cellulose; ADL, acid detergent lignin; TP, total Phenols; TT, total tannins.

Browse species preference as measured by dry matter intake

Intake measurements were divided into three consecutive 10-min intervals with the first 10-min measurement used to compare preference among browse species as the subsequent 10-min periods are confounded as unequal amounts of browse species were available to the animals. Given the range of tannin concentration in browse species, preference was not against the high tannin-containing browse species. Despite the high tannin and phenol contents, intakes of *D. cinerea*, *R. natalensis* and *A. etbaica* were higher and considered as the most preferred species, similar to the reports by Yayneshet et al. (2008). The latter authors allowed goats to browse naturally while in the study described here, goats were offered air-dried browse species. Drying increases forage cell wall fractions which may contribute to reduced intake of the same forage by ruminants. Diet selection by ruminants is associated with reducing the risk of over ingesting toxic forage components and the need to meet nutritional requirements. Provenza (1996), however, indicated that neither could be the case and preference is related to the association between sensory input upon feed apprehension and post-ingestive effects which occurs involuntarily. This may partly explain the observation that goats prefer high tannin/phenol containing browse based on a previous learned experience. Goats in the present experiment were bought from the same area where browse species were obtained, and therefore, they had previous exposure to the browse species. As such, the animals were experienced and previously had learned to consume a mixture of nutritious as well as potentially toxic plants (Provenza et al., 2003). The goats' previous exposure to the browse species also suggests that a non-cognitive feedback mechanism was established based on past experience, and that decision on preference during the current experiment was based on sensory feedback signals, a non-cognitive phenomenon as described by Provenza (1996). However, in non-experienced animals, the feedback mechanism has to be first established and decision on preference would not be on such mechanism. Thus, past experience and the associated adaptive behaviours of the goats with the apparent positive (or not negative) feedback may partly contribute to preferences for the high tannin browse species in the present experiment. Similar to our observation, Jansen et al. (2007) reported selection of Acacia species by goats with high tannin content regardless of the presence of low tannin content alternatives. Moreover, these authors indicated that tannin contents of the Acacia species were tolerated to a threshold level while minimizing ADF. In the present study, selection against the lower tannin/phenol, high CP and low fibre in *C. farinosa*, *C. tomentosa* and *M. angolensis* could suggest a deliberate selection by goats for higher NDF intake while minimizing ADF intake and also the additional benefits from tannins in increasing ruminal bypass protein. As the intakes of other high tannin/phenol-rich browse species (e.g. *D. angustifolia* and *E. racemosa*) were limited, this could indicate that tannin/phenol levels were minimized to a certain threshold level.

The voluntary intake for a high tannin concentration could be attributed to the natural tendency of proline-rich protein in the saliva of goats to attenuate the negative effects of tannins. Saliva of Criollo goats from Mexico (Ventura-Cordero et al., 2015) and Damascus and Mamber goats of the Mediterranean region (Hanovice-Ziony et al., 2010) exhibited tannin binding characteristics regardless of a prior tannin stimulus indicating that goats are naturally tolerant to relatively high level of tannins. Supplementation of PEG increased total browse species and hence tannin intake as found in previous studies with goats browsing on a tannin-rich forage, *Pistacia lentiscus* L. (Decandia et al., 2000; Landau et al., 2002) as well as a quebracho tannin supplement in lambs (Titus et al., 2000). The effect of PEG in increasing intake could be related to positive effects on digestion in the rumen rather than astringency as PEG exerts effect in the rumen (Silanikove et al., 1996). However, preference for individual browse species was not affected by PEG addition as found by Hernández-Orduño et al. (2012) in short-term trials with goats that had previous browsing experience.

Browse species intake, intake per visit and intake rate during 30 min

The higher consumption of *A. etbaica*, *D. cinerea* and *R. natalensis* during the first 10 min, regardless of PEG presence, is likely to have had an effect on the intake of the remaining browse species. In the second 10 min, increased consumption of *M. senegalensis*, *E. racemosa* followed by *S. singueana* was observed. It is noteworthy that the goats still maintained a preference for browse species with high tannin levels supporting the existence of a tannin intake threshold level (Jansen et al., 2007). The increase in intake for *M. senegalensis* and *E. racemosa* in the second 10 min suggests transition to more fibrous browse species as the second choice, despite the accompanied high tannin levels. When tannin intake is kept below the threshold level, intake of tannin-containing forages is a function of the fibre fraction (Jansen et al., 2007; Alonso-Díaz et al., 2008). The significant increase in *E. racemosa* intake after PEG addition might be associated with its high tannin content neutralized by PEG. Although the concentration of condensed tannins in *S. singueana*, *C. tomentosa* and *C. farinosa* is relatively low, their level of intake increased significantly after inclusion of PEG. The presence of PEG reverses the beneficial role of tannin–protein complex in supplying protein to the lower tract, and therefore, it appeared that goats targeted browse species with high protein but still with reasonable NDF contents, such as *S. singueana*, *C. tomentosa* and *C. farinosa*. Besides, in these species, preference may be influenced more by tannin composition, structural configuration and degree of polymerization associated with sensory properties (Robichaud and Noble, 1990). Although *M. angolensis* had the highest CP content, its consumption was not increased by PEG and this could be associated with its lower NDF content. The effect of day mainly arose from an increasing trend in intake of *E. racemosa*, *S. singueana*, *C. tomentosa* and *C. farinosa*. The interaction between browse species and PEG indicates an effect of PEG on intake that differed with species of browse. Of note is that the highly preferred species had higher intake per visit showing goats maximize intake of the preferred browse species per visit. This result is contrary to the general characteristics of herbivores to reduce polyphenolic intake by reducing meal size (Torregrossa and Dearing, 2009). The discrepancy could suggest that tannin/polyphenolic levels of the browse species did not influence intake per visit. The relationship between intake and intake rate revealed that goats spent more time on the most preferred species and, therefore, targeted species with higher intake rates as reported with grasses (Illius et al., 1999).

Principal component analysis for browse species components and intake prediction

The principal component analysis clustered browse species into three groups. The positive association between TP and tannin contents with fibre fractions was in line with earlier work on a range of browse species (Kaitho et al., 1998). The inverse relationship between CP and CT, TT and TP could be due to the formation of tannin–protein complexes increasing the proportion of indigestible CP (Reed, 1986). A close relationship between browse species intake and hemicellulose was observed which may suggest that the preference for browse species was rather based on the digestible fibre fraction. The positive association between tannin-containing forages intake and their digestible fibre fractions was reported in goats (Alonso-Díaz et al., 2008).

The contribution of CT and TT was not evident in the prediction of browse species intake in the absence of PEG. This result also substantiates our observation that discrimination of browse species by goats was not primarily based on tannins, under the conditions of the present experiment. However, TP contributed to the prediction of DMI indicating phenolic components other than tannins may have influence on browse species intake. In the presence of PEG, the contribution of TT to browse species DMI could be associated with the increase in intake resulting from neutralization of tannins. The association between browse species intake and phenols was in line with results of Alonso-Díaz et al. (2008). However, the positive association between intake and TP was contrary to the findings of Alonso-Díaz et al. (2008) which could be explained by the apparent preference of goats for high tannin/phenol browse species in the present experiment.

Conclusions

The 10 browse species investigated were distinct in chemical composition (including phenols and tannins) and contained a high crude protein content allowing supplementation of grass hay. Independent of PEG supplementation, the goats preferred high tannin-containing browse species, *D. cinerea*, *A. etbaica* and *R. natalensis*. Our results suggest the possibility that goats tend to ingest a certain level of tannins while targeting maximization of intake of other nutrients such as digestible fibre fraction (e.g. hemicellulose) and crude protein. Therefore, tannin content did not primarily determine the preference of goats that have been pre-exposed to tannin-containing forages early in life.

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