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Behavioural response of pure Ankole and crossbred (Ankole × Holstein) cows to seasonal pasture variations in south-western Uganda

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ABSTRACT

This study evaluated the effects of season and pasture species on variations in sward composition, pasture quantity (plant-height and biomass) and quality [crude protein (CP), neutral detergent fibre (NDF) and in vitro organic matter digestibility (IVOMD)]. Behavioural responses of a group of 10 pure Ankole and another of 10 crossbred (Ankole × Holstein) cows to the seasonal variations in pasture quantity and quality were also examined. Irrespective of season, the dominant pasture species was *Brachiaria decumbens*, with scanty presence of *Hyparrhenia rufa*, *Themeda triandra*, *Sporobolus pyramidalis* and *Cymbopogon afronardus*. The sward height, biomass, CP, NDF and IVOMD were dependent on both season and species ($P < 0.001$). Whereas the sward-height and biomass of *B. decumbens*, *H. rufa*, and *T. triandra* peaked during the rainy season, that of *C. afronardus* and *S. pyramidalis* peaked in the dry season. During the grazing cycle, a minimum plant-height of 31 cm and forage biomass of 118 g/m^2, an equivalent of 1180 kg/ha, was recorded for most of the pasture species. The CP content of the pasture species were below 7%, irrespective of season, except for *B. decumbens* which had 8.7% CP in the rainy season. Minimum NDF content for all the pasture species was 67% and 50% during the dry and rainy seasons, respectively. Consequently, IVOMD ranged between 29–61% and 51–65% during the dry and rainy seasons, respectively. Ankole and the crossbred cows increased the number of feeding stations, bites and residence time in patches of species, which were scantly grazed in the rainy season. They also increased standing ($P < 0.01$) at the expense of walking ($P < 0.001$) and social activities ($P < 0.001$). Irrespective of season, more than 40% of grazing occurred in *B. decumbens* patches and both genotypes grazed for ¾ of the time on pasture. However, the crossbred cows required extended grazing duration, resulting into less lying and rumination ($P < 0.05$) on pasture than the Ankole cows. Ankole and the crossbred cows grazed locales with high pasture groundcover and biomass. However, locales with high CP but low forage quantity were also grazed. This study revealed that at an appropriate stocking rate, sufficient forage supply was possible in both seasons. However, the low CP content and less preference for majority of the dominant species compelled the Ankole and the crossbred cows to graze for a long time. Thus, the crossbred cows were constrained by time in both the dry and rainy seasons.

1. Introduction

Pasture quantity and quality are the most important factors that affect the amount of nutrients obtained during grazing. The quantity and quality of natural pastures often fluctuate depending on environmental factors (Tallowin and Jefferson, 1999; Yiruhan et al., 2004), pasture species and grazing management (Motazedian and Sharrow, 1990; Milchunas et al., 1995; Cop et al., 2009). However, Yiruhan et al. (2004) recognized that season and pasture species considerably modify the effects of management on pasture quantity and quality. Consequently, availability of different pasture species may minimize the impact of temporal fluctuations in pasture quantity and quality on livestock production (Fehmi et al., 2002).

Animals react to seasonal pasture quantity and quality constraints by altering their grazing behaviour which affects their wellbeing and productivity (Butler et al., 1997). Such response may include selective foraging which is aimed at maximizing daily

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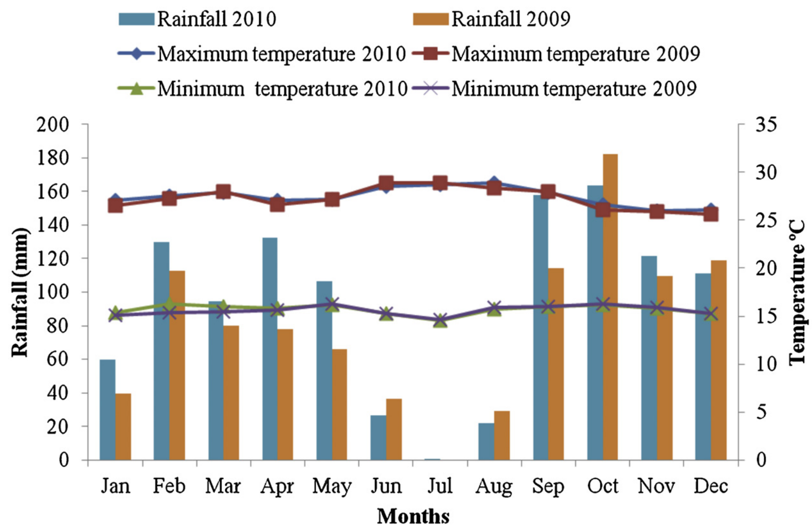

Fig. 1. Means for monthly rainfall and environmental temperature in south-western Uganda during the study.

nutrient intake and may involve a trade-off between pasture availability and quality (WallisDeVries et al., 1999; Ganskopp and Bohnert, 2009). Therefore, animals that are behaviourally well-adapted to environmental changes remain productive (Butler et al., 1997). Usually animals of the same age and physiological status show similar behavioural response to environmental variation although the response may be modified by differences in species or breed and prior experience of the animals in the environment (Mirkena et al., 2010).

In Uganda, natural pastures are found mainly in the rangeland, which is an important herbage resource to about 92% of the national cattle herd (Sabiiti and Mugasi, 2004; MAAIF and UBOS, 2008). The rangeland has heterogeneous pasture species, among which *Hyparrhenia rufa* (*H. rufa*), *Brachiaria decumbens* (*B. decumbens*), *Themeda triandra* (*T. triandra*) and *Chloris gayana* (*C. gayana*) were identified as grass species of high nutritive value (Langdale-Brown et al., 1964; Byenkya, 2004; Roschinsky et al., 2012). Grass species which have low nutritive value like *Cymbopogon afronardus* (*C. afronardus*) and *Sporobolus pyramidalis* (*S. pyramidalis*) lace the pastures, especially pasture fields that are allocated to indigenous cattle breeds (Roschinsky et al., 2012). Rainfall seasonality has a strong modifying effect on the pasture composition, quantity and quality. As a result of low rainfall, cattle face a reduction in the quantity of forage because of the decline in plant cover, plant-height and biomass. Similarly, nutritional quality in terms of crude protein, fibre content and digestibility of the forage also decline during the dry season (Byenkya, 2004; Okello et al., 2005; Roschinsky et al., 2012).

The southwestern rangeland of Uganda is a home to Ankole cattle breed, which was traditionally kept by nomadic pastoralists (Ford and Clifford, 1968). The breed holds a unique place in the livelihood of cattle farmers not only in Uganda but also in the entire Great Lakes region (Wurzinger et al., 2006). However, of late, most of the farmers are changing from the traditional pastoralism to a sedentary life and practice continuous stocking and rotational grazing (Reid et al., 2005; Wurzinger et al., 2006). The farmers also keep mixed herds of Ankole and its crosses with Holstein (Wurzinger et al., 2006; MAAIF and UBOS, 2008).

In a situation where such a fragile ecosystem is experiencing introduction of new cattle genotypes and grazing management (Wurzinger et al., 2006), it is important to gain more information about the pastures and how to utilize this resource properly. This requires drawing together studies on grazing behaviour of the herbivores with knowledge of quantity and nutritional quality of available pasture species to inform grazing management decisions (Dumont and Gordon, 2003). Although earlier research in the area indicated seasonal fluctuations in pasture quantity and quality (Byenkya, 2004; Okello et al., 2005; Roschinsky et al., 2012), there could be a pasture species that may significantly stabilize forage quantity and quality in southwestern Uganda. Moreover, even though the Ankole and the crossbred cattle have been reported to have similar grazing behaviour, how the two genotypes respond to seasonal fluctuations in pasture quantity and quality in the area remained to be understood (Huber et al., 2008). The main objective of the study was to understand seasonal fluctuations in pasture quantity and quality and behavioural adaptation of the two cattle genotypes for rational grazing management in southwestern Uganda.

2. Materials and methods

2.1. Study area

The study was conducted at Ruhengyere ranch (0°35′ S, 30°31′ E) in the south-western rangeland of Uganda. The topography of the area is gently undulating hilly terrains with valleys. The area has bimodal rainfall, which peaked from February to May and September to December. We recorded an annual mean rainfall of 966.2 mm and 1286 mm in 2009 and 2010, respectively (Fig. 1). The dry season was from June to August but July was the driest month. The lowest diurnal minimum and maximum environmental temperatures were 15.6 °C and 27.3 °C, respectively, and both were experienced in the dry season (Fig. 1). Grass species, *H. rufa*, *B. decumbens*, *T. triandra*, *C. afronardus* and *S. pyramidalis* dominated the pastures. *Panicum maximum* (*P. maximum*), *C. gayan*, and *Cynodon dactylon* (*C. dactylon*) were also present but had less than 2% prevalence on the farm.

2.2. Experimental pastures

The experimental pasture consisted of two pasture fields, each measured 20-ha, of which 19.7 ha was in use as pasture and 0.3 ha was for night kraal. The pasture fields had both mixed species and discrete monoculture pastures. The discrete monoculture patches were on a 7-ha pasture block, curved out of each pasture field. Each block was partitioned into 7 paddocks of 1 ha each, resulting into a total of 14 paddocks. These paddocks were marked into 25 m^2 patches of monocultures (≥80% pure stands) of *B. decumbens*, *H. rufa*, *C. afronardus*, *S. pyramidalis* and *T. triandra* in a randomized complete block distribution. Based on relative uniformity in spatial distribution of the dominant pasture species, 5 paddocks which had 72 ± 4 patches containing ≥80% monoculture of each species were selected per pasture block to constitute 10 designated paddocks for the study. The patches which had considerable presence of *C. dactylon*, *P. maximum* and *C. gayana*, in addition to the major species were referred to as "other species" and were included in the study.

2.3. Experimental animals and grazing management

We obtained a group of 10 lactating pure Ankole and another of 10 Ankole × Holstein crossbred cows from the breeding herds at Ruhengyere ranch. Each cow and group represented about 1.4 and 14 Tropical Livestock Units (TLU), respectively. One TLU was defined as a 250 kg ruminant (Jahnke, 1982). Different cows were used for the dry and rainy season studies but were selected to be as similar as possible. The cows were raised under similar environmental and management conditions from birth to the experimental period and would not show conspicuous change in behaviour when approached to a 2 m distance.

Each group was allocated to one of the pasture fields, resulting into the recommended stocking rate of 1 TLU per 1.41 ha (Mulindwa et al., 2009). The groups grazed the 7 paddocks therein at a rotation of 1-day per paddock and grazed the 12.7 ha portion of the unimproved pasture for 13 days, constituting a rotation cycle of 20 days. At the end of every rotation cycle, the groups were alternated to experience grazing in both pasture fields. Other management activities were conducted according to the local husbandry practices in the area. Milking was completed by 7:00 h and grazing was started at 8:00 h and ended at 19:00 h. The cows were guided by herdsmen and watered twice daily at about 13:00 h and 18:00 h at a nearby valley dam. In the evening, the cows were driven back to their night kraals and supplemented with rock salt.

2.4. Data collection

Pasture and behaviour data were collected in two seasons: at the peak of the dry season in July 2009 and the rainy season in October 2010. Each period lasted for 24 days of which 10 days were for data collection. Pasture groundcover (i.e. species composition) was measured in the unimproved portion of the pasture fields using point sampling method (Long et al., 1972). Measurements for plant-height, biomass, CP, NDF and IVOMD were taken in the sampling paddocks a day before each paddock was grazed. Plant height was determined by measuring the tallest culm heights of 10 plants per species per paddock using a common ruler. A 1 m^2 quadrant was thrown into five randomly selected patches of each pasture species. The pasture within the quadrants were cut at 2 cm stubble heights and weighed before submission to the laboratory. The samples were oven dried at 65 °C to a constant weight and weighed to determine dry biomass and later ground to pass a 2 mm sieve. Ground samples were analyzed for crude protein (CP) using the Kjeldahl procedure (AOAC, 1990), neutral detergent fibre (Van Soest et al., 1991) and in vitro digestibility of organic matter (Tilley and Terry, 1963).

Behavioural data were collected from 9:00 h until 13:00 h and from 14:00 h until 18:00 h to account for diurnal variations in grazing behaviour (Rutter et al., 2004). Behavioural pattern data was collected by scan sampling each cow at 10 min intervals (Hull et al., 1960; Jensen et al., 1986), thrice per observation hour, 8 observation hours per day for 10 days per season. Principal behaviour pattern recorded included: grazing i.e. cows were searching with their heads close to the ground, severing, chewing or swallowing herbage; cows moving with their heads up (walking); cows were motionless but on their feet (standing), lying and chewing the cud (ruminating). Meanwhile, suckling, licking, scratching of self or group-mate and agonistic or playful fighting were collectively termed as social behaviour. Data were tallied for each cow within a paddock and individual averages were used in data analyses.

To determine preference for the pasture species, behaviour of each cow was continuously observed (Mitlöhner et al., 2001) in nine sessions. Each session lasted for 10 min to obtain 90 min of preference records. The sessions were spread in nine paddocks and covered all the observation hours. Trained observers recorded the patches visited, the pasture species therein, patch residence time, number of feeding stations in each patch and the number of bites per feeding station. The observers also counted the number of bites taken in the visited patches in a minute (bite rate). A patch was considered visited when the cow had at least one bite in it and a feeding station was defined as an area in which an animal could make one or more bites without moving its fore feet. The preference data was tallied by pasture species across the cows nested under genotype and season. The composition of the diet was determined by comparing the proportion of total grazing time spent on monocultures of each pasture species (Bjugstad et al., 1970). All preference variable data were adjusted for proportions of monoculture patches of each pasture species in a paddock (Stuth, 2000).

2.5. Data analyses

Pasture data were analyzed using the GLM procedure of SAS (2001) in a factorial structure. The model used was: $Y_{ijk} = \mu + \alpha_i + \beta_j + \alpha\beta_{ij} + \varepsilon_{ijk}$. Where Y_{ijk} is the pasture variable measured, μ is the overall mean, α_i is the effect of season (rainy, dry), β_j is the effect of pasture species, $\alpha\beta_{ij}$ is the interaction between pasture species and season, and ε_{ijk} is the residual.

Behaviour pattern and preference data were analyzed using a mixed model of SAS (2001) in a nested-factorial structure. The factorial factors included in behaviour pattern data analysis were season (dry and rainy) and genotype (Ankole and Ankole × Holstein). Meanwhile, an experimental cow was the random factor. The experimental cows were either Ankole or crossbred (Ankole × Holstein) and different cows were selected for dry and rainy seasons studies. Therefore, cows were nested within the genotype and season in the analyses. The model used for behaviour pattern data was: $Y_{ijkl} = \mu + \alpha_i + \beta_j + \gamma_{k(ij)} + \alpha\beta_{ij} + \varepsilon_{ijkl}$. Where Y_{ijkl} is the behaviour pattern observed, μ is the overall mean, α_i is the effect of season, β_j is the effect of genotype, $\gamma_{k(ij)}$ is the random effect of kth cow nested in genotype j and observed in season i, $\alpha\beta_{ij}$ is the interaction between genotype and season and ε_{ijkl} is the residual.

The factorial factors included in the analysis of preference data were season (dry and rainy) and pasture species (*B. decumbens*, *C. afronardus*, *H. rufa*, *T. triandra*, *S. pyramidalis* and "other species"). Meanwhile, the cows constituted the random factor and were nested within season. Genotype was eliminated in the model for preference data because it did not influence preference. The model for preference data analysis was: $Y_{ijkl} = \mu + \alpha_i + \beta_j + \gamma_{k(i)} + \alpha\beta_{ij} + \varepsilon_{ijkl}$. Where Y_{ijkl} is the observed behaviour variable l, μ is the overall mean, α_i is the effect of season, β_j is the effect of pasture species, $\gamma_{k(i)}$ is the effect of kth cow nested in season i, and $\alpha\beta_{ij}$ is the effect of interaction between season and pasture species, and ε_{ijkl} is the residual. Least square means of the response variables generated were separated using the probability of difference option. Pearson's correlation matrix was used to explore relationships between pasture utilization by two different genotypes and pasture quality and quantity parameters during the dry and rainy seasons.

Table 1
Means of variables describing quantity and quality of pasture species during the dry and rainy seasons in southwestern Uganda.

	Ground cover (%)	Sward height (cm)	Patch biomass (g/m^2)	Dry matter (%)	CP (%)	NDF (%)	IVOMD (%)
Dry season							
B. decumbens	37.23^{a}	28.10^{d}	159.15^{fg}	83.90^{c}	6.00^{c}	71.98^{d}	61.11^{b}
C. afronardus	3.44^{d}	54.17^{a}	284.94^{a}	85.08^{c}	4.81^{e}	77.76^{a}	36.89^{f}
H. rufa	16.82^{b}	44.42^{b}	160.75^{f}	88.14^{b}	3.95^{f}	75.35^{b}	42.92^{e}
S. pyramidalis	7.28^{cd}	32.33^{c}	218.22^{c}	91.28^{a}	3.92^{f}	78.46^{a}	29.40^{g}
T. triandra	10.92^{bc}	32.86^{c}	118.17^{h}	83.12^{c}	3.25^{g}	74.88^{b}	56.09^{c}
"*Other species*"	2.13^{d}	28.00^{d}	35.01^{i}	85.42^{c}	5.87^{c}	67.42^{f}	59.88^{b}
Mean	–	36.59	163.01	86.09	4.63	73.25	44.27
Rainy season							
B. decumbens	42.27^{a}	32.78^{c}	174.52^{e}	30.92^{g}	8.71^{a}	54.41^{j}	64.66^{a}
C. afronardus	3.91^{d}	32.97^{c}	271.61^{b}	35.42^{f}	5.57^{d}	73.56^{c}	51.42^{d}
H. rufa	19.28^{b}	30.86^{c}	155.56^{g}	38.82^{e}	6.22^{c}	50.86^{i}	54.29^{c}
S. pyramidalis	9.33^{cd}	31.41^{c}	191.17^{d}	41.72^{d}	5.61^{d}	68.86^{e}	53.67^{cd}
T. triandra	12.65^{bc}	32.86^{c}	170.68^{e}	36.38^{f}	5.90^{cd}	68.50^{e}	55.67^{c}
"*Other species*"	2.56^{d}	32.25^{c}	26.764^{j}	35.42^{f}	7.35^{b}	63.98^{g}	60.45^{b}
Mean	–	31.71	165.35	36.44	6.75	64.42	56.69
S.E.M	2.66	1.31	7.35	0.93	0.32	1.36	1.10
Significance							
Season (S)	ns	***	**	***	***	***	***
Spp (P)	***	***	***	***	***	***	***
S × P	ns	***	***	***	***	***	***

DM: dry matter; NDF: neutral detergent fibre; IVOMD: in vitro organic matter digestibility; SEM: standard error of mean; ^{ab} Least square means for the same parameter within a column with similar superscripts do not differ ($P > 0.05$).

3. Results

3.1. Pasture quantity

The mean groundcover of all the pasture species was not affected by the season (Table 1). However, point sampling indicated that the percentage of bare patches increased from 10% in the rainy season to 22.2% in the dry season. Among the pasture species, *B. decumbens* was the most dominant species; followed by *H. rufa*, *T. triandra*, and *S. pyramidalis* (Table 1). Sward heights of all the pasture species were above 20 cm but plant-heights were affected by both season and pasture species. Surprisingly, *C. afronardus* and *H. rufa* were taller during the dry season than in the rainy season. In contrast, all the pasture species did not vary ($P > 0.05$) in sward heights during the rainy season which was about 31 cm tall as opposed to variation ($P < 0.001$) in dry season, which ranged between 28.0 and 54.0 cm.

The effect of season on biomass and dry matter (DM) content of forage depended ($P < 0.001$) on pasture species (Table 1). Apart from less defoliated *C. afronardus* and *S. pyramidalis* that offered high biomass in the dry and rainy seasons, *B. decumbens* and *H. rufa* provided the highest biomass ($P < 0.001$) among the most grazed species in the dry season. However, in the rainy season, the biomass of *T. triandra* regenerated to match the biomass of *B. decumbens*. The dry matter (DM) contents of all the pasture species were above 83% in the dry-season but it declined to below 42% during the rainy season. *S. pyramidalis* had the highest DM in both the dry and rainy seasons and was followed by *H. rufa*. On the other hand, *B. decumbens* was the most succulent pasture species in the dry and rainy seasons with DM contents of 31 and 84%, respectively.

3.2. Pasture quality

All pasture quality parameters measured depended on season and type of pasture species (Table 1). The crude protein levels for all the pasture species were below 7%, irrespective of season, with the exception of *B. decumbens* which had CP of 8.7% in the rainy season. All the pasture species had fibre levels (NDF) which ranged between 67% and 78% in the dry season, but improved to a range of 50–73% during the rainy season. Consequently, IVOMD ranged between 29–61% and 51–65% during the dry and rainy seasons, respectively. In both the dry and rainy seasons, *B. decumbens* had the highest ($P < 0.001$) IVOMD.

3.3. Grazing behaviour

Season and genotype influenced behaviour pattern of the cows (Table 2). The variables that were significantly influenced by season included standing ($P < 0.01$), walking and social activities ($P < 0.001$). The cows prolonged their standing durations in the dry season at the expenses of walking and social behaviour, which occurred mainly in the rainy season. In both genotype and season, grazing accounted for more than 70% of the total observation time. However, irrespective of season, the crossbreds grazed for longer durations ($P < 0.05$) than pure Ankole cows. The shorter grazing time shown by Ankole cows enabled them to lie and ruminate on pasture longer ($P < 0.05$) than the crossbreds.

Ankole and the crossbred cows responded to the dry season by decreasing their frequency of visits to the different pasture patches but increased the number of feeding stations utilized per patch ($P < 0.05$) (Table 3). However, the bite rate of the cows were significantly low ($P < 0.05$) in the dry season, resulting into significantly less number of bites taken at each feeding station ($P < 0.05$) and pasture patch ($P < 0.001$) in the dry season. *B. decumbens* patches were the most visited in both the dry and rainy seasons (Table 4). However, the number of visits to *B. decumbens* patches was fewer in the dry season. The cows increased the bite rate in *B. decumbens* patches but the number of feeding stations and bites per patch were fewer due to the reduction in residence time. Instead, both the Ankole and the crossbred cows increased the number of feeding stations, bite rates and the number of bites per feeding station in *C. afronardus*, *H. rufa*, *S. pyramidalis* and *T. triandra* patches in the dry season. In both the dry and rainy seasons, groundcover, patch-biomass and crude protein content of the various pasture species were positively correlated with proportions of the pasture species in the diets of pure Ankole and Ankole × Holstein crossbred cows (Table 5).

4. Discussion

All the five dominant pasture species in the area maintained their relative contributions to groundcover in both the dry and

Table 2
Means for activity patterns of Ankole and the crossbred cows during the dry and rainy seasons in southwestern Uganda.

% of observation time on pasture (240 min)								
Season	Dry season		Rainy season		SEM	Significance		
Genotype	Ankole	Crossbred	Ankole	Crossbred		S	G	SG
Activity								
Grazing	76.8^{ab}	78.7^{a}	74.5^{b}	78.2^{a}	1.3	ns	*	ns
Lying	6.5^{a}	4.8^{b}	7.3^{a}	5.1^{b}	0.4	ns	*	ns
Standing	8.0^{a}	7.2^{ab}	5.5^{b}	4.8^{b}	0.8	**	ns	ns
Walking	7.4^{b}	7.7^{b}	9.7^{a}	10.0^{a}	0.4	***	ns	ns
Socializing	1.6^{b}	1.8^{b}	3.1^{a}	2.6^{a}	0.2	***	ns	ns
Ruminating	11.1^{a}	7.7^{b}	11.9^{a}	7.0^{b}	1.7	ns	*	ns

SEM: standard error of mean; S: season; G: genotype; SG: season by genotype interaction; [ab] Means within a row with similar superscripts are not significantly different ($P > 0.05$). $n = 10$; $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$. ns: not significant ($P > 0.05$).

Table 3
Means of preference variables for pure Ankole and the crossbred cows during the dry and rainy seasons in southwestern Uganda.

Season	Dry season		Rainy season		SEM	*P*-Value		
Genotype	Ank	Cross	Ank	Cross		S	G	SG
Preference variables								
Visits per patch (#)	18.6^{b}	18.4^{b}	19.9^{a}	19.5^{a}	0.2	*	ns	ns
Feeding stations patch^{-1} (#)	4.8^{ab}	5.0^{a}	4.6^{b}	4.7^{ab}	0.1	*	ns	ns
Bites per feeding station (#)	4.3^{ab}	4.1^{b}	4.4^{ab}	4.7^{a}	0.1	*	ns	ns
Bites per patch (#)	21.8^{b}	20.8^{b}	26.0^{a}	26.8^{a}	0.5	***	ns	ns
Bites per minute (#)	35.5^{b}	35.2^{b}	38.8^{a}	39.6^{a}	0.3	*	ns	ns
Residence time (s)	34.7^{a}	33.4^{a}	34.4^{a}	35.0^{a}	0.6	ns	ns	ns

Ank: Ankole, cross: Ankole × Holstein crossbreds, SEM: standard error of the mean, S: season, G: cattle genotype, SG: season by genotype interaction, #: number; [ab] Least square means within a row with similar superscripts are not significantly different ($P > 0.05$), $^{*}P < 0.05$, $^{***}P < 0.001$. $n = 10$.

Table 4
Means of variables describing preference of cows for different native grass species in southwestern Uganda during the dry and rainy seasons.

Pasture species	Visits per patch (#)	Number of feeding stations	Bites per feeding station (#)	Bites per patch (#)	Bites per minute (#)	Patch residence time (s)	Proportion in diet (%)
Dry season							
B. decumbens	25.3^{b}	5.5^{b}	7.8^{b}	43.0^{c}	59.5^{a}	43.5^{b}	41.4^{b}
C. afronardus	15.0^{e}	5.6^{b}	2.5^{f}	10.7^{h}	20.3^{g}	32.2^{d}	6.2^{g}
H. rufa	18.6^{cd}	5.3^{bc}	4.3^{d}	22.1^{e}	33.1^{e}	40.0^{c}	15.8^{e}
S. pyramidalis	14.3^{e}	5.0^{c}	4.3^{d}	16.6^{f}	31.0^{e}	32.3^{d}	9.2^{f}
T. triandra	12.3^{e}	3.6^{e}	2.4^{f}	5.4^{i}	28.0^{f}	11.6^{g}	2.6^{h}
"*Other species*"	21.5^{c}	4.6^{d}	5.6^{c}	30.2^{d}	40.5^{c}	44.7^{b}	24.9^{d}
Rainy season							
B. decumbens	31.5^{a}	7.3^{a}	7.4^{b}	56.5^{b}	50.1^{b}	67.3^{a}	45.6^{a}
C. afronardus	15.6^{e}	2.1^{f}	1.6^{g}	2.6^{j}	27.0^{f}	9.9^{g}	1.0^{h}
H. rufa	18.5^{d}	4.1^{d}	3.3^{e}	13.1^{g}	32.2^{e}	25.0^{f}	6.3^{g}
S. pyramidalis	15.2^{e}	4.1^{d}	3.5^{e}	17.7^{f}	36.8^{d}	29.2^{e}	6.9^{g}
T. triandra	13.2^{e}	3.2^{e}	1.6^{g}	6.7^{i}	37.0^{d}	11.1^{g}	2.2^{h}
"*Other species*"	24.3^{b}	7.0^{a}	8.7^{a}	61.7^{a}	52.5^{b}	65.6^{a}	37.9^{c}
S.E.M	0.40	0.20	0.26	0.90	0.57	1.04	0.55
Significance							
Season (S)	***	*	*	***	***	ns	ns
Species (F)	***	***	***	***	***	***	***
S × F	***	***	***	***	***	***	***

#: number; s: seconds; least square means within a column sharing common superscripts are not significantly different ($P > 0.05$); $^{*}P < 0.05$), $^{***}P < 0.001$); S × F: season by pasture species interactions. $n = 20$.

Table 5
Correlations between pasture characteristics and foraging behaviour of Ankole cattle and the crossbred cows in southwestern Uganda.

Pasture spp. characteristic	Likelihood of being grazed by Ankole and crossbreds in dry and rainy seasons ($n = 10$)							
	Dry season				Rainy season			
	Ankole		Crossbred		Ankole		Crossbred	
	r	*P*	*r*	*P*	*r*	*P*	*r*	*P*
Groundcover	0.680	0.137	0.738	0.094	0.935	0.006	0.939	0.005
Patch biomass	0.696	0.124	0.752	0.085	0.951	0.004	0.957	0.003
Crude protein	0.595	0.213	0.533	0.276	0.935	0.006	0.922	0.009
NDF	0.594	0.214	0.599	0.209	−0.455	0.365	−0.415	0.414
IVOMD	0.065	0.903	0.060	0.911	0.626	0.184	0.575	0.233

Crossbred: Ankole × Holstein Friesian crossbred; *r*: Pearson's correlation coefficient; *P*: probability value; NDF: neutral detergent fibre; IVOMD: in vitro organic matter digestibility. Relationship is significant if $P < 0.05$.

rainy seasons, suggesting that the grass community in the sward was stable under the set stocking rates and variations in season. A minimum plant-height of 31 cm and forage biomass of 118 g/m^2, an equivalent of 1180 kg/ha, was recorded for all the dominant species in both seasons. The average body weight for Ankole and the crossbred cows is about 341 kg and 432 kg, respectively (Petersen et al., 2004; Johansson, 2013). At an estimated dry matter intake of 2.5% live body weight (Dias et al., 2011), it can be assumed that in the absence of other constraints, monocultures of the dominant pasture species would be sufficient to support daily forage requirements of the cattle at the present stocking rate.

On the basis of pasture quality, *B. decumbens* and a collection of the minor species, termed "other species" had the best crude protein content in both the dry and rainy seasons. Amongst the studied species, *B. decumbens* and the "other species" were the only ones that met the minimum of 7% protein requirements of cattle only in the rainy season (Bowman et al., 1995; Cochran, 1995). The consequence was that *B. decumbens* and the minor species were also the only species which had ≥60% organic matter digestibility in both seasons. This underscored the close linkage between crude protein content and digestibility of feed in earlier reports (Bowman et al., 1995; Cochran, 1995). It is therefore, likely that without protein supplementation, cattle that grazes in the area in the dry season or swards in which *B. decumbens* is not a dominant species will have low digestibility. Thus, affirming the desire to maintain a dominant *B. decumbens* and integration of drought-tolerant nitrogen fixing fodder legumes such as *Stylosanthes* spp. in the sward (Harrington and Thornton, 1969; Stobbs, 1969; Byenkya, 2004; Roschinsky et al., 2012).

One of the main effects of season on grazing behaviour of Ankole and the crossbred cows was an increased standing duration in the dry season. Increased resting duration during the dry season was also earlier observed in Zebu cattle in Uganda (Wilson, 1961) and dairy cattle elsewhere (Ginane and Petit, 2005; Hejecmanova et al., 2009). According to Hayasaka and Yamagishi (1990) standing serves a purpose of heat regulation, which could be responsible for the relatively stable grazing time of the cattle in both seasons (Albright and Arave, 1997). The cows chose to reduce walking and social activities to extend the standing duration without compromising grazing in the dry season. This could be because grazing is important in meeting animals' nutritional requirements at the circadian level (Linnane et al., 2001).

Previous reports indicated that walking is associated with forage search and selection (Baumont et al., 2000; Canas et al., 2003). It can be assumed that the reduced walking duration in the dry season was responsible for the decrease in visits to patches which contained *B. decumbens*, the most preferred species. The number of feeding stations, number of bites and residence time in *B. decumbens* and "other species" patches also declined in the dry season. On the other hand, it could also explain the increase in the duration of residence in *C. afronardus*, *S. pyramidalis* and *H. rufa* patches in the dry season. The cattle grazed the latter three species moderately in both seasons but the number of feeding stations; bites per feeding station and patches were relatively high in the dry season.

The result of Pearson's correlation matrix positively linked the grazing decisions of Ankole and the crossbred cows to pasture crude protein content, biomass and ground cover. WallisDeVries et al. (1999) and Ganskopp and Bohnert (2009) also reported the central role both pasture quality and quantity hold in shaping grazing behaviour of ruminants. This resulted into *B. decumbens* and the "minor species", which had the best crude protein content, constituting the bulk of the diet of the cattle in both seasons. The biomass and crude protein content of *B. decumbens* was above that of the sward average in the rainy season. This caused the pattern of selective utilization of pastures to persist in the rainy season (Ganskopp et al., 1997), which possibly resulted into the high plant-height and biomass of *C. afronardus* and *S. pyramidalis* patches in the dry season. However, the number of feeding stations and the proportions of the latter two species in the diet increased in the dry season. Thus, under controlled grazing, the dry season provides an opportunity for utilization of the less valuable pasture species (Harrington and Thornton, 1969).

The reduced bite rate in the dry season was expected since the cattle showed relative increase in the number of feeding stations, number of bites per feeding station and residence time in *S. pyramidalis* and *C. afronardus* patches. These species had exceptionally high biomass and fibre contents, which could compromise bite rate (Hejecmanova et al., 2009; Komwihangilo et al., 2007). Since bite rate is the link between short-term intake rate and daily herbage intake (Arnold, 1981), probably forage intake of the cattle was reduced during the dry season.

Both Ankole and the crossbred cows grazed for three quarters of the total observation time on pasture in both the dry and rainy seasons. According to Albright and Arave (1997), grazing activity reduce when the environmental temperatures are above the thermoneutral zone. Environmental temperature probably did not constrain the cows because the maximum environmental temperature in the study area was 29.4 °C, which was less than 32 °C, the upper thermoneutral limit of lactating Holstein cows (Igono et al., 1992). On the other hand, the quantity of forage was also sufficient and grazing was expected to be relatively short (Popp et al., 1997). It was likely that less preference for majority of the pasture species and low crude protein content in the dry season compelled the cows to increase forage search; consequently, grazing time was also increased (Utsumi et al., 2009). Meanwhile, the longer grazing time shown by the crossbred cows could be because they were producing more milk than Ankole cows (Grimaund et al., 2007; Galukande et al., 2008). High milk yields often lead to increase in grazing time to match nutrient intake with milk production demands (Linnane et al., 2001; Casasus et al., 2002).

A longer rumination time was expected during the dry season because of the poor pasture quality (Hejecmanova et al., 2009). However, this study showed that the duration of rumination was similar in both the dry and rainy seasons. Analyses of the relationship between foraging time and rumination duration in the present study are consistent with an earlier study which suggested that long grazing duration shown by both genotypes impeded rumination duration (Bayer, 1990). In this study, whereas a relatively shorter grazing time resulted into a longer rumination time for Ankole cows, on the other hand, a longer grazing duration thwarted rumination time in the crossbred cows. Meanwhile, a similar grazing time for Ankole and the crossbred heifers also resulted into a similar rumination time for both genotypes (Huber et al., 2008). According to Bayer (1990) and Kilgour (2012) grazing always takes precedence over any other activity during the day. Therefore, the crossbred cows could have postponed rumination and other activities to night hours in preference for grazing during the day.

5. Conclusions

Understanding variations in forage resources and its impact on grazing behaviour of animals can support development of novel and modification of existing grazing management. This study suggested that all the dominant pasture species could supply sufficient pasture quantities for cattle throughout the year, implicating possible overstocking for earlier reported forage insufficiencies, especially during the dry season, in south-western Uganda. The most competitive and nutritious pasture species under the grazing management was *B. decumbens*. However, in the dry season, all the pasture species were low in crude protein, necessitating supplementation as a management intervention.

Ankole and the crossbred cows grazed mainly *B. decumbens* but the less prevalent pasture species containing good quality were also considerably grazed in both seasons. However, attempts by both cattle genotypes to graze the rest of the dominant pasture species in the dry season constrained bite rates. Foraging the high nutritive value species required extensive search since the majority were scarce in the sward and the less preferred species constrained bite rate. The combined effect was long grazing duration in both genotypes and the crossbred cows reduced lying and rumination. These were indications that the crossbred cows were constrained by time on pasture in both the dry and rainy seasons. Therefore, regardless of forage quantity, the crossbred cows require ample time when grazing swards containing mixed pasture species with varied nutritive value and preference.

Conflicts of interest

The authors declare no conflicts of interest.

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