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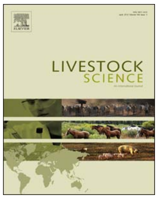

Effects of feeding systems on rumen environment, degradability and passage kinetics in Ankole × Friesian crossbred steers

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ABSTRACT

Natural pastures constitute a large proportion of the feed resource base for meat and milk production in Sub-Saharan Africa. However, there is increasing use of agro-industrial by-products, especially those that are cereal-based as supplementary feedstuff to grazing animals and in diets under semi-intensive and intensive production systems. This study evaluated the influence of feeding systems on rumen environment, degradability and passage kinetics. Six Ankole x Friesian F1 crossbred steers weighing 339 ± 29 kg (about two years of age), each fitted with permanent rumen cannula were used in a replicated 3 × 3 Latin square design ($n_s = 2$). Two steers were allocated per period to one of three feeding systems i.e. (1) sole grazing (control), (2) control plus concentrate supplement (composition g/kg DM: 375 maize bran, 559 brewer's spent grain, 62.5 molasses and 3.75 NaCl), and (3) feedlot systems where steers were fed total mixed ration (TMR) comprising g/kg DM: 200 maize stover, 300 maize bran, 447 brewers' spent grain, 50 molasses and 3 NaCl. Data was collected on rumen pH, ammonia-nitrogen (NH_3-N), volatile fatty acids (VFA) and degradability of dry matter (DM), crude protein (CP) and neutral detergent fiber (NDF). Rumen pH was lowest ($P < 0.001$) at feedlot (5.3) but highest ($P < 0.001$) under sole grazing (6.2). Rumen NH_3-N ranged between 62.8 and 120 mg/l and was higher ($P < 0.001$) in sole grazing than in grazing but supplemented steers and those at the feedlot. Total VFA concentration for sole grazing steers (124 mmol/Mol) was higher ($P < 0.05$) than values observed under feedlot (102 mmol/Mol) while grazing but supplemented steers showed an intermediate value (108 mmol/Mol), not differing significantly from the two other systems. Molar proportion of acetate was higher ($P < 0.001$) in grazing steers compared to values for either grazing but supplemented or those under feedlot while the reverse was true for propionate. The degradation characteristics of DM, CP and NDF were generally higher in sole grazing steers. Although, in most cases, the influence of feeding system on degradability was dependent on the type of feedstuff, feeding systems did not influence total mean retention time. The high extent of DM, CP and fiber degradation in grazing steers compared to supplemented and feedlot steers demonstrates that forage diversity under grazing positively influences degradability. However, attention to the nature and fermentation characteristics of proteins and carbohydrate sources and how they modify rumen environment in different production systems is needed to improve utilization of supplements and TMR.

1. Introduction

Natural pastures constitute a large proportion of the feed resource base for meat and milk production in Sub-Saharan Africa. Most animals subsist on natural pastures, which vary greatly in quantity and quality between the wet and dry seasons (Safari et al., 2011; Selemani et al., 2013). However, there is increasing use of agro-industrial by-products (Ben Salem and Nefzaoui, 2003), especially cereal-based by-products as either supplementary feed to grazing animals or in diets of animals fed under semi-intensive and intensive production systems (Bebe et al., 2003). Semi-intensive and intensive production practices are growing in mixed crop-livestock and agro-pastoral production systems, especially in communities where land for grazing has become limiting (Bouwman et al., 2005). However, most of the changes in the

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production systems occur with limited knowledge on the influence of diets on rumen environment, passage kinetics and the digestibility of feeds which have bearing on the health (Galyean and Rivera, 2003; Mickdam et al., 2016) and performance (González et al., 2012; Shoukun et al., 2016) of the animals. Moreover, the compositions of animal products such as saturated fatty acids in milk are also influenced by the rumen fermentation patterns (Shingfield et al., 2008). Therefore, understanding rumen fermentation characteristics in the fast changing livestock productions systems in the tropics would provide a better planning for improved animal performance and product quality.

Further still, most feeding practices in Sub-Saharan Africa occur without the use of locally developed feeding standards that could guide diet formulation. Subsequently, dietary and nutrient imbalances are common among animals fed concentrates under intensive or semi-intensive practices. However, the extent to which different diets and different production systems affect rumen environment, passage kinetics and digestibility of feeds is an area that is scarcely researched in the tropics (Madsen et al., 1997). Changes in concentrations of volatile fatty acids, ammonia-nitrogen and ruminal pH levels are good markers for describing nutrient utilization by ruminants. Also, information on ruminal fermentation pattern and nutrient supply (Annison and Bryden, 1998) and degradation parameters of feeds (McDonald et al., 1987) are considered important for the development of feeding systems for ruminants. Since concentrate diets are associated with low rumen pH and higher concentration of propionate, it was hypothesized that the influence of feeding systems on degradation characteristics is also affected by the type of feeds on offer which also affects passage kinetics and rumen environment. This study was, therefore, aimed at evaluating the influence of natural grazing pastures, supplementation of grazing with concentrate and feedlot systems on rumen environment, degradability of feeds and passage kinetics in steers.

2. Materials and methods

2.1. Study site

This study was conducted between February and August 2012 on a private ranch located in Mubende district found within the cattle corridor in central Uganda. The study was part of a broader beef production research where the effects of the feeding systems on daily growth and feed efficiency were evaluated (Asizua et al., 2017). Mubende district lies along the longitude 31°40΄E and latitude 00°30΄N at an altitude of 1300 m above sea level. Annual rainfall in the area ranges between 850 mm and 1300 mm distributed between two wet seasons of April-May and September-November. Mean daily temperature ranges between 15 and 28 °C. The predominant grass pasture species in the area include Signal grass (*Brachiaria brizantha, Brachiaria ruziziensis*), Rat's tail (*Sporobolous pyramidalis*), Star grass (*Cynodon dactylon*), Couch grass (*Digitaria scalarum*) with sparse distribution of legumes such as Glycine (*Neonotonia wightii*), Greenleaf desmodium (*Desmodium intortum*) and Silver leaf desmodium (*Desmodium uncinatum*). Predominant tree species included Acacia (*Acacia hockii*), Albizia (*Albizia coriaria, Albizia zygia*) and Bushwillow trees (*Combretum* spp.).

2.2. Animals, treatments and experimental design

Six Ankole × Friesian F1 crossbred steers weighing 339 ± 29 kg initially (about two years of age), each fitted with a permanent rumen cannula of size 8c (Bar diamond Inc., Parma, USA) were used in a 3 × 3 replicated Latin square design ($n_s = 2$). All procedures were conducted within the provisions of section 12 of the Uganda animals (preventions and cruelty) act (ULII, 2000). The treatments included; 1 - Sole grazing (GZ) as control, 2 - Grazing plus supplementation with concentrate (GZS) and 3 – Confinement feeding in a feedlot with a total mixed ration (TMR) comprising maize stover and concentrate formulated from locally available agro-industrial by-products. Three steers of similar body weights were randomly allocated to one of the three feeding systems in each of the three periods. The Latin square was then replicated and conducted simultaneously with a different set of three other steers. Each period lasted for 21 days, 16 of which were for adaptation and 5 for sampling and data collection. The steers were kept on natural pastures for 30 days during the acclimatization period used as a transition between periods. Grazing steers were released at 08:00 h for grazing and returned by 18:00 h. Grazing and supplemented as well as the feedlot steers received a locally formulated concentrate which targeted to meet requirements for 1.0 kg live body weight gain per steer per day (NRC, 1984; Asizua et al., 2009). The grazing steers that were supplemented received the concentrate overnight as 1.5% of their live body weight in experimental pens, which allowed at least 12 m^2 of space per steer. The feedlot steers received the concentrate as part of a total mixed ration (TMR) comprising 80% concentrate and 20% maize stover. The TMR was offered every morning between 08:00 and 09:00 h in similar pens described for the grazing and supplemented steers. Refusals were collected and weighed every morning to estimate previous day's intake. Feed and refusal samples were collected daily, air dried at the farm and merged to form weekly samples and taken for laboratory analysis.

2.3. Experimental feeds

Grazing animals had access to three paddocks (7.5 ± 2.3 ha) containing natural heterogeneous pastures. Two of the paddocks were on adjacent hills while the third paddock was along the valley separating the two hills. The area was originally natural tropical savanna vegetation reclaimed for pasture through bush clearing about two years before the experiments were conducted. The heterogeneous natural pastures in the paddocks were maintained through continuous weeding using hand slasher and hand hoe. Watering points distributed at random points with an average of at least one trough per square kilometre provided water for the grazing animals. The paddocks were also accessible to a herd of about 110 animals at least once in a week during the experimental period as there was no strict grazing management scheme on the ranch.

Pasture biomass yield in the paddocks was assessed using the stratified random sampling procedures for large grazing areas (Cayley and Bird, 1996). Paddocks were stratified to at least five strata by slope. Five samples were taken randomly using a 1 m^2 wooden quadrat from each stratum for biomass yield. Samples were clipped at a height of about 5 – 10 cm above ground depending on forage mass. Fresh samples were stored in polythene bags and weighed immediately. Samples were transferred to the laboratory and dried at 60 °C in a forced air oven for at least 48 h for dry matter determination (DM). Average pasture biomass during the experimental period was 1.7 ± 2.4 t DM/ha. Subsamples were taken and thoroughly mixed and later used for analysis of chemical composition and degradability studies.

Grazing steers that were supplemented received the locally formulated concentrate. The concentrate comprised (g/kg DM); 375 maize bran, 559 brewers' spent grain, 62.5 molasses and 3.75 NaCl. For ease of uniform mixing, the molasses was diluted with water in a ratio of 1:1. Meanwhile, the feedlot steers were offered a TMR comprising the concentrate but mixed with maize stover in proportions stated before. The maize stover was collected from the surrounding crop farms and chopped to pieces of about 3–6 cm using a John Deere forage chopper. The concentrate was then blended with maize stover to form the TMR. The TMR subsequently comprised (g/kg DM): 200 maize stover, 300 maize bran, 447 brewers’ spent grain, 50 molasses and 3 NaCl. The TMR was formulated to provide 130 g/kg DM of CP and 10 MJ ME/kg DM. The formulated ration targeted to meet requirements for average daily gain (ADG) of 1000 g/animal/day (NRC, 1984). The TMR was offered ad libitum by adding 10% of the previous day's intake to the daily offer. Throughout the experimental period, free access was provided to water and Maclik mineral block, which consisted of the following elemental components (%): Ca (2.6), P (1.4), Na (31.93), Cl (49.28), Mg (1.8), Cu (0.32), Co (0.04), Fe (0.5), K (0.006), I (0.02), Zn (0.36), Mn (0.28) and S (0.36); and compounds (%): CaO (3.64), P_2O_5 (3.21) and NaCl (81.21).

2.4. Experimental procedures

2.4.1. Rumen fermentation

On the 21st day of each experimental period, rumen contents were taken by hand at 07:00, 10:00, 13:00, 16:00, 22:00, 01:00, 04:00 and 07:00 h from every animal to measure rumen fermentation characteristics. On the days of sampling, the steers were deliberately confined in a paddock with a crush facility to enable restraining when needed. Approximately 250 ml of rumen contents (i.e. liquid with fiber) were removed from the medial rumen of each steer and separately placed in 500 ml beakers. Ruminal pH was immediately measured using a glass rod probe digital pH meter (Knick, Portamess® 922) with a daily 2-point calibration (pH 4.0 and 7.0). Ruminal fluid was strained through four layers of cheesecloth and acidified with 1 ml of 3 M H_2SO_4 per 100 ml rumen fluid from each steer, packed on ice during transport to the laboratory and then stored at −20 °C for subsequent analysis of volatile fatty acids and ammonia-nitrogen.

2.4.2. Degradability of feeds

Degradability of feeds was conducted according to procedures described by the International Livestock Centre (Osuji et al., 1993). At 13:00 h on day 16 of each experimental period, duplicate nylon bags (5 × 10 cm; pore size 53 ± 10 µm, Bar diamond, Inc., Parma, USA) containing about 3.5 g of feed samples ground to pass a 2 mm screen in a hammer mill were suspended in the rumen of each steer for 0, 3, 6, 12, 24, 36, 48, 72 and 96 h for all feedstuffs. The sequential addition method of bag placement into the rumen as earlier described by Osuji et al. (1993) was used. After removal, bags were repeatedly rinsed in cold tap water until the rinse was clear. Bags were stored on ice for transport to the laboratory where it was dried in a forced air oven (60 °C) for at least 24 h until constant weight to determine DM degradability and the residues were further analyzed for crude protein (CP) and neutral detergent fiber (NDF). Degradation parameters were estimated by fitting the exponential equation of Ørskov and McDonald (1979) using Statistical Analysis Systems (SAS, Institute Inc.).

2.4.3. Passage kinetics

Chromium mordanted fiber (57.6 g Cr/kg DM of fiber) from pastures and stover were prepared according to Udén et al. (1980). The mordanted straw was then ground through a 5 mm screen of a hammer mill and stored in polythene bags pending administration. At 07:00 h on day 16 of each experimental period, fecal grab samples were taken from each steer for 0 h samples. Steers were then dosed through the rumen cannula with 80.8 ± 0.9 g of mordanted fiber wrapped in paper tissue. The fiber was slightly wetted in the paper with water before introduction into the rumen. Steers on pasture were dosed with fiber from pasture while steers at the feedlot were dosed with fiber from maize stover. Further fecal grab samples were taken after 3, 6, 12, 18, 24, 27, 30, 33, 37, 48, 54, 60, 72, 84, 96 and 120 h post dosing. Fecal samples were packed in polythene bags and transferred for drying in forced air oven at 60 °C for 48 h. Samples were ground through a 2 mm sieve in a hammer mill and stored awaiting analysis of chromium.

2.5. Chemical analysis

2.5.1. Chemical composition

Chromium concentration in dosed fiber and fecal grab samples were analyzed using atomic absorption spectrophotometry (GBC scientific equipment, Dandenog, Australia) with air-acetylene flame. Samples were prepared by heating at 360 °C with a digestion mixture comprising selenium, lithium sulphate, concentrated sulfuric acid and 30% hydrogen peroxide in a block digester. Dry matter of feeds was determined in a forced air draft oven at 60 °C until constant weight. Ash corrected Neutral Detergent Fiber (NDF) determined without the use of amylase and ash corrected Acid Detergent Fiber (ADF) were analyzed according to the procedures of Van soest et al. (1991) while ADL was determined by solubilization of cellulose with sulfuric acid and corrected for acid insoluble ash. Crude protein (CP), calcium (Ca), phosphorous (P) and total ash were determined according to the procedures of AOAC (1990). Crude protein was determined using the Kjeldahl method while Ca and P were determined using flame photometry and spectrophotometry, respectively. Crude fat was extracted with diethyl ether using the Soxtech method. The sulfuric acid anthrone method was used to determine the starch content. Samples were incinerated at 600 °C for 8 h to determine total ash contents. Metabolisable energy (ME) was estimated from chemical composition of feeds following the equation: $\mathrm{ME\ (MJ/kg\ DM)} = 0.012\mathrm{CP} + 0.031\mathrm{EE} + 0.005\mathrm{CF} + 0.014\mathrm{NFE}$ (MAFF, 1975).

2.5.2. Ammonia-nitrogen, volatile fatty acids and passage kinetics

Frozen samples were thawed and analyzed for ammonia-nitrogen (NH_3-N) and volatile fatty acids (VFA). Ammonia-nitrogen was analyzed after 5 ml were drawn from the thawed rumen fluid samples which were centrifuged at (4000 × *g*, 20 min) and the supernatants analyzed according to the procedures of micro-Kjeldahl.

Volatile fatty acids (VFAs) were analyzed according to Erwin et al. (1961) and Cottyn and Boucque (1968). After thawing at room temperature, 1 ml sub-samples were taken from each sample and 30 µl of 34% orthophosphoric acid was added and left to stand for 30 min. Samples were centrifuged (pico-Heraeus, Kendro) at (12,879 × *g*, 10 min). Supernatants were transferred to GC-vials and immediately stored at −20 °C until analysis. After thawing at room temperature, 1 µl was analyzed in a gas chromatograph (Perkin Elmer, Clarus 500, USA) equipped with flame-ionisation detector (FID) using TR-FFAP column – 30 m × 0.25 mm (internal diameter) and a stationary phase of 0.25 µm thickness (Teknokroma). Hydrogen gas was used as mobile phase at 12 kPa column head pressure. The injector temperature was set at 260 °C and detector at 330 °C. The oven was programmed at 110 °C, 8 °C/min to 190 °C, then 20 °C/min to 230 °C where it was left isothermal for 1 min before cooling for the next run. The flame-ionisation detector (FID) was used to detect components eluting from the column. The detector output signal was captured and recorded using Perkin Elmer interface with TotalChrom workstation 6.3.1 software data system for processing and storage of chromatographic data. The peaks were identified by comparison with standard chromatogram of standard mixture of seven VFAs (Volatile Acid Standard Mix, SUPELCO, Bellefonte, PA, USA) analyzed using the same procedure. Volatile fatty acid concentrations were quantified using standard curves plotted from analysis of individual standard VFAs (Sigma-Aldrich, Germany).

Passage kinetics was calculated according to Huhtanen and Kukkonen (1995). Fecal marker excretion curves were fitted to two compartment models (G3G1) assuming age-dependent distribution of residence time in the first compartment and exponentially distributed residence times in the second compartment. Curve fitting was carried out using the iterative Marquardt method in PROC NLIN procedures of Statistical Analysis Systems Institute Inc. as described by Moore et al. (1992). Detailed explanation of the terminology and calculations are found in Pond et al. (1988). The model estimates the passage rate from two compartments and transit time (TT). The mean retention time in the first, age-dependent compartment ($CMRT_1$), was calculated as $3/\lambda$ and in the second, age-independent compartment ($CMRT_2$) as $1/k$. Total compartmental retention time (CMRT) was calculated as $CMRT_1 + CMRT_2$ and the total mean retention time (TMRT) as CMRT + TT.

2.6. Data analysis

The MIXED procedure of SAS with repeated measures was used to analyze data on rumen environment (pH, NH_3-N and VFAs) using Statistical Analysis Systems (SAS Institute Inc.). The following model was used:

$$Y_{ijkl} = \mu + F_i + T_j + p_k + s_l + (FT)_{ij} + \varepsilon_{ijkl}$$

Where Y_{ijkl} represents the observation on steer l given treatment i at time j and period k; F_i represents the fixed effect of the i^{th} feeding system (i = 1,2,3); T_j represents the fixed effects of the j^{th} time (j = 1, 2, …, 8); p_k represents the random effects of the k^{th} period (k = 1, 2, 3); s_l represents the random effects of the l^{th} steer (j = 1, 2, ….., 6), $(FT)_{ij}$ represents the interaction effects between the i^{th} feeding system and the j^{th} time and ε_{ijkl} is random error.

Data on degradability was analyzed using the MIXED procedure of SAS Inst. The fixed effects included feeding system, feedstuff and the interaction between feeding system and feedstuff. Each steer was included as random effect. However, for passage kinetics data, feeding system was the main effect while period and steer were included as random effects to reduce on variability attributed to size of steers. Least squares means were separated using the probability of difference option.

3. Results

3.1. Chemical composition of feeds and Rumen environment

While concentrates were high in CP continent (173 ± 12 g/kg DM), pasture and maize stover had relatively lower values of 95 ± 16 g/kg DM and 39 ± 5 g/kg DM, respectively. However, the reverse was true for NDF and ADF composition. The proportion of ME content of pasture and stover were 0.7 and 0.64, respectively, relative to that in the concentrate. The partitioning of the CP showed that the concentrate had close to more than double the effective degradability than pastures.

Rumen ammonia-nitrogen (NH_3-N) was higher ($P < 0.001$) in sole grazing steers than in those grazing and supplemented. However, steers under feedlot had the lowest ($P < 0.001$) levels of NH_3-N (Table 2). Peak concentration of NH_3-N for sole grazing steers occurred at 13:00 h while the concentrations for the steers under feedlot and those under grazing but supplemented were generally consistent throughout 24 h with slightly lower values in the night (Fig. 1A). Rumen pH was similarly higher ($P < 0.001$) in grazing steers than those that were grazed but supplemented and steers fed at the feedlot. Although pH values were fairly consistent throughout the 24 h, lowest values occurred between 19:00 and 22:00 h for all feeding systems (Fig. 1B). Total VFA concentration for sole grazing steers (124 mmol/Mol) was higher ($P < 0.05$) than values observed under feedlot (102 mmol/Mol) while grazing but supplemented steers showed an intermediate value (108 mmol/Mol), not differing significantly from the two other systems. Concentration of total VFAs for grazing but supplemented steers had two peaks, one in the morning, the other in the evening; however, sole grazing steers and feedlot steers generally had similar patterns with a single peak in the evening (Fig. 2). The proportion of acetic acid was

Table 1
Chemical and nutritional composition of feeds.

	Concentrate	Pasture	Stover	Brewers' sp ent grain
DM (g/kg feed)	490 ± 42	310 ± 47	880 ± 23	270 ± 51
CP (g/kg DM)	173 ± 12	95 ± 16	39 ± 5	235 ± 31
Crude fat (g/kg DM)	36.3 ± 6.1	6.2 ± 2.1	0.05 ± 0.1	54 ± 14
Crude fiber (g/kg DM)	113 ± 3	298 ± 6	502 ± 9	124 ± 7
NDF (g/kg DM)	425 ± 31	781 ± 34	868 ± 11	649 ± 30
ADF (g/kg DM)	119 ± 30	360 ± 67	487 ± 26	134 ± 10
ADL (g/kg DM)	49.0 ± 14	42 ± 18	42 ± 14	31 ± 10
Starch (g/kg DM)	104 ± 15	nd	nd	31.3 ± 2.9
Ash (g/kg DM)	108 ± 19	114 ± 16	82 ± 11	54 ± 15
P (g/kg DM)	4.8 ± 2.2	3.7 ± 0.2	5.6 ± 1.0	3.4 ± 0.1
Ca (g/kg DM)	5.3 ± 0.3	5.6 ± 0.3	6.2 ± 1.0	5.5 ± 0.2
ME (MJ/kg DM)	11.4 ± 1.0	8.0 ± 1.1	7.3 ± 0.4	11.8 ± 1.2
QDP g/kg DM)	129 ± 3.1	74.2 ± 1.6	24.7 ± 0.6	75.0 ± 5.8
SDP (g/kg DM)	14.3 ± 3.1	3.7 ± 1.7	2.8 ± 0.6	85.2 ± 6.9
ERDP (g/kg DM)	118 ± 8.6	63.1 ± 0.6	22.5 ± 0.9	145 ± 2.5
UDP (g/kg DM)	29.3 ± 0.7	17.10.5	11.5 ± 0.3	74.8 ± 1.1

CP: Crude protein; nd: not detected, ME (MJ/Kg DM) = 0.012CP + 0.031EE + 0.005CF + 0.014NFE (MAFF, 1975), QDP: Quickly degradable CP = $a \times$ CP; SDP: Slowly degradable CP = $[(b \times c)/(c + r)] \times$ CP, where r is an assumed rumen outflow rate (0.03) for solids; ERDP: Effective rumen degradable CP = (0.8 × QDP) + SDP; UDP: Undegradable CP = CP - (QDP + SDP) (Source: Kabi and Bareeba, 2008).

Table 2
Least squares means showing the effects of feeding system on rumen environment and fermentation pattern in Ankole x Holstein Friesian crossbred steers.

	GZ	GZS[†]	Feedlot	SEM	Significance
DMI (concentrate, kg/steer/day)	na	4.3 ± 0.8	6.5 ± 1.2	na	na
DMI (stover kg/steer/day)	na	na	1.3 ± 0.2	na	na
Total CP intake (g/steer/day)	na	743 ± 138	1332 ± 225	na	na
Total ME intake (MJ/steer/day)	na	49 ± 9.1	83 ± 14.7	na	na
NH3-N (mg/l)	120^a	88.3^b	62.8^c	3.1	***
pH	6.2^a	5.6^b	5.3^c	0.04	***
Total VFAs (mmol/l)	124^a	108^{ab}	102^b	6.8	*
Individual VFAs (mole/100 mol)					
Acetic acid	63.6^a	57.1^b	50.5^c	1.6	***
Propionic acid	16.0^c	21.3^b	24.2^a	1.34	***
Butyric acid	15.4^b	17.1^b	20.9^a	1.24	**
Isobutyric acid	1.5^a	1.1^b	0.8^c	0.16	***
Isovaleric acid	2.0	1.6	1.8	0.20	ns
Valeric acid	1.4	1.4	1.7	0.15	ns
Caproic acid	0.06^b	0.06^b	0.1^a	0.01	***
A:P	4.0^a	2.7^b	2.1^c	0.19	***

^{abc}Means with similar superscripts within rows are similar, ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$, GZ – Sole grazing, GZS – grazing plus concentrate supplement, SEM – Standard error of the mean, A:P – Acetic acid to propionic acid ration, na – not determined.

[†] Values provided for DM, CP and ME intakes are limited to concentrate supplement.

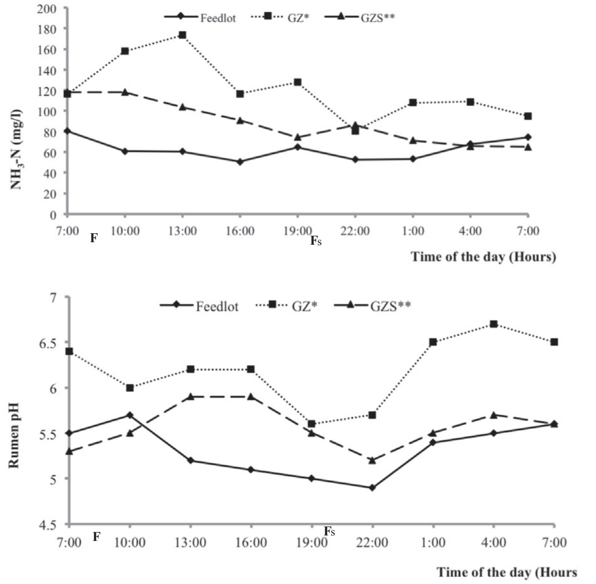

Fig. 1. Interactive effects of feeding system and time on daily variation of NH_3-N (A) and pH (B) with time of the day in Ankole x Holstein Friesian crossbred steers. *GZ – Grazing, **GZS – Grazing plus concentrate supplement, F – Morning feeding time (between 08:00 and 09:00 h), Fs - evening feeding time (19:00 – 20:00, concentrate supplement for grazing only).

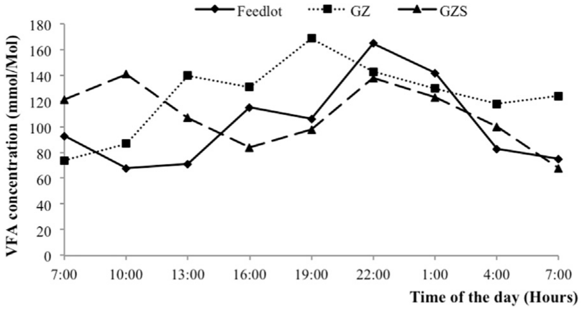

Fig. 2. Interactive effects of feeding system and time on total concentration of volatile fatty acids in Ankole x Holstein Friesian crossbred steers. GZ- Sole grazing, GZS – Grazing plus supplementation with concentrate.

higher ($P < 0.001$) in sole grazing steers than for those grazing but supplemented and those under feedlot system, but the reverse was true for propionic acid concentration. Butyric acid proportion in the rumen ranged between 15.4 and 20.9 (mole/100 mol) for all treatments, however, feedlot steers had higher ($P < 0.01$) proportions than for sole grazing and the grazing but supplemented steers. The ratio of acetic acid to propionic acid in sole grazing steers was more than double that of steers at feedlot, however, the ratios were different ($P < 0.001$) among the steers in the different feeding systems.

3.2. Degradability characteristics of DM, CP and NDF

The degradation characteristics of DM, CP and NDF for concentrate, pasture and maize stover in the rumen environment of steers as influenced by the different feeding systems are presented in Table 3. The readily soluble fraction (*a*) and the potentially degradable but not soluble fraction (*b*), potential degradability (PD) and effective degradability (ED) of DM varied ($P < 0.001$) between feedstuffs and feeding systems ($P < 0.001$), however, rate of degradation of *b* presented as *c* only varied between feeds. Interaction between feeding system and feedstuffs was also significant ($P < 0.001$) for all DM degradation characteristics except for *c*. The highest *a* fraction of DM for the three feedstuffs was observed under grazing, however, the least *a* fraction for concentrate was observed under grazing but supplemented steers while that for pasture was observed at the feedlot. Effective DM degradability was highest under sole grazing system for all feedstuffs. Stover had the least values of ED while highest values were observed for concentrate in all production systems.

Degradation characteristics of CP varied between feedstuffs ($P < 0.001$) except the rate of degradation *c* while fractions *a,* PD and ED were affected by feeding systems. Interactions between feeding system and feedstuffs were observed for *a* fraction and ED of CP. While the lowest values of *a* fraction of CP for concentrate (741 g/kg) and stover (572 g/kg) were observed under grazing but supplemented, the lowest values for pasture (635 g/kg) was observed under feedlot system. Highest ED of CP for pasture were observed in the grazing (908 g/kg) and grazing but supplemented (899 g/kg) feeding systems but differed ($P < 0.001$) from values observed for concentrate (878 g/kg) and stover (767 g/kg) in the grazing system. Stover had the lowest ED in all feeding systems.

The *b* fraction, PD and ED of NDF differed between feedstuffs ($P < 0.001$) and feeding systems ($P < 0.05$) although only ED was influenced ($P < 0.001$) by the interaction between feedstuffs and feeding system. The *b* fractions for NDF degradation ranged between 250 and 401 (g/kg DM) for pasture and stover in all feeding systems. Except under grazing, the ED of NDF was similar for pasture and stover and was also lower than the ED of the concentrate.

3.3. Passage kinetics

The retention time of the second age-dependent compartment ($CMRT_2$) under feedlot was more than twice ($P < 0.05$) the value observed under sole grazing but slightly greater than one and half times the observed value under grazing but supplemented feeding system (Table 4). Total mean retention time ranged between 55.5 h at the feedlot and 60.8 h under grazing, but with no differences ($P > 0.05$) between the feeding systems. Similarly, there were no differences ($P > 0.05$) observed between feeding systems for the other measured parameters of passage kinetics.

4. Discussion

Although natural pastures traditionally constitute a large proportion of the feed resource on which most ruminants subsist for meat and milk production under sole grazing, the emerging trends of production systems demand for increased use of agro-industrial by-products and crop residues not only to enhance nutrient supply through a diversity of feedstuffs (Table 1) but also for economic optimization. However, as ruminant production systems and feedstuff composition of the diets

Table 3
Least squares means showing the degradation characteristics of DM, CP and NDF for concentrate, pasture and stover in rumen environment of Ankole × Holstein Friesian crossbred steers under three production systems.

		Feedlot			GZ			GZS			SEM	Significance		
		Conc	Pasture	Stover	Conc	Pasture	Stover	Conc	Pasture	Stover		FS	Feedstuff	FSxFeedstuff
DM	a (g/kg)	396^{b}	104^{e}	27^{f}	509^{a}	131^{d}	95^{e}	334^{c}	114^{d}	24^{f}	9.0	***	***	***
	b (g/kg)	366^{b}	280^{d}	368^{b}	336^{bc}	335^{bc}	272^{d}	430^{a}	302^{c}	316^{cd}	17.9	*	***	***
	c (h^{-1})	37.4^{a}	35.9^{a}	15.0^{b}	39.5^{a}	27.2^{ab}	16.6^{b}	38.7^{a}	35.3^{a}	16.3^{b}	5.8	ns	**	ns
	PD (g/kg)	762^{b}	384^{de}	395^{d}	845^{a}	466^{c}	366^{de}	764^{b}	417^{cd}	339^{e}	19.5	**	***	*
	ED (g/kg)	584^{b}	244^{d}	148^{e}	697^{a}	290^{c}	223^{de}	571^{b}	267^{cd}	135^{e}	11.3	***	***	***
CP	a (g/kg)	748^{d}	781^{c}	635^{f}	827^{b}	862^{a}	696^{e}	741^{d}	857^{ab}	572^{g}	12.7	***	***	***
	b (g/kg)	164^{ab}	84^{c}	119^{ab}	115^{bc}	58^{c}	161^{ab}	176^{a}	64^{c}	156^{ab}	24.2	ns	***	ns
	c (h^{-1})	35.7	65.1	46.1	28.1	10.9	27.7	25.6	56.2	81	47	ns	ns	ns
	PD (g/kg)	911^{ab}	865^{b}	753^{c}	942^{a}	920^{ab}	856^{b}	917^{ab}	922^{ab}	729^{c}	25.3	**	***	ns
	ED (g/kg)	831^{c}	820^{c}	705^{e}	878^{b}	908^{a}	767^{d}	817^{c}	899^{a}	644^{f}	7.6	***	***	***
NDF	a (g/kg)	0	0	0	0	0	0	0	0	0	0	na	na	na
	b (g/kg)	488^{b}	388^{bc}	280^{d}	727^{a}	337^{cd}	401^{bc}	523^{b}	374^{b}	253^{d}	57.7	*	***	ns
	c (h^{-1})	33.8	29.4	27.8	30.9	26.4	29.9	24.6	31	28.3	7.7	ns	ns	ns
	PD (g/kg)	522^{b}	392^{bc}	280^{e}	729^{a}	352^{c}	404^{bc}	523^{b}	378^{c}	253^{c}	57.2	*	***	ns
	ED (g/kg)	285^{b}	140^{de}	133^{de}	366^{a}	171^{d}	128^{e}	227^{c}	152^{de}	121^{e}	20.3	***	***	***

Means with similar superscripts within rows are similar, ****$P < 0.001$, **$P < 0.01$, *$P < 0.05$,* GZ – Sole grazing, GZS – grazing plus concentrate supplement, SEM – Standard error of the mean, FS – effects of feeding system, F – effects of feed, FxFS–Interaction effects of feeding system with feed, DM – Dry matter, CP – Crude protein, NDF – neutral detergent fiber, a – readily degradable (soluble) fraction, b –degradable, not soluble fraction, c – rate of degradation of b fraction, PD – potential degradability, ED - effective degradability ($k = 0.03$).

Table 4

Least squares means showing effects of feeding system on passage kinetics[#].

Item	GZ	GZS	Feedlot	SEM	Significance
CMRT1	37.1	30.8	22.3	4.5	ns
CMRT2	12.0^{b}	13.1^{ab}	24.4^{a}	5.1	**
CMRT	49.1	43.6	46.8	4.9	ns
TD	11.4	14.2	8.7	1.8	ns
TMRT	60.8	57.7	55.5	4.6	ns

Means with similar superscripts within rows are similar, $^{***}P < 0.001$, $^{**}P < 0.01$, $^{*}P < 0.05$, ns – not significant, GZ – Sole grazing, GZS – grazing plus concentrate supplement, SEM – Standard error of the mean, CMRT$_1$ – mean retention time in the first age-dependent compartment, CMRT$_2$ – mean retention time in the second age-independent compartment, CMRT – total compartmental retention, TD – Time delay, TMRT – total mean retention time. [#]Mordanted pasture was used for the grazing steers while mordanted maize stover was used for the feedlot steers.

change, various fermentation patterns within the rumen are eminent with their associated influence on growth and feed utilization of animals (Asizua et al., 2017). This study, therefore, is one of the few attempts to understand in vivo feed utilization in the different ruminant production systems in Africa where major changes are occurring.

4.1. Rumen environment

The rumen fermentation characteristics in this study demonstrated the distinction in rumen environment and fermentation pattern observed in the different production systems. The higher rumen ammonia-nitrogen (NH_3-N) concentration in sole grazing steers compared to those grazing but supplemented and those under feedlot confirms the disparities in nitrogen (N) transaction pathways (Nolan and Dobos, 2005). The N transaction pathways imply that the source of both nitrogen and energy and how fermentable the source of energy is, will determine N metabolism (Hristov and Ropp, 2003; Nolan and Dobos, 2005). Such pathways influence the concentration of NH_3-N and other products of N metabolism in the rumen (Bach et al., 2005). The higher peak of NH_3-N in the rumen of sole grazing animals 4–5 h post prandial observed in this study has also been reported (Khalili and Sairanen, 2000). Meanwhile, Paster et al. (1993) and Attwood et al. (1998) observed that higher NH_3-N in ruminants under sole grazing could also be attributed to bacteria such as *Clostridium sticklandii, Peptostreptococcus anaerobius* and *Clostridium aminophilum,* which are associated with higher concentration of NH_3-N. However, the concentration of NH_3-N for all the feeding systems was within the critical range of 50–250 mg/l (Preston and Leng, 1987).

The pH values under sole grazing compared favorably with previous studies involving grazing animals (McCracken et al., 1993; Khalili and Sairanen, 2000; de Carvalho et al., 2017). However, the pH values were slightly lower for grazing but supplemented and feedlot steers and were within the range for sub-acute ruminal acidosis (SARA) of 5.0–5.6 as earlier reported (Nagaraja and Lechtenberg, 2007; González et al., 2012). The diurnal pattern of pH in feedlot steers tended to approach acute acidosis especially after offering feed in the morning. Various factors explain rumen pH levels in ruminants; however, most probable causes of low pH in the rumen environments of grazing but supplemented and feedlot steers was the source and level of fermentation of the carbohydrates (especially starch) in the concentrate (Robinson et al., 1987). However, selection against stover in preference for the concentrate in the TMR at the feedlot, as indicated by the relatively lower fraction of stover DM intake (about 148 g stover /kg TMR) instead of the intended 200 g stover/kg TMR, may have also contributed to the low pH. The concentrate contained brewers' spent grain and maize bran, which accounted for over 90% of the total DM. Arguably, such selection provides high concentrations of starch as shown by the starch content (104 ± 15 g/kg DM) and DM intake (6.5 ± 1.2 kg DM/steer/day for feedlot) of the concentrate in Table 2. Therefore, the lower pH observed under supplementation of grazing and the feedlot was associated with readily fermentable carbohydrate intake. Nagaraja and Lechtenberg (2007) argued that fermentable substrates such as starch and sugars increase fermentative activities in the rumen resulting in increased concentration of VFAs leading to lower pH. While brewers' spent grain was used in this study as a cheaper source of protein, it is likely that its high inclusion level together with molasses and maize bran in the concentrate contributed more fermentable carbohydrates relative to protein. The current results, therefore, imply that more attention should be paid to the level of inclusion and nature of fermentation of proteins and carbohydrate in different supplemental sources to optimize the rumen environment. Although no detrimental health effects of the low pH were observed in the animals, especially at the feedlot, the low pH could have affected the rumen function, which may have a bearing on production performance.

The total VFA concentrations were within the reported normal range between 70 and 130 mmol/l (France and Dijkstra, 2005). However, total VFA concentration for grazing as well as grazing but supplemented steers were similar but higher than values observed in feedlot steers. Khalili and Sairanen (2000) reported similar VFA concentration for sole grazing cows and those supplemented with concentrate. Although total VFA concentration for the sole grazing and the grazing but supplemented steers is comparable to results elsewhere (McCracken et al., 1993; Khalili and Sairanen, 2000), the comparatively lower values observed in the feedlot steers is possibly attributed to the influence of maize stover inclusion in the TMR. Presence of more structural carbohydrates and lignin, resistant to microbial degradation in maize stover (Atuhaire et al., 2016) possibly explains the low total VFA of TMR. Therefore the less degradable cell wall contents of the stover in the TMR also demonstrates the assertion that total VFA concentration in the rumen at any given time is a result of the balance between the rate of their production and the rate of disappearance (France and Dijkstra, 2005). Meanwhile the diurnal patterns of the total VFA concentrations showed a double peak for grazing but supplemented steers and a single peak for the sole grazing as well as the feedlot steers. This demonstrates the fact that rumen fermentation pattern also follows the frequency of feeding. Furthermore, the peak of total VFA was attained after at least 8 h from the start of feeding unlike NH_3-N, which surged 4–5 h after the steers were released for grazing. The molar proportions of acetate, propionate and their ratio followed the commonly reported patterns as influenced by forage or concentrate diets, although unique to this study was the higher molar fractions of butyrate (France and Dijkstra, 2005). Butyrate proportion was higher under feedlot than in the two grazing systems. This supports the argument that under certain conditions, concentrate diets may encourage the development of a large protozoal population, which may be accompanied by an increase in butyrate rather than propionate (Williams and Coleman, 1997). The fermentation patterns with high levels of butyrate could, therefore, negatively have impacted gluconeogenesis, which is mainly known to be influenced by propionate. Ultimately, these results are interpreted to mean that sole grazing encourages acetate production while starch rich concentrate diets commonly used in grazed but supplemented and feedlot management systems favour production of propionate, which is associated with more efficient feed utilization and production as earlier reported in the growth and feed utilization study (Asizua et al., 2017).

4.2. Degradability characteristics of DM, CP and NDF

The degradation coefficients were generally higher for all feedstuffs in the rumen of sole grazing steers. However, in most cases, the influence of feeding system on the degradation characteristics was dependent on the type of feedstuff. For concentrate, the degradation characteristics were higher in sole grazing followed by feedlot but for pasture and stover, degradation characteristics were also higher in sole grazing and followed by grazed but supplemented system. The high extent of DM, CP and fiber degradation in grazing steers compared to the supplemented and feedlot steers demonstrates that forage diversity under grazing positively influences degradability of feeds in the rumen. It is reported that, feed utilization in the rumen is dependent on a balance between energy and protein, although the rate and extent of degradation of feeds is determined by cellulolytic, amylolytic and proteolytic activity of the ruminal microflora all of which are influenced by pH (Bach et al., 2005). Abdoun et al. (2007) also reported that degradation of protein depends on solubility, susceptibility to microbial proteases and residence time in the rumen. The lower NDF degradation in the rumen environments of feedlot and the grazing but supplemented steers also confirmed the reports that NDF degradation tends to reduce with increase in starch and soluble carbohydrate intake (Bannik and Tamminga, 2005).

4.3. Passage kinetics

Mean retention time was similar for the three production systems except for the second age-dependent compartment (CMRT2) where the retention time at the feedlot was lower than for sole grazing and the grazing but supplemented steers. It is generally known that mean retention times in the gastrointestinal tracts are determined by type and nature of the fiber consumed, although the type of marker and the choice of model used are also important determinants. Krämer et al. (2013) concluded that forage type, rather than ration composition, seemed to determine total-tract retention time of forage. It would imply that the dynamics of the pasture fiber particles in sole grazed and grazing but supplemented steers was not different from the behaviour of stover fiber particles in the feedlot diet. However, the longer retention time in the first age-dependent compartment than the second age-dependent compartment was different from various studies (Lund et al., 2006; Krämer et al., 2013). Since digestion in ruminants is a function of the two competing processes of degradation and passage, similarity in the total mean retention time irrespective of the feeding system suggests that the extent of digestion of feedstuffs with higher levels of structural carbohydrates is influenced more by the potential degradability other than residence time in the gastro intestinal tract. Therefore, efforts that can improve feed quality to enhance rumen environment for improved digestibility is a crucial intervention in the current production systems.

5. Conclusion

The results of rumen environment showed that feedlot and grazing but supplemented systems resulted in improved fermentation pattern compared to sole grazing. However, precautionary measures should be taken on the inclusion rates of highly soluble carbohydrates in total mixed ration to avoid sub acute or acute acidosis. The high extent of DM, CP and fiber degradation in grazing steers compared to the grazing but supplemented and feedlot steers demonstrates that forage diversity under grazing positively influences degradability of feeds in the rumen. However, balancing the inclusion levels of supplements with emphasis on fermentation characteristics of their carbohydrates and protein and how they influence the rumen environment requires more attention in the current feeding systems.

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