fecal composition2

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The effect of feed quality and feeding level on fecal composition in East African cattle farming systems

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Abstract

The effects of feeding levels below maintenance requirements of metabolizable energy (MER) and of feed supplementation on fecal nutrient and microbial C concentrations were evaluated in two experiments. In Exp. 1, twelve Boran steers were allotted to four feeding levels during four periods. Rhodes grass hay only was offered at 80%, 60%, and 40% of individual MER, while steers at 100% MER additionally received a concentrate mixture. In Exp. 2, six Holstein x Boran heifers were offered three different diets during two periods. Per 100 g of dry matter (DM), the roughage (R) diet consisted of 61.4 g wheat straw plus 38.6 g Rhodes grass hay. Roughage was either supplemented with sweet potato vine silage (R+SPVS) or with a urea-molasses block (R+UMB). Both trials quantified feed intake and total fecal excretion, and determined the fecal concentration of bacterial, fungal and total microbial mass by analysis of amino sugars.

In Exp. 1, fecal DM, organic matter (OM), and acid detergent fiber (ADF) concentrations increased as feeding levels decreased ($P < 0.001$), while the concentration of fecal nitrogen (N) and neutral detergent fiber (NDF) remained constant. The highest concentration of fungal carbon (C) and total microbial C was observed at 60% MER ($P < 0.01$). Concentrate supplementation (100% MER) increased fecal OM and N contents ($P < 0.001$) and reduced the ratio of fungal-to-bacterial C. In Exp. 2, SPVS and UMB supplementation increased the fecal concentration of bacterial C ($P < 0.01$)

but decreased total microbial C and the ratios of fungal-to-bacterial C as and of fungal-to-microbial C. The results indicate that at feeding levels below MER feces tend to host more fungi, whereas supplementation with concentrates (100% MER), SPVS and UMB increases fecal N and fosters bacterial populations. Implications of these changes for the recycling of nutrients via animal manure to crop fields merit further scientific investigation.

Key words: sub-Saharan Africa, Boran cattle, diet composition, fecal excretion, feed intake, manure quality, nutrient cycling.

1. Introduction

Livestock is a very important component for the livelihoods of small-scale farmers in sub-Saharan Africa (Otte & Chilonda, 2002; Odero-Waitituh, 2017), and a key factor for the sustainable intensification of their predominantly mixed crop-livestock systems (Duncan et al., 2013; Herrero et al., 2013). On the other hand, especially extensively managed ruminant livestock are accused for a substantial contribution to the greenhouse gas emissions (Tubiello et al., 2014) from enteric fermentation as well as from manure. Furthermore, inappropriate management of livestock dung can also contribute to contamination of groundwater and surface waterbodies with organic matter, nitrate, and organic phosphates (Hristov et al., 2013). Previous work (Al-Asfoor et al., 2013; Jost et al., 2013b) has shown that feed quality strongly affects the quality of manure and the rate and pattern of its decomposition and release of nutrients. In sub-Saharan Africa (SSA), cattle and other ruminants are seasonally exposed to a lack of forage, particularly at the end of the dry season and in drought years. In addition, in these periods the available roughages are also of very poor quality – low in protein and energy concentration, and high in fiber fractions (Leng, 1990; Bayala et al., 2014). This results in low production of milk and no or negative body weight gain (Yahaya et al., 1999; Koralagama et al., 2008; Abdou et al., 2011), but also affects feces –and thus manure– quality. However, in the SSA context of smallholder cattle farming, little information has been provided on how diet composition and feeding level affect the nutrient concentration as well as the microbial composition of feces, even though this is a crucial aspect in the context of nutrient balance studies (Rufino et al., 2006).

Previous work described negative effects of low feed intake on nutrient digestibility (Doreau et al., 2003) and animal physiology, nutrient and energy metabolism (Chilliard et al., 2000; Ferraris &

Carey, 2000). The drop in digestibility when ruminants are fed below their maintenance energy requirement (MER) may increase the amount and the nutrient concentration of feces. For Holstein cows offered natural grassland hay, soybean meal, and barley (83:8.5:8.5, on fresh matter - FM - basis), fecal nitrogen (N) loss increased from 350 to 450 g N kg^{-1} N intake when feeding level declined from 110% to 65% MER (Grimaud & Doreau, 1995). Likewise, in a trial with Holstein cows fed grassland hay, straw, and ground maize (60:30:10, on FM basis) with and without urea supplementation at 80% and 27% MER, fecal N loss increased from 430 to 810 g N kg^{-1} N intake (Doreau et al., 2004). For sheep fed vetch-oats hay at 100% and 20% MER, Atti et al. (2002) observed an increase in fecal N loss from 410 to 830 g N kg^{-1} N intake. The higher fecal N loss was paralleled by a reduced N retention and an increased blood urea concentration (Atti et al., 2002), and a higher loss of endogenous N (Doreau et al., 2003).

On the other hand, supplementing ruminants with locally available energy- and/or protein-rich feedstuffs also affects the nutrient concentration in feces, and an increased fecal N concentration as well as a higher content of bacterial carbon (C) and total microbial C might be observed in the supplemented diets (Van Vliet et al., 2007; Jost et al., 2013a). For dry cows fed eight different diets *ad libitum*, Van Vliet et al. (2007) showed that fecal nutrient and microbial composition varied with diet concentration of metabolizable energy (ME), neutral detergent fiber (NDF), starch, and crude protein (CP). Feces from cows on a high fiber and low CP diet had a higher carbon-to-nitrogen (C/N) ratio than feces from cows on a low fiber and high CP diet, whereas fecal bacterial biomass was highest for the diet with highest energy and protein content. A difference in fecal composition and microbial biomass C/N ratio was also reported for Holstein cows on two diets differing in N concentration (Jost et al., 2013a). Fecal NDF concentration along with the C/N ratio was higher in the low CP diet as compared to the high CP diet, whereby the concentrations of the amino sugars muramic acid, glucosamine, and galactosamine, which are used to determine the fecal bacterial and fungal biomass, were not different. When a diet high in fiber and low in CP is fed to cattle at below 100% MER levels, microbial growth in the hindgut might increase due to lowered rumen fermentation, resulting in increased fecal N concentration from both bacterial mass and undigested feed N (Lapierre & Lobley, 2001). Similarly, Al-Kindi et al. (2016) reported that glucosamine and galactosamine concentrations markedly varied when Boer goats consumed a mixture of ryegrass hay and concentrate that contained different levels of quebracho tannin and activated charcoal. Tannin and charcoal additions lowered the digestibility of OM, CP, NDF, and

acid detergent fiber (ADF), and as a result, changed the fecal composition and increased fungal C concentration.

Given the importance of organic manure for the fertilization of crop fields and vegetable gardens in SSA (Wiig et al., 2001; Baijukya et al., 2005), as well as the potential nutrient losses that may occur with inappropriate manure management (Predotova et al., 2010), insights into the effects of common feeding situations in SSA - from sub-maintenance roughage feeding to quality supplementation of roughage diets - on the concentration of C, N, and microbial biomass in feces might be useful for reducing nutrient wastage and greenhouse gas emissions in the ecoregion. We hypothesized that (i) feed intake at levels below 100% MER leads to declining nutrient digestibility, increasing fecal N concentration and higher fecal microbial biomass, and that (ii) supplementation of a poor roughage diet with quality supplements improves nutrient digestibility but again increases fecal N concentration and fecal microbial biomass.

2. Materials and Methods

2.1. Experimental feeding and animals

One trial of sub-maintenance feeding (Exp. 1) and one supplementation trial (Exp. 2) were conducted at the Mazingira Centre of the International Livestock Research Institute, Nairobi, Kenya. The average minimum and maximum ambient air temperature during Exp.1 was 18°C and 20°C, and relative air humidity ranged from an average minimum of 55% to an average maximum of 69%. During Exp. 2, the average temperature and relative humidity ranged from 14 to 26°C and from 17% to 93%, respectively. Animals in both experimental trials were kept in individual pens (1.8 m x 2.8 m) in an open barn during three weeks of adaptation, and in individual pens (1.1 m x 2.2 m) inside a closed barn during one week of measurements (see below).

In the sub-maintenance trial, twelve purebred Boran steers (183 ± 15.2 kg) were assigned to four feeding levels, namely 100%, 80%, 60%, and 40% of their individual maintenance requirement of metabolizable energy (MER) of 0.74 MJ $kg^{-0.75}$ live weight (LW) for mature bulls (NRC, 1989). Steers at 80% MER (MER80) as well as at MER60 and MER40 were only fed Rhodes grass hay, whereas steers at MER100 were receiving hay at 20 g kg^{-1} LW plus a concentrate mixture of cotton seed meal (CSM) and sugar cane molasses at 16 g concentrate per 100 g diet dry matter (DM) The experiment run over four periods and each period consisted of three weeks adaptation, one week of total fecal collection, one week of respiration chamber measurements (not reported here) and two weeks of refeeding.

In the supplementation trial, six Holstein Friesian x Boran heifers (148 ± 4.6 kg) were allocated to three diets, namely a pure roughage (R) diet (61.4 g of wheat straw and 38.6 g of Rhodes grass hay per 100 g DM), a diet consisting of roughage and sweet potato vine silage (R+SPVS), and a roughage diet plus urea molasses blocks (R+UMB). The experiment was running for two consecutive periods and each period consisted of three weeks of adaptation, one week of total fecal collection and one week of respiration chamber measurements (not reported here). The amount of roughage offered to each heifer was calculated from the weekly measured individual LW, allowing for a refusal of 5 to 10 g per 100 g offered roughage. The UMB was available *ad libitum* while SPVS was offered at 2.5 g SPVS per 100 g LW (as fed), equivalent to 19 g SPVS per 100 g DM of R+SPVS. The roughages were chaffed to 5 – 20 cm particle size and mixed daily, while the silage was prepared according to Lukuyu et al. (2012). The UMB contained (in g per 100 g FM): water (5.0), magnesium sulfate (5.0), vegetable oil (1.0), sugarcane molasses (35.0), urea (10.0), sodium chloride (10.0), dicalcium phosphate (18.9), a trace mineral premix (Mn, Zn, Cu, Se; 0.1), cement (10.0), and CSM (5.0). In the both trials, drinking water was provided *ad libitum* and in the sub-maintenance trial steers had always access to a mineral lick block.

2.2. Determination of feed intake and fecal excretion

After chaffing and mixing, 100 g FM of offered roughage was sampled weekly and stored in a paper bag. Approximately 300 g FM of SPVS was collected when a new silage bag was opened; a sample of UMB (100 g FM) was collected in a plastic zipper bag at the moment of UMB preparation and stored at -20°C. Molasses (70 g FM) and CSM (100 g FM) were sampled once per period. For each animal, refusals of roughage and SPVS were collected and weighed daily while intake of UMB was quantified by calculating the weight difference of the block between two subsequent mornings during the whole measurement week. In the end of each measurement week, refusal of roughage were mixed, pooled and subsampled (100 g FM; Citizen CTG6H scale, Citizen Scales Inc., New York, USA; capacity 6000 g, accuracy 0.1 g). Quantification of refusals was done before morning feeding; in Exp. 1 no refusals of the CSM-molasses mixture were left.

The total amount of fecal FM was collected per animal into a 10-l bucket from the clean floor at each time an animal defecated. Total fecal mass was weighed at 8:00 a.m. daily throughout the measurement week. The feces were thoroughly mixed and a subsample of 300 g FM was dried at 50°C for 72 h (Genlab SDO/425/DIG oven, Genlab Ltd., Widnes, UK) and then reweighed. For N analysis, another fecal subsample of 60 g FM was collected and then stored (-20°C). The dried samples were ground (IKA® Werke grinder MF 10 basic, Staufen, Germany) to pass a 1 mm mesh

at the end of each experimental period. The ground fecal subsamples were pooled per period based on the daily amount of fecal excretion, homogenized, and sample of 100 g was kept for analyses. The frozen fecal samples were thawed, pooled (also based on the amount of daily excretion), mixed, and directly analyzed for N concentration. To determine fecal amino sugars as markers for microbial biomass and its composition, about 50 g of fresh feces were sampled immediately after defecation at three different sampling times (12:00, 18:00, and 24:00 h) on day 2, 4, and 6 during each measurement week. If needed, the animals were manually stimulated at the anus to provoke defecation. After overnight storage in a zipper bag at -20°C, each sample was transferred to a paper bag for vacuum freeze-drying during 48 h at -55°C and 0.4 mbar in a Telstar LyoQuest-55 freeze dryer. After freeze-drying the sample was store in an air-conditioned room (ca. 20°C) until amino sugar analysis.

2.3. Chemical analysis of samples

The ground and dried samples of feed, refusals and feces were analyzed for DM and organic matter (OM) concentrations (AOAC, 1990; methods no 967.03 & 924.05), while NDF and ADF (VDLUFA, 2012; methods no. 6.5.1 & 6.5.2) were determined in a Fibertec™ FOSS analyzer (Foss GmbH, Hamburg, Germany). The N concentration in pooled samples of frozen feces was determined according to the Kjeldahl procedure (AOAC, 1990; method no. 988.05). Analysis of mannosamine, muramic acid, glucosamine, and galactosamine concentration in the freeze-dried fecal samples was done according to Indorf et al. (2011). To this end, the sample (0.4 g ±0.01 g; Sartorius 224i-1-S balance) was hydrolyzed with 10 ml of 6 M hydrochloric acid for 3 h at 115°C, and filtered afterwards. From a 0.3 ml aliquot of the hydrolysate, the acid was removed using a Heidolph vacuum rotary evaporator (Schwabach, Germany) at 40°C. After that, the residue was dissolved in 1 ml bi-distilled water and centrifuged at 13000 rpm (Centrifuge 5910 R, Eppendorf) for 10 min, afterwards transferred to a plastic vial, sealed and stored at -18°C. The chromatographic separation of amino sugars was performed using a Phenomenex (Aschaffenburg, Germany) Hyperclone C18 column at 35°C. The HPLC system consisted of a Dionex (Germering, Germany) P 580 gradient pump and a Dionex Ultimate WPS-3000TSL analytical autosampler with in-line split-loop injection and thermostat; a temperature of 15°C was used using ortho-phthalaldehyde reagent. Fungal C was estimated from glucosamine and muramic acid concentrations (mmol) as follows:

$$\text{Fungal C} = 9 \times (\text{glucosamine} - 2 \times \text{muramic acid}), \qquad \text{[Eq. 1]}$$

thereby assuming that the muramic acid to glucosamine ratio in bacterial cells is 1:2 (Engelking et al., 2007), and 9 being the conversion value of fungal glucosamine to fungal C.

Bacterial C was calculated by multiplying the muramic acid concentration by 45 (Appuhn & Joergensen, 2006), and microbial C was calculated as the sum of fungal C plus bacterial C.

2.4. Data analysis

Daily nutrient intake of the individual animal was calculated from the amount of daily feed offered and refused and its respective nutrient content. Apparent digestibility of DM, OM, CP, NDF, and ADF was calculated by subtracting the amount of fecal excretion from the amount of ingested feed and dividing the difference by the ingested amount. The data of fecal DM, OM, N, NDF, and ADF concentrations in the sub-maintenance trial (12 steers x 4 periods) and the supplementation trial (6 heifers x 2 periods), was analyzed by experiment with the following model:

$$y_{ijk} = \mu + d_i + p_j + dp_{ij} + a_k + e_{ijkl} \quad \text{[Eq. 2]}$$

where y_{ijk} is the dependent variable for a particular ijk case, μ is the overall mean, d_i and p_j are the fixed effects of diet and period, respectively, dp_{ij} is the interaction of diet and period, a_k is the random effect of animal, and e_{ijkl} is the residual error.

For the data on amino sugar concentrations and microbial biomass, the data of Exp. 1 (12 steers, 4 periods, 3 sampling hours, 3 sampling days) and Exp. 2 (6 heifers, 2 periods, 3 sampling hours, 3 sampling days) were again analyzed separately using the following model:

$$y_{ijkl} = \mu + d_i + p_j + dp_{ij} + s_k + ds_{ik} + a_l + e_{ijklm}, \quad \text{[Eq. 3]}$$

where y_{ijkl} is the dependent variable for a particular ijkl case, μ is the overall mean, diet (d_i) and period (p_j) are fixed effects and their interaction (dp_{ij}), the repeated measurements are accounted for via sampling day (s_k) and its interaction with diet (ds_{ik}), a_l is the random effect of animal and e_{ijklm} is the residual error. The Tukey post-hoc test was applied to detect significant differences ($P \leq 0.05$) between diet, period, sampling day, and the interactions of diet with period and sampling day.

In a first step, the data from the three sampling hours had been included in the model to test for systematic diurnal variation in microbial markers. Since no significant differences in the concentrations of amino sugars and microbial C were observed between the different sampling hours within a day in both experiments (Table S1), only one data point per sampling day (the 12:00 h sample) was considered in the final analysis [Eq. 2; Eq. 3]. Statistical analyses were done using R v3.4.3 (R Core Team, 2017). For ANOVA, the *lme* function was used while a covariance structure with compound symmetry was fitted in the repeated measurement models using *gls*

function. For the Pearson correlation, the *cor* function was used. All results are presented as arithmetic treatment means and standard error of the mean (SEM).

3. Results

3.1. Feed intake and digestibility

In Exp. 1, even though the steers at MER80, MER60, and MER40 only consumed Rhodes grass hay, ingesta compositions was greatly modified as intake declined from 81 to 40 g $kg^{-0.75}$ LW. At MER80, OM, NDF, and ADF contents were lower, while CP content was higher than at MER40, while at MER60 the nutrient concentrations were in between MER80 and MER40 levels. As a consequence, a higher CP and ADF digestibility was found at MER80. On other hand, the higher CP and lower fiber fraction content of the concentrate mixture (MER100) increased ingesta energy and protein contents as well as CP digestibility, whereas NDF and ADF digestibility were lowered (Table 1). In Exp. 2, SPVS supplementation increased the CP content of the ingesta whereas NDF and ADF contents were not modified. As a result, diet R+SPVS had a higher DM digestibility than diet R and diet R+UMB (Table 2). However, the higher CP content of diet R+SPVS did not improve nutrient intake and a slight increase of OM and NDF digestibility was found as compared to the other two diets.

3.2. Feces quality

In Exp. 1, intake level as well as experimental period and their interaction influenced fecal concentrations of DM, OM, N, and ADF ($P < 0.05$). At MER100, fecal concentration of DM was lower and concentration of OM and N were higher compared to feces at lower intake levels, whereby feces at MER40 had the highest DM and ADF concentration. Among the pure hay diets (MER80, MER60, MER40), fecal DM, OM and ADF concentrations were lowest at MER80 ($P < 0.05$), while N concentration was similar (Table 1). A difference in the nutrient concentration of feces in Exp. 2 was only observed with respect to the OM content, with similar values for diets R+SPVS and R and a lower value for R+UMB (Table 2).

3.3. Microbial composition of feces

No influence of sampling day (and no interaction of day and diet) was observed for the concentrations of amino sugars and fecal microbial composition in Exp. 1. Diet as well as period and their interaction affected fecal concentrations of galactosamine and glucosamine ($P < 0.01$), while muramic acid only differed ($P < 0.01$) between experimental periods (Table 1).

Galactosamine and glucosamine concentrations were lowest at MER100 and highest at MER60 ($P < 0.01$), but similar for MER100 and MER80 as well as for MER60 and MER40. Fungal C concentration was highest at MER60 and was lowest during period 3 ($P < 0.001$). Likewise, total microbial C was highest at MER60 ($P < 0.01$). Fungal-to-bacterial C ratio was lower at MER100 than at MER80 and MER60 ($P < 0.05$). A significantly ($P < 0.05$) lower ratio of fungal-to-microbial C was also calculated for MER100 as compared to MER60 (Table 1).

In Exp. 2, the concentration of muramic acid was affected by diet and was higher for R+SPVS and R+UMB than for R ($P < 0.01$). The same result was obtained for galactosamine and glucosamine concentrations ($P < 0.001$). Furthermore, a difference in the concentrations of galactosamine and glucosamine was observed between experimental periods 1 and 2. Fungal C concentrations also varied between periods but were not affected by diet. Being derived from muramic acid concentrations, diet and period effects on bacterial C concentrations followed the same patterns as described for muramic acid. In diet R, microbial C was lower and the ratio of fungal-to-bacterial C and of fungal-to-microbial C was higher than in the two supplemented diets. The latter resulted in a similar ratio of fungal-to-microbial C, whereas the ratio of fungal-to-bacterial C was higher ($P < 0.01$) in R+UMB than that in R+SPVS (Table 2).

Table 1. Intake, digestibility and fecal concentrations of dry matter (DM), organic matter (OM), nitrogen (N), neutral detergent fiber (NDF) and acid detergent fiber (ADF), as well as amino sugar components of fungal and bacterial biomass in feces of Boran steers fed diets corresponding to different levels (%) of maintenance energy requirements (MER). Values are arithmetic means and standard error of the mean (SEM).

Variable	Diet				Period				SEM	Significance		
	MER100	MER80	MER60	MER40	1	2	3	4		D	P	D*P
Intake (g kg$^{-0.75}$ LW d^{-1})												
DM	81.3 d	64.3 c	56.6 b	40.3 a	65.9 b	58.5 a	55.7 a	62.4 b	2.29	***	***	**
OM	74.4 d	58.6 c	51.8 b	36.9 a	60.4 c	53.4 ab	51.3 a	56.6 b	2.09	***	***	**
CP	5.5 d	2.2 c	1.9 b	1.3 a	2.7 b	2.9 c	2.4 a	2.9 c	0.24	***	***	*
NDF	56.0 d	49.2 c	43.5 b	31.0 a	48.4 c	43.9 ab	41.6 a	45.8 bc	1.45	***	***	**
ADF	36.1 d	31.5 c	27.9 b	19.9 a	31.3 c	27.7 ab	27.4 a	29.1 ab	0.93	***	***	**
Digestibility (g kg^{-1})												
DM	567	569	560	541	574 b	544 a	546 ab	573 ab	4.7	(*)	*	
OM	591	601	590	574	607 c	571 a	577 ab	601 bc	4.6	(*)	**	
CP	492 c	203 b	133 ab	103 a	192 a	319 b	206 a	215 a	26.3	***	**	(*)
NDF	562 a	608 b	597 b	581 ab	605 b	576 ab	570 a	597 ab	5.3	**	*	
ADF	512 a	568 c	549 bc	527 ab	559 b	514 a	532 ab	551 b	5.8	***	**	
Fecal composition (g kg^{-1}DM)												
DM (in FM)	227 a	241 ab	248 b	270 c	239 a	241 ab	259 ab	247 b	3.5	***	*	
OM	862 c	845 a	852 b	851 b	846 a	859 b	857 b	848 a	1.5	***	***	
N	12.8 b	10.3 a	10.4 a	10.2 a	11.0 ab	10.5 a	10.1 a	12.0 b	0.22	***	***	
NDF	695	696	703	702	684 a	703 bc	712 c	698 b	2.1		***	(*)
ADF	500 ab	492 a	505 b	510 b	494 a	508 b	511 b	494 a	2.1	***	***	*
Fecal microbial parameters (mg g^{-1} DW)												
Muramic acid	0.62	0.62	0.67	0.65	0.54 a	0.55 a	0.74 b	0.74 b	0.013		***	*
Galactosamine	1.83 a	1.98 ab	2.28 c	2.17 bc	1.96 ab	2.21 bc	1.787 a	2.30 c	0.043	***	***	**
Glucosamine	2.60 a	2.69 a	3.02 b	2.79 ab	2.66 b	3.02 c	2.392 a	3.04 c	0.046	***	***	***
Fungal C	12.1 a	13.1 a	15.1 b	13.4 a	14.2 b	13.9 b	11.6 a	14.0 b	0.27	***	***	***
Bacterial C	28.1	27.8	30.4	29.2	24.3 a	33.1 a	24.8 b	33.3 b	0.60		***	*
Microbial C	40.2 a	40.9 a	45.4 b	42.7 ab	38.5 a	47.0 b	36.4 a	47.3 b	0.73	**	***	**
Fungal C to bacterial C ratio	0.45 a	0.52 b	0.52 b	0.47 ab	0.61 b	0.43 a	0.49 a	0.43 a	0.012	*	***	*
Fungal C to microbial C ratio	0.31 a	0.33 ab	0.34 b	0.31 ab	0.37 c	0.29 a	0.32 b	0.30 ab	0.005	*	***	*

DW: dry weight; FM: fresh matter;
Periods: 1 = 25/07 - 11/09/2016; 2 = 12/09 - 30/10/2016; 3 = 31/10 - 18/12/2016; 4 = 19/12/2016 - 23/01/2017.
Within rows, means with different superscripts differ at $P < 0.05$ (Tukey post-hoc test).
Statistical significance: (*) $P \leq 0.10$; *$P \leq 0.05$; **$P \leq 0.01$; ***$P \leq 0.001$ of diet (D), period (P), and diet x period interaction (D*P) obtained with *lme* function.
An empty cell indicates non-significant effects.

Table 2. Intake, digestibility and fecal concentrations of dry matter (DM), organic matter (OM), nitrogen (N), neutral detergent fiber (NDF), acid detergent fiber (ADF), and amino sugar components of fungal and bacterial biomass in feces of Holstein x Boran heifers offered roughage alone (R; wheat straw and Rhodes grass hay), or R supplemented with sweet potato vine silage (R+SPVS) and urea-molasses blocks (R+UMB). Values are arithmetic means and standard error of the mean (SEM).

Variable	Diet			Period		SEM	Significance		
	R	R+SPVS	R+UMB	1	2		D	P	D*P
Intake (g $kg^{-0.75}$ LW d^{-1})									
DM	70.9	76.0	66.8	64.3	78.2	3.08			
OM	63.1	67.5	59.0	56.8	69.6	2.79			
CP	5.6	6.7	5.5	5.4	6.5	0.31			
NDF	50.4	52.6	47.7	44.5	55.9	2.22			
ADF	32.3	33.9	30.2	29.4	35.0	1.30			
Digestibility (g kg^{-1})									
DM	474 ^{a}	510 ^{b}	480 ^{ab}	476	500	10.07	*	(*)	
OM	509	539	512	515	525	7.78	(*)	(*)	*
CP	337	385	325	356	342	16.7			
NDF	496	530	506	496	525	8.28	(*)		
ADF	428	458	429	427	449	6.79			
Fecal composition (g kg^{-1} DM)									
DM (in FM)	172	171	166	183 ^{b}	156 ^{a}	5.2		*	
OM	832 ^{ab}	836 ^{b}	829 ^{a}	819 ^{a}	846 ^{b}	4.2	*	**	(*)
N	16.0	17.8	17.1	16.5	17.4	0.53			
NDF	679	662	679	667	680	3.9			
ADF	496	495	497	500	493	2.6			
Fecal microbial parameters (mg g^{-1} DW)									
Muramic acid	0.42 ^{a}	0.53 ^{b}	0.52 ^{ab}	0.47	0.51	0.024	**		
Galactosamine	1.30 ^{a}	1.54 ^{b}	1.57 ^{b}	1.34 ^{a}	1.60 ^{b}	0.054	***	*	*
Glucosamine	2.53 ^{a}	2.87 ^{b}	2.90 ^{b}	2.56 ^{a}	2.98 ^{b}	0.099	***	*	(*)
Fungal C	15.3	16.2	16.8	14.6 ^{a}	17.6 ^{b}	0.58		*	**
Bacterial C	18.7 ^{a}	23.9 ^{b}	23.3 ^{ab}	21.0	23.0	1.07	**		
Microbial C	34.0 ^{a}	40.1 ^{b}	40.1 ^{b}	35.6	40.6	1.47	**		
Fungal C to bacterial C ratio	0.85 ^{c}	0.69 ^{a}	0.76 ^{b}	0.74	0.80	0.031	***		**
Fungal C to microbial C ratio	0.45 ^{b}	0.41 ^{a}	0.42 ^{a}	0.42	0.44	0.010	***		*

DW: dry weight; FM: fresh matter;

Period 1: from 07/09 to 11/10/2015; period 2: from 12/10 to 15/11/2015

Within rows, means with different superscripts differ at $P < 0.05$ (Tukey post-hoc test).

Statistical significance: (*) P ≤ 0.10; *P ≤ 0.05; **P ≤ 0.01; ***P ≤ 0.001 of diet (D), period (P), and diet x period interaction (D*P) obtained with *lme* function. An empty cell indicates non-significant effects

3.4. Influence of feed intake and diet quality on fecal composition

Table 3 shows that across the two experiments, fecal DM concentration was negatively correlated with nutrient intake, ingesta CP concentration, and CP digestibility ($P < 0.001$), whereas a positive correlation was found with ingesta OM, NDF, and ADF contents ($P < 0.001$). Fecal N increased as nutrient intake ($P < 0.001$), ingesta CP content, and CP digestibility increased ($P < 0.01$). However, fecal N declined when ingesta OM, NDF, and ADF concentration increased, and with an increase in NDF and ADF digestibility ($P < 0.001$ in each case). Fecal NDF and ADF concentrations decreased with increasing nutrient intake ($P < 0.05$).

Table 3. Pearson correlation coefficients (r) and significance levels[1] between fecal concentration of dry matter (DM), organic matter (OM), crude protein (CP), neutral detergent fiber (NDF) and acid detergent fiber (ADF) and nutrient intake, ingesta composition and diet digestibility, across Exp. 1 and Exp. 2 data sets[2].

Variable	Fecal composition (g kg^{-1} DM)				
	DM	**OM**	**N**	**NDF**	**ADF**
Nutrient intake (g kg$^{-0.75}$ LW)					
DM	-0.62 ***	0.06	0.50 ***	-0.35 **	-0.42 ***
OM	-0.59 ***	0.10	0.46 ***	-0.32 *	-0.41 **
CP	-0.76 ***	-0.07	0.79 ***	-0.49 ***	-0.26 *
NDF	-0.59 ***	0.07	0.42 ***	-0.29 *	-0.44 ***
ADF	-0.58 ***	0.05	0.41 **	-0.30 *	-0.42 ***
Ingesta composition (g kg^{-1})					
OM	0.72 ***	0.65***	-0.82 ***	0.60 ***	0.29 *
CP	-0.78 ***	-0.20	0.86 ***	-0.53 ***	-0.18
NDF	0.57 ***	0.09	-0.70 ***	0.51 ***	0.25 (*)
ADF	0.65 ***	0.04	-0.75 ***	0.50 ***	0.34 **
Digestibility (g kg^{-1})					
DM	0.50 ***	0.32 *	-0.41 **	0.08	-0.11
OM	0.52 ***	0.24(*)	-0.44 ***	0.05	-0.13
CP	-0.44 ***	0.15	0.37 **	-0.26 *	-0.11
NDF	0.55 ***	0.17	-0.52 ***	0.08	-0.08
ADF	0.63 ***	0.19	-0.59 ***	0.19	-0.18

[1] Statistical significance: (*) $P \leq 0.10$; *$P \leq 0.05$; **$P \leq 0.01$; ***$P \leq 0.001$. An empty cell indicates non-significant correlation

[2] Exp. 1: Boran steers fed at different levels (%) of maintenance energy requirements (MER) with Rhodes grass hay alone (MER40, MER60, MER80) or supplemented with concentrate (MER100); Exp. 2: Holstein x Boran heifers fed roughage (R) alone or supplemented with sweet potato vine silage (R+SPVS) and urea molasses block (R+UMB).

Table 4. Pearson correlation coefficients (r) and significance levels[1] between fecal concentrations of galactosamine (Gal), glucosamine (Glu), fungal C, bacterial C (muramic acid), and microbial C and nutrient intake, ingesta composition, diet digestibility and fecal composition, across Exp. 1 and Exp. 2 data sets[2].

Variable	Gal	Glu	Fungal C	Bacterial C	Microbial C	Fungal-to-bacterial C	Fungal-to-microbial C
	mg g^{-1} DW						
Nutrient intake (g kg$^{-0.75}$ LW)							
DM	-0.31 *	-0.08	0.03	-0.16	-0.13	0.19	0.18
OM	-0.30 *	-0.09	0.01	-0.15	-0.13	0.16	0.15
CP	-0.48 ***	-0.08	0.13	-0.26 *	-0.18	0.34 **	0.31 *
NDF	-0.25 (*)	-0.04	0.05	-0.13	-0.09	0.18	0.17
ADF	-0.29 *	-0.10	0.01	-0.17	-0.14	0.19	0.17
Ingesta composition (g kg^{-1})							
OM	0.35 **	-0.14	-0.39 **	0.22 (*)	0.04	-0.53 ***	-0.50 ***
CP	-0.52 ***	-0.07	0.17	-0.30 *	-0.20	0.40 **	0.37 **
NDF	0.47 ***	0.20	0.02	0.29 *	0.26 *	-0.24 (*)	-0.23 (*)
ADF	0.33 *	-0.03	-0.14	0.11	0.04	-0.21	-0.20
Digestibility (g kg^{-1})							
DM	0.38 **	0.06	-0.16	0.27 *	0.17	-0.38 **	-0.34 **
OM	0.36 **	0.02	-0.18	0.23 (*)	0.13	-0.36 **	-0.32 *
CP	-0.32 *	-0.09	-0.06	-0.07	-0.08	0.03	0.03
NDF	0.46 ***	0.12	-0.07	0.27 *	0.21	-0.31 *	-0.28 *
ADF	0.43 ***	0.04	-0.16	0.24 (*)	0.15	-0.35 **	-0.31 *
Fecal composition (g kg^{-1} DM)							
DM	0.53 ***	0.02	-0.26 *	0.32 *	0.18	-0.54 ***	-0.49 ***
OM	0.34 **	0.10	-0.20	0.38 **	0.26 *	-0.53 ***	-0.50 ***
N	-0.45 ***	0.02	0.31 *	-0.32 *	-0.16	0.52 ***	0.49 ***
NDF	0.41 **	0.10	-0.24 (*)	0.43 ***	0.28 *	-0.56 ***	-0.54 ***
ADF	0.12	-0.02	-0.16	0.14	0.06	-0.25 (*)	-0.24 (*)

[1] Statistical significance: (*) $P \leq 0.10$; *$P \leq 0.05$; **$P \leq 0.01$; ***$P \leq 0.001$. An empty cell indicates non-significant correlation. DW: dry weight, DM: dry matter, OM: organic matter, CP: crude protein, N: nitrogen, NDF: neutral detergent fiber, ADF: acid detergent fiber.

[2] Exp. 1: Boran steers fed at different levels (%) of maintenance energy requirements (MER) with Rhodes grass hay alone (MER40, MER60, MER80) or supplemented with concentrate (MER100); Exp. 2: Holstein x Boran heifers fed roughage (R) alone or supplemented with sweet potato vine silage (R+SPVS) and urea molasses block (R+UMB).

Muramic acid (and thus bacterial C) concentration correlated negatively with CP intake as well as with ingesta and fecal N concentrations ($P < 0.05$), but positively with ingesta NDF concentration, NDF digestibility ($P < 0.05$) and fecal NDF concentration ($P < 0.001$). Moreover, it also positively correlated with DM digestibility, as well as fecal DM and OM concentrations ($P < 0.05$). As shown

in Table 4, galactosamine concentration correlated negatively with intake of DM, OM, CP, and ADF ($P < 0.05$). Similar to muramic acid, galactosamine also correlated negatively with ingesta CP and fecal N content ($P < 0.001$) and positively with ingesta NDF and ADF concentrations ($P < 0.05$). Besides a positive correlation with NDF and ADF digestibility ($P < 0.001$), galactosamine also showed a positive correlation with DM and OM digestibility and fecal DM, OM, and NDF concentrations ($P < 0.01$) but a negative correlation with CP digestibility ($P < 0.05$).

Fungal C correlated negatively with ingesta OM and fecal DM content but positively with fecal N content (Table 4), while microbial C associated positively with ingesta and fecal NDF ($P < 0.05$). The ratio of fungal-to-bacterial C and that of fungal-to-microbial C correlated positively with N intake, ingesta CP content and fecal N concentration ($P < 0.01$), whereas a negative correlation existed with ingesta OM content ($P < 0.001$), digestibility of DM, OM, NDF and ADF ($P < 0.05$), and fecal DM, OM, and NDF concentration ($P < 0.001$).

4. Discussion

4.1. Effects of diet quality and feed intake on feces quality

Smallholder farmers dominate livestock production in SSA and their systems greatly differ between agro-ecological regions (Otte & Chilonda, 2002). For feeding their cattle, they mainly depend on locally available roughage feeds that seasonally fluctuate in quantity and quality (Nyaata et al., 2000; Debele et al., 2013; Bayala et al., 2014). As a result, the quality of fecal excreta and hence the manure available for fertilizing field crops and vegetables also differs. The present differences in fecal nutrient concentration reflect such conditions. Beside the difference in diet quality between supplemented diet MER100 and pure hay diets MER80, MER60 and MER40, differences in ingesta quality between the four periods of Exp. 1 (Table 1) resulted in fluctuations of the nutrient concentration in fecal excreta. Moreover, fecal nutrient concentrations were also influenced by feed intake: increasing fecal DM content with decreasing feed intake may be due to a higher water reabsorption in the large intestine (Hecker & Grovum, 1975) as ingesta retention time increased (Ali et al., 2018). This was furthermore indicated by a strong correlation between fecal DM content and retention time of liquid digesta in the lower GIT ($r = 0.83$; data not shown). When considering the pure hay diets only, the lower fecal OM concentration at MER80 than at MER60 and MER40 (Table 1) is in line with the result of Jost et al. (2013a) that OM content is higher in feces of an N-deficient diet.

The fecal N concentrations in both experiments are comparable to average values of 9 g N kg^{-1} DM reported for Friesian x Ayrshire steers in Kenya fed a pure barley straw diet, and to the 11 – 17 g N kg^{-1} DM in feces when barley straw was supplemented with tree legumes and poultry manure (Delve et al., 2001). Feces obtained with a pure hay diet fed below maintenance (MER80, MER80, MER40) had a much lower fecal N concentration (10 g N kg^{-1} DM) than feces from the supplemented diets (MER100: 13 g N kg^{-1}DM, R+SPVS / R+UMB: 17 – 18 g N kg^{-1} DM) but also than diet R fed *quasi ad libitum* in Exp. 2 (16 g N kg^{-1} DM). Across both experiments and all diets, fecal N concentrations were lower than values reported for forage alone and supplemented cattle diets in temperate regions of 17 – 38 g N kg^{-1} DM (Sørensen et al., 2003; Van Vliet et al., 2007; Jost et al., 2013a). While poor to medium quality diets as tested in the present work obviously generate only medium quality manure, the nitrous oxide emissions from such manure are lower than those of manures in temperate regions as was proven by Zhu et al. (2018) in a companion study on greenhouse gas emissions from the manure generated in the sub-maintenance trial. From our correlation analysis it appeared that fecal N concentration was more closely related to ingesta NDF and ADF concentration than to CP digestibility because CP digestibility declined as intake decreased (Ali et al., under review). In contrast, Kyvsgaard et al. (2000) reported that fecal N concentration was more related to CP digestibility (r = 0.88) than to diet NDF (r = -0.64) and ADF (r = -0.70) content. The present correlation between fecal N content and ingesta composition (Table 3) points to the strong influence of diet on fecal N content.

In Exp. 1, fecal NDF and ADF concentrations increased as feed intake declined, mainly caused by a higher share of fiber fractions and a lower share of CP in the ingesta. As a result, feces from diets MER60 and MER40 had a higher C/N ratio than feces from MER100 (Zhu et al., 2018). This is congruent with the higher C/N ratio along with a higher fecal ADF concentration of feces excreted by dairy cows fed N-poor as compared to N-rich diets (Jost et al., 2013a). The lower carbon dioxide and nitrous oxide emissions reported for these C-rich feces (Zhu et al., 2018) might be explained by the lack of N for denitrification processes (McNeill & Unkovich, 2006) or by higher N immobilization due to the high fecal fiber content (Delve et al., 2001). This is further supported by the fact that mineralization of N was negatively related with dietary NDF and positively related with dietary CP (Sørensen et al., 2003). Diets low in CP lead to lower soil inorganic N concentrations and lower plant DM and N uptake in the short term (Powell et al., 2006).

4.2. Effects of diet quality and feed intake on fecal microbial composition

In both experiments, the average concentrations (in mg g^{-1} dry weight; DW) of muramic acid, galactosamine, and glucosamine were higher than those reported for Holstein heifers and lactating cows (Jost et al., 2013b) on a 50:50 maize silage and concentrate mixture, where muramic acid ranged from 0.22 - 0.45, galactosamine from 0.79 - 1.15, and glucosamine from 1.50 - 2.00. They were also lower than the concentrations of 0.28 - 0.47 (muramic acid), 1.10 - 1.60 (galactosamine) and 1.70 - 2.50 (glucosamine) reported for Holstein heifers fed a mixed ration of grass silage, maize silage, and sugar beet leaves silage (Jost et al., 2011). Whereas the concentrations of microbial C across bot experiments (34 - 40.9 mg g^{-1} DW) were higher than the 21 - 32 mg g^{-1} DW reported by Jost et al. (2013b), they corresponded to the concentrations of 25 - 37 mg g^{-1} DW published by Jost et al. (2011). Considering that in both experiments N concentration of ingesta (5 – 14 g N kg^{-1} DM) was lower and NDF concentration (674 – 780 g NDF kg^{-1} DM) was higher than the values (21 – 25 g N kg^{-1} DW; 445 – 491 g NDF kg^{-1} DW) reported by Jost et al. (2013b), the higher fecal concentrations of amino sugars and microbial C in our samples cannot be explained by ingesta composition. The different results of the present study might relate to the animals' negative energy and balance (see below).

In Exp. 1, the higher N and lower fiber concentration in the supplemented diet MER100 did not alter fecal amino sugar concentrations but fungal-to-bacterial C ratio was lower than in feces derived from diet MER80. Similarly, in Exp. 2, a lower fungal-to-bacterial C ratio along with a lower fungal-to-microbial C ratio and a higher bacterial C and microbial C content was obtained for diet R+SPVS (with higher N and lower NDF and ADF content) than for diet R. The lower ratios of fungal-to-bacterial C and fungal-to-microbial C in supplemented diets MER100 and R+SPVS and the higher bacterial C and microbial C content of feces derived from R+SPVS are in agreement with previous findings that a higher dietary N content enhances fecal microbial biomass (Van Vliet et al., 2007; Jost et al., 2011; Jost et al., 2013a; Jost et al., 2013b).

Furthermore, Jost et al. (2013b) reported that microbial C and muramic acid concentrations were higher in feces derived from a diet with higher N and lower NDF concentration, and that fungal-to-bacterial C ratio is negatively related to diet N concentration (Jost et al., 2013a). Furthermore, Van Vliet et al. (2007) observed that a N-rich diet supports higher fecal microbial and bacterial biomass. In Exp. 1, the highest fungal C and microbial C concentration were obtained at MER60, when the ingested diet was low in N and high in fiber fractions. The lower CP and ADF digestibility at MER60 and MER40 than at MER100 and MER80 might have enhanced the supply of undigested

feed N and fiber fractions to the lower gastrointestinal tract, stimulating fungal growth in the hindgut. A shift in the fecal microbial community towards fungal C was also reported by Al-Kindi et al. (2016) when diet digestibility dropped due to addition of quebracho tannin to the diet. This microbial community sift was ascribed to a lowered N availability in rumen and hindgut due to complexation of feed protein by tannins (Al-Kindi et al., 2016). In the present study, the higher fungal C concentration at MER60 and the higher fungal- to-microbial C ratio at MER60 and MER40 (where ingesta fiber fraction was higher and CP content lower than in the other diets), were in agreement with previous findings. However, the positive correlation of ingesta CP content with fungal-to-bacterial C as well as fungal-to-microbial C ratio and the negative correlations of ingesta CP content with muramic acid (bacterial C) and galactosamine concentrations (Table 4) seem to contradict these results. One reason could be that the higher fecal amino sugar concentrations at MER60 and MER40 might overestimate fungal C and microbial C concentrations. This might relate to the negative energy and N balance of animals subjected to MER60 and MER40 feeding (Wassie et al., 2019), because fecal excretion of endogenous amino sugars might have been elevated. This would also be supported by the drop in CP digestibility and the higher fecal N loss as feed intake declined (Table 1). Amino sugars such as N-acetyl-glucosamine, N-acetyl-galactosamine, and sialic acids have been found in the glycoprotein of mucin in the intestinal mucosa, and these substances are regularly excreted by animals given their functions to lubricate and protect the mucosal epithelia (Mantle & Allen, 1981; Montagne et al., 2000). A review by Doreau et al. (2003) related the lowered OM and CP digestibility when intake level declined bellow MER to the higher excretion of mucosa, yet data is lacking in cattle, whereas sloughed mucosal tissue was observed in undernourished chicken (Bayer et al., 1981), rat (Habold et al., 2007), and weaned pigs (Lallès & David, 2011). Moreover, a higher ratio of fecal glucosamine to fecal N was observed in pigs on a diet of maize starch, sucrose, and glucose (free-protein diet) than in pigs fed either a diet of wheat bran or a mixture of barley and wheat (Fuller & Cadenhead, 1991). Therefore, further research is needed to compare the presently used methods of amino sugar quantification in animal feces to alternative methods of fungal and bacterial quantification in severely undernourished animals.

5. Conclusions

The present study confirmed that the nutrient composition of the diet greatly modifies the fecal concentration of nutrients and amino sugars as well as the fecal microbial community. A declining feed intake of poor quality roughage, very common in the course of the dry season, results in an

increase of C-rich fecal fractions with no effects on the concentration of bacterial C but with an increase of fungal C concentration. Supplementation of poor roughage diets, mostly practiced in dairy cows, may increase fecal OM and N content, depending on the supplement. Fecal nitrogen losses were higher in supplemented cattle, whereas the concentration of bacterial C was unaffected by concentrate supplementation but increased with SPVS supplementation; the fungal-to-bacterial C ratio was lowered by all supplementations strategies. At low levels of feed intake, an increased fecal concentration of slowly decomposable fiber fractions along with a higher fungal C content entails lower greenhouse gas emissions from manure and a longer term supply of soil nutrients to plants.

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Table S1. Non-significant influence of different sampling hours within a sampling day on fecal concentrations of amino sugars and microbial C (mg g^{-1} dry weight; DW) in trials of sub-maintenance feeding (Exp.1) and supplementation (Exp.2).

Variable	hour			SEM	P value
	24:00	12:00	18:00		
Experiment 1					
Amino sugars (mg g^{-1} DW)					
Muramic acid	0.57	0.54	0.56	0.013	0.1911
Galactosamine	2.04	1.96	2.04	0.057	0.4482
Glucosamine	2.88	2.66	2.82	0.060	0.0984
Microbial C (mg g^{-1} DW)					
Fungal C	15.72	14.22	15.24	0.390	0.6910
Bacterial C	25.59	24.28	25.26	0.606	0.1911
Microbial C	41.31	38.50	40.50	0.850	0.2078
Fungal-to-bacterial C ratio	0.65	0.61	0.63	0.019	0.2624
Fungal-to-microbial C ratio	0.38	0.37	0.38	0.007	0.4029
Experiment 2					
Amino sugars (mg g^{-1} DW)					
Muramic acid	0.48	0.47	0.44	0.019	0.7908
Galactosamine	1.30	1.34	1.27	0.041	0.4170
Glucosamine	2.73	2.56	2.47	0.102	0.4170
Microbial C (mg g^{-1} DW)					
Fungal C	15.98	14.63	14.25	0.660	0.3259
Bacterial C	21.54	20.98	19.86	0.876	0.5291
Microbial C	37.52	35.61	34.11	1.382	0.5291
Fungal-to-bacterial C ratio	0.76	0.74	0.74	0.029	0.8294
Fungal-to-microbial C ratio	0.43	0.42	0.41	0.009	0.7906

fecal composition2

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