digesta passage

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Digesta passage and nutrient digestibility in Boran steers at low feed intake levels

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Summary

The present study evaluated the effects of energetic undernutrition on liquid and solid digesta passage and on nutrient digestibility as well as their interdependencies. Using a 4 x 4 Latin square design, 12 growing Boran steers (183 ± 15.2 kg live weight) were allocated to four levels of metabolizable energy (ME) supply fixed at 100, 80, 60, and 40% of individual maintenance energy requirements (MER) during four experimental periods. Each period ran for three weeks of adaptation and two weeks of data collection. Diets MER80, MER60 and MER40 only consisted of Rhodes grass hay (RGH), whereas diet MER100 contained (as fed) 83% RGH, 8% cotton seed meal and 9% sugarcane molasses. Feed intake differed between treatments ($p < 0.001$) and ranged from 40 ± 0.6 g dry matter (DM) per kg of metabolic weight ($kg^{0.75}$) in MER40 to 81 ± 1.3 g DM in MER100. Parameters of digesta passage and digestibility of proximate diet components were affected by treatment, with 8% higher digestibility of neutral and acid detergent fiber (NDF, ADF) at MER80 as compared to MER100 and MER40, even though rumen retention time of liquid and solid digesta was longest at MER40. Rumen retention time of liquid and solid digesta was weakly, but positively, correlated with the digestibility of proximate diet components whereas the -negative- correlation with quantitative feed and nutrient intake was strong ($p < 0.01$). Our results suggest that tropical cattle are able to buffer a moderate energy deficit by an increased rumen retention time of digesta and hence an improved diet digestibility. Conversely, a severe energy deficit cannot be buffered by digestive adaptation mechanisms and will inevitably lead to productivity losses.

Keywords: dry season; energy deficiency; passage rate; roughage diet; ruminants.

1 INTRODUCTION

In sub-Saharan Africa, cattle are regularly exposed to situations of undernutrition due to limited availability of feed, often coupled with low crude protein (CP) and high neutral and acid detergent fiber (NDF, ADF) concentrations during the long dry season (Angassa & Beyene, 2003; Debele, Guru, Hundessa, & Duguma, 2013; Bezabih, Pellikaan, Tolera, Khan, & Hendriks, 2014). Low feed intake has been shown to increase rumination time (Galvani, Pires, Wommer, Oliveira, & Santos, 2010), the percentage of fine feed particles in solid digesta (Luginbuhl, Pond, & Burns, 1990; Okine & Mathison, 1991) and overall diet digestibility

(Galvani et al., 2010; Schulze, Weisbjerg, & Nørgaard, 2014). However, findings at and above maintenance energy intake are different from sub-maintenance feeding levels: In Holstein steers fed grass silage and soybean hulls, Mulligan et al. (2002) observed a decline of the ruminal passage rate of solid digesta and a concomitant increase of the digestibility of dry matter (DM), organic matter (OM), CP, NDF, and ADF as feed intake decreased from 160 to 100% maintenance energy requirements (MER). Recently, Chaokaur, Nishida, Phaowphaisal, and Sommart (2015) tested four intake levels above MER in a tropical cattle breed and concluded that digestibility of DM, OM, CP, and NDF increased by 58% as intake decreased from *ad libitum* to maintenance. Likewise Okine and Mathison (1991) observed an increase in feed particle retention time in the rumen and total gastrointestinal tract (GIT) and an increase of DM, OM, and ADF digestibility as intake of a hay ration decreased from 170 to 100% MER. An increase of particle retention time in the total GIT and of DM and OM digestibility was also observed in Hereford steers when feeding level decreased from *ad libitum* to 2.5, 2.0 and 1.5% of live weight (Dias et al., 2011). Improvement of DM, NDF, and ADF digestibility was observed in a low forage (32% forage, 68% concentrate) and high forage (83% forage, 17% concentrate) diet as particulate passage rate decreased when feeding level declined from *ad libitum* to maintenance in Holstein cows (Colucci, Chase, & Van Soest, 1982).

At intake levels below MER, effects of declining feed intake are less conclusive: For sheep fed hay at 100, 60, and 20% MER, Michalet-Doreau and Doreau (2001) reported that NDF and ADF digestibility were higher at 20% MER than at the higher feeding levels, while DM digestibility was unaffected. When two different grass hay qualities were offered to dry cows at 80, 50 and 20 g DM/kg$^{0.75}$ live weight (LW), rumen and total GIT retention time of particles were greater at 20 g DM/kg$^{0.75}$ LW than at higher intake levels (Doreau & Diawara, 2003). Conversely, the digestibility of DM, OM, NDF, and ADF was only modified by hay quality and not by intake level (Doreau & Diawara, 2003). In contrast to this, a decreasing DM and OM digestibility was recorded for non-lactating Holstein cows on 83% natural grassland hay, 8.5% soybean meal, and 8.5% barley as intake declined from 110 to 65% MER (Grimaud & Doreau, 1995), whereas NDF and ADF digestibility remained constant. Ruminal DM and OM degradation as well as rumen passage of solid digesta were not altered, while passage of liquid digesta through rumen and lower GIT decreased with decreasing feed intake (Grimaud & Doreau, 1995). In Holstein cows fed 60% grassland hay, 30% straw, and 10% ground maize with and without urea supplementation, digestibility of DM, OM, NDF and ADF decreased while ruminal passage rate of particles remained constant as feed intake decreased from 80% to 30% MER (Doreau, Michalet-Doreau, &

Béchet, 2004). For *Bos indicus* and *Bos taurus* cows fed 79% rice straw and a 21% cotton seed meal plus molasses mixture, digestibility of DM, OM, NDF, and ADF were reduced and liquid and solid outflow rate from the rumen declined as intake dropped from 120% to 60% MER (Grimaud, Richard, Kanwé, Durier, & Doreau, 1998).

The above findings suggest that above MER declining intake levels increase digesta retention time and improve digestibility of diet components. Below MER, declining intake does either not affect or reduce rumen and total tract retention time of solid and liquid digesta as well as digestibility of proximate diet components. As an improved digestibility of feed is crucial for enhancing energy extraction from scarce and poor quality feed in a tropical dry season situation (Savadogo, Zemmelink, Nianogo, & Van Keulen, 2000; Abdou, Nsahlai, & Chimonyo, 2011), the current study aimed at reexamining these conflicting consequences of above-/maintenance and sub-maintenance feed intake for diet digestibility and solid and liquid digesta passage. We thereby hypothesized that in environmentally well-adapted tropical cattle a decline in feed intake from 100 to 40% MER (1) consistently results in a longer rumen and total tract retention time of liquid and solid digesta, which (2) improves digestibility of proximate diet components. Furthermore, the collected data was used to verify maintenance energy requirements of housed tropical cattle.

2 MATERIALS AND METHODS

An experiment was conducted at Mazingira Centre, a state-of-the-art environmental research facility within the International Livestock Research Institute, Nairobi, Kenya, from July 2016 to January 2017. During this period, daily average ambient air temperature and relative humidity ranged from 18 to 20°C and from 55 to 69%, respectively (recorded on site with a H08-032-08 HOBO® Temp/RH logger at 15-min intervals; Table 1). The experiment was approved by the Animal Care and Use Committee of ILRI (No. IACUC-RC2016-11).

2.1 Experimental design and animals

In a trial set up as a complete 4 x 4 Latin square design, 12 Kenyan Boran steers aged 1.5 years with initially 183 ± 15.2 kg LW were stratified by LW and allocated to four experimental treatments. Before the trial, animals were ear-tagged and treated against foot-and-mouth disease (inactivated FMD virus strains, 3 ml/animal subcutaneously; Kenya Veterinary Vaccines Production Institute, Nairobi, Kenya), intestinal helminths (Albendazole 10 g/L; 20 ml/animal orally; NORBROOK Kenya Ltd., Nairobi, Kenya) and ticks (Flumethrin 1 g/L, 30 ml/animal pour-on; Bayer New Zealand Ltd., Glenfield, New Zealand).

The trial consisted of four 7-week experimental periods, each starting with three weeks of adaptation to the diet. These were followed by two experimental weeks including one week of digesta passage and digestibility measurements when feed intake and fecal and urine excretion were measured, and one week of methane (CH_4) measurements in respiration chambers (three days per animal, every second day – Goopy et al., *submitted*). Finally, two weeks of recovery feeding concluded each experimental period. Due to the fact that only three respiration chambers were available, six animals were randomly allotted to the digestibility plus digesta passage measurements and six to the CH_4 measurements in experimental week 1. In experimental week 2, the animals were swapped and allocated to the respective other measurements (see Appendix, Table A1). Steers were housed in individual pens (1.8 m x 2.8 m) in an open barn during adaptation and recovery weeks, and in individual pens (1.1 m x 2.2 m) inside a closed barn during the digestibility measurements. Throughout the whole trial, the animals' LW was determined at weekly intervals before morning feeding (Gallagher weighing scale W210; FarmShop Australia, Kenmore, Australia; weighing capacity 2000 kg, accuracy 1%).

2.2 Feeding

The experimental treatments comprised of four feeding levels calculated to cover 100, 80, 60, and 40% of the individual animal's maintenance requirement for metabolizable energy (MER; 0.74 MJ/kg$^{0.75}$ LW for mature bulls; NRC, 1989). For all animals, the diet consisted of Rhodes grass hay (*Chloris gayana* Kunth) harvested at the seed stage and chaffed to about 5 cm particle length. The Rhodes grass hay used in the experiment was purchased from a commercial farm but consisted of different batches. Therefore, its CP concentration in period 3 was similar to that in period 1 but lower than in periods 2 and 4. The OM concentration of the hay in period 1 was similar to that in period 2, higher than in period 4 and lower than in period 3. For animals at 100% MER (abbreviated MER100), 20% of the metabolizable energy (ME) was offered in the form of a cotton seed meal (CSM) and sugarcane molasses mixture (10 : 10% of ME; Table 1) to meet the animals' MER at maximum voluntary feed intake. Amounts of feed offered were adjusted to the individual animal's LW at the start of each of the four adaptation periods and remained constant until the start of the first recovery week.

Each animal's daily ration of hay was weighed into a large plastic bag one day before being offered. Feeding started at 9:30 a.m. after hay refusals from the previous day had been removed and weighed. During daily feeding, only a small portion of hay was placed in the feeding trough at a time. When two thirds of the portion were consumed, new hay was added until the bag was completely empty; this was the case at around 2:00 p.m.

for animals of treatments MER40 and MER60, around 6:00 p.m. for MER80 and around midnight for MER100. The two components of the concentrate mixture for treatment MER100 were weighed separately and mixed thoroughly before being offered once per day (in the morning) in a separate bucket. The concentrate mixture was completely consumed within 15 min. Animals always had *ad libitum* access to drinking water and mineral lick blocks.

During the recovery weeks, animals were offered good-quality Rhodes grass hay *ad libitum*, 2 kg/animal of CSM, 1 kg/animal of molasses and about 100 g of Brachiaria grass (*Brachiaria decumbens* Stapf.) (all weights as fed) to regain LW before the next experimental period.

2.3 Determination of digestibility and digesta passage

A subsample of 100 g fresh matter (FM) of the hay on offer was collected on day 1 of each measurement week. Cotton seed meal (100 g FM) and molasses (70 g FM) offered to MER100 animals were sampled once per experimental period. To determine diet digestibility, the weighed feed on offer as well as refusals of hay were recorded per animal and day (Citizen CTG6H scale, Citizen Scales Inc., New York, USA; capacity 6000 g, accuracy 0.1 g). No refusals of the concentrate mixture were encountered. Total hay refusals were stored as collected and, at the end of each experimental week, pooled per animal, thoroughly homogenized, and sampled (100 g FM). Samples of offered and refused feed were dried at 50°C for 72 h (Genlab forced-air oven SDO/425/DIG, Genlab Ltd., Widnes, UK) and reweighed to determine dry weight.

As soon as an animal defecated, total fecal mass was collected directly from the clean pen floor throughout the week of digestibility determination. For each animal, all feces were collected into a 10-liter bucket and weighed (Citizen CTG6H scale, Citizen Scales Inc., New York, USA; capacity 6000 g, accuracy 0.1 g) once every 24 h (at 8:00 a.m.). Afterwards, feces were thoroughly mixed by hand and a subsample of 300 g FM was dried at 50°C for 72 h (see above) and reweighed. Another subsample of 60 g FM was taken and stored at -20°C for nitrogen (N) analysis.

Dried samples of offered and refused feed and of feces were stored in air-tight polyethylene zipper bags at room temperature. At the end of each experimental period, the dried samples were ground to pass a 1-mm mesh (MF 10 basic, IKA® Werke, Staufen, Germany), pooled per animal and period, and homogenized. A subsample of 100 g dry feces was kept for analysis. Frozen fecal samples were thawed, pooled per animal and

period (proportionally to the daily amount of air dry feces excreted), thoroughly mixed, and directly weighed for N analysis (see below).

The passage of liquid and solid digesta through the GIT was determined using ytterbium (Yb)-marked fiber particles and cobalt (Co)-EDTA (ethylene diamine tetra-acetic acid). To prepare Yb-marked fiber, wheat straw was first cut with scissors to pieces of 3 to 5 cm length and then sieved through a 2-cm mesh to remove debris. Particles remaining on the sieve were boiled in EDTA-free neutral detergent solution for 1 h and then rinsed repeatedly with tap water. Washed fiber particles were dried at 70°C and thereafter soaked for 24 h in 12.4 mmol/L aqueous solution of Yb (III) acetate hydrate. Afterwards the fiber was again rinsed with tap water. To remove excess Yb, the marked particles were soaked for 6 h in a solution of 100 mmol/L of acetic acid, rinsed with tap water and dried at 70°C (Teeter, Owens, & Mader, 1984). The final concentration of Yb (8.46 mg/g DM) was determined from 10 g of marked fiber sample (see below). The Co-EDTA marker was prepared according to Uden, Colucci, and Van Soest (1980). In brief, 249.08 g Co (II) acetate tetrahydrate, 43 g lithium hydroxide, and 292.24 g EDTA were dissolved in a 10-L beaker containing 2 L of Milli-Q distilled water. Hydrogen peroxide (200 ml of 30% v/v) was added to the solution and the mixture was left overnight. On the next day, 3 L of ethanol (95% v/v) were added, then the solution was refrigerated at 4°C. The resulting precipitate was filtered (Whatman No. 2 filter paper) and washed thoroughly with 80% (v/v) ethanol. The precipitate was dried overnight at 65°C and stored in an air-tight bag.

On the first day of the digestibility measurements, each animal was offered a single pulse dose of Yb-marked fiber (560 mg/kg LW; Richter & Schlecht, 2006) mixed with 20 g molasses before morning feeding. After the marked fiber had been completely consumed, the animal was drenched with Co-EDTA (23.56 mg/kg LW). The dosing time (t_0) was individually defined as the moment when an animal had been drenched with Co-EDTA. To determine the Yb and Co concentration in feces, gentle anal stimulation and grab-sampling of fresh feces occurred at 0, 4, 6, 8, 10, 12, 14, 16, 20, 24, 28, 32, 36, 40, 46, 52, 58, 64, 70, 76, 82, 88, 96, 104, 112, 120, 128, 136, and 148 h post dosing. The fresh feces were weighed, homogenized, and 60 g FM were kept for marker determination. The residual material was collected into the 10-L bucket of daily fecal sampling (see above). Fecal samples collected for marker determination were dried at 50°C for 72 h, reweighed, ground to pass a 1-mm mesh (see above), and stored in air-tight polyethylene bags until analysis.

2.4 Chemical analysis of samples

Ground samples of hay, CSM, sugarcane molasses, hay refusals, and feces (hourly samples for Yb and Co concentrations, and weekly pooled samples) were analyzed for DM (AOAC, 1990; method 967.03) and crude ash (AOAC, 1990; method 942.05). The concentration of OM was calculated by subtracting the concentration of crude ash (g/100 g DM) from 100. A Fibertec™ FOSS analyser (Foss GmbH; Hamburg, Germany) was used to determine NDF and ADF concentrations (VDLUFA, 1976; methods 6.5.1 and 6.5.2). The N concentration in feedstuffs offered, hay refusals, and thawed feces was determined by the Kjeldahl procedure (AOAC, 1990; method 984.13) using a Tecator 1028 distilling unit (Tecator GmbH; Hagen, Germany). The CP concentration was calculated by multiplying N concentration with factor 6.25. Crude lipid concentrations of feedstuffs offered were analyzed according to AOAC (1990; method 920.29), and their ME concentration was estimated from 24 h gas production *in vitro* and proximate nutrient concentrations according to Menke and Steingass (1988). All analyses were done in duplicate (for gas production: 2 triplicate incubations) and analysis was repeated if replicate results differed by more than 5%.

Samples of Yb-marked fiber and of dried feces collected for marker determination were subjected to sealed chamber digestion for determination of Yb and Co concentrations (Anderson & Henderson, 1986). Of each dried sample 0.2 g (± 0.01; Toledo XP205 balance; Mettler, Giessen, Germany) was placed in a tared 100-ml Schott bottle. Two ml of a freshly prepared mixture of perchloric acid and hydrogen peroxide (7:3 v/v) were added to the sample. The bottle was loosely capped and stored overnight at room temperature. On the following day, 1 ml of H_2O_2 was added, the bottle was tightly sealed and placed in an oven (Genlab SDO/425/DIG, Genlab Ltd., Widnes, UK) at 80°C for 30 min. After the bottle had cooled down, another 1 ml of hydrogen peroxide was added and the tightly sealed bottle was placed in the oven at 80°C for 60 min. Afterwards, the sample solution was equilibrated to 20 g by addition of distilled water, shaken, and filtered (Whatman No. 1 filter paper) to remove silica precipitates. The solute was collected into a vial, sealed and stored at 2°C until analysis. This digestion procedure was done in duplicate for every 10th sample. Yb and Co concentrations of the solution (mg/L) were determined by inductively coupled plasma optical emission spectroscopy (ICP-OES 5100 VDV, Agilent Technologies, Santa Clara, USA) after 1:10 dilution, and the concentration of Yb and Co in the dried fecal sample (mg/g DM) was calculated based on initial sample weight and dilution factors.

2.5 Data analysis

Individual feed and nutrient intake were calculated by subtracting the animal's daily amount of feed refusals (and the nutrients contained therein, respectively) from the daily amount of feed (nutrients) offered. Apparent total tract digestibility ('digestibility') of feed DM and other proximate diet components (OM, CP, NDF, ADF) were calculated by subtracting the amount excreted via feces from the respective amount ingested and dividing the difference by the ingested amount. The cumulative quantity of Yb and Co excreted during an experimental week was calculated from the elements' concentration in individual fecal samples multiplied by the respective total fecal mass excreted at time t_i (sampling time). The NLIN procedure (PROC NLIN method=dud) was applied using the Type N model of Richter and Schlecht (2006) for parameters of both liquid and solid digesta passage. The following parameters were calculated by applying this one-compartment Gamma-2 model: first-time appearance of the markers in feces (TT; equivalent to post-ruminal laminar flow), ruminal passage rate (λ), half time in the mixing compartment (T_{50}: 0.8392 x $2\lambda^{-1}$), retention time in the mixing compartment (i.e., rumen; CMRT: $2\lambda^{-1}$), and retention time in the total GIT (TMRT: CMRT+TT).

The software package SAS 9.1 (SAS Institute Inc. Cary. CA. USA) was used for data analysis. After confirming normal distribution of data residuals (Kolmogorov-Smirnov test, PROC UNIVARIATE), analysis of variance was performed using the MIXED procedure. Data on feed intake, ingesta composition, digestibility of diet components and digesta passage parameters were analyzed with the following model:

$$y_{ijk} = \mu + f_i + p_j + fp_{ij} + a_k + e_{ijk} \quad [1]$$

where y_{ijkl} is the dependent variable for a particular ijk case, μ is the overall mean, f_i and p_j are the fixed effects of feeding level and period, respectively, fp_{ij} is the interaction of feeding level and period, a_k is the random effect of animal, and e_{ijk} is the random residual error. Significance was declared at $p \leq 0.05$. Differences between treatments at $0.05 > p \leq 0.10$ were considered as a trend towards significance. The Tukey post-hoc test was applied to detect significant differences between means of feeding levels and periods, respectively. Linear and quadratic effects of feeding levels were analyzed for diets below MER using orthogonal polynomial contrast. A Spearman rank correlation was performed to test the relationship between feed intake, ingesta quality, and rate of passage parameters using the CORR procedure. The REG procedure was applied to predict MER at zero LW gain using the data on daily LW changes during four 5-week periods (adaptation plus

experimental weeks). If not stated otherwise, results are presented as arithmetic means and standard error of the mean.

3 RESULTS

3.1 Feed and nutrient intake, digestibility and live weight change

Decreasing feeding levels decreased intake of DM, OM, CP, NDF, ADF, and ME (Table 2). Moreover, below MER100 the amount of hay refusals decreased ($p < 0.001$) with decreasing feeding level (140, 16, and 0 g/kg DM offer for MER80, MER60, and MER40 *versus* 77 g/kg DM offer for MER100). Feed intake varied between experimental periods (Table 2) and was lowest in period 3. Intake of NDF and ADF was highest in period 1, whereas CP intake was higher in period 1 than in period 3 but lower than in periods 2 and 4 (Table 2). Interactions between feeding level and period were observed for the intake of all nutrients (Table 2), whereby intake of DM, OM, NDF, and ADF fluctuated most at MER80 compared to all other levels (Appendix, Tables A2, A3). Ingesta CP concentration fluctuated between experimental periods and peaked in period 2 (Table 2); lowest ME intake was recorded for MER40 in periods 2 and 3 ($p < 0.001$) and highest ME intake values were determined for MER100 in period 1.

Nutrient digestibility varied between experimental periods with highest values for DM, OM, NDF, and ADF digestibility observed in period 1. Digestibility of DM, OM, and ADF declined while CP digestibility peaked in period 2 ($p < 0.05$). For the fiber fractions, the fluctuations in digestibility were consistent with the higher ingesta NDF and ADF concentrations in periods 2 and 3, respectively (Table 2). Ingesta composition as well as CP, NDF and ADF digestibility were affected by feeding level (Table 2), while digestibility of DM ($p = 0.07$) and OM ($p = 0.09$) were only influenced by trend. Ingesta of steers at MER40 contained more NDF and ADF but less CP than ingesta of animals at MER80 and MER100 ($p = 0.001$). Yet, NDF as well as ADF digestibility was similar for MER40 and MER100 ($p > 0.05$) but differed from MER80 ($p < 0.001$). The Spearman correlation was negative for the relationship between ingesta NDF concentration and the digestibility of DM ($r_s = -0.41$, $p < 0.01$), OM ($r_s = -0.38$, $p < 0.01$), and CP ($r_s = -0.43$, $p < 0.01$). Similarly, ingesta ADF concentration correlated negatively with the digestibility of DM ($r_s = -0.32$, $p < 0.05$) and CP ($r_s = -0.63$, $p < 0.001$), whereas ingesta CP concentration only correlated with CP digestibility ($r_s = 0.87$, $p < 0.001$).

Decreasing feeding levels introduced LW losses and only animals at MER100 gained LW (Table 2). Linear regression analysis (Figure 1) showed that LW change was ($p < 0.001$) correlated with ME and DM intake (ME intake: $R^2 = 0.62$; DM intake: $R^2 = 0.68$). From the regression of ME intake on LW change a daily ME requirement of 0.48 MJ/kg$^{0.75}$ LW was calculated for the steers across the duration of the experiment.

Tables 1, 2 and Figure 1 near here

3.2 Digesta passage

Feeding level influenced liquid (*l*) and solid (*s*) digesta passage parameters (Table 3). The hourly outflow rates from the rumen, λl and λs, were >21% higher at MER100 than at the lower feeding levels. In consequence, rumen retention time (CMRT*s*, CMRT*l*) as well as total tract retention time (TMRT*s*, TMRT*l*) were >16% shorter at MER100 than at the lower feeding levels. The laminar flow of fiber particles (TT*s*) and liquid digesta (TT*l*) through the lower GIT was slowest at MER40 ($p < 0.05$), whereas halftime of liquid and solid digesta in the rumen ($T_{50}l$ and $T_{50}s$) were similar among feeding levels below MER and >18% longer than at MER100 ($p < 0.05$). All liquid digesta passage parameters fluctuated between experimental periods, with λl being highest in period 4 ($p < 0.05$). As a result, liquid retention time in the rumen (CMRT*l*) as well as in the total GIT (TMRT*l*) was shortest ($p < 0.05$) in this period. For animals fed hay only (MER80, MER60, and MER40), the parameters λl and λs, $T_{50}l$ and $T_{50}s$, CMRT*l* and CMRT*s*, as well as TMRT*s* were similar among feeding levels ($p > 0.05$), whereas TT*l*, TT*s*, and TMRT*l* were highest in MER40 ($p < 0.05$).

Liquid and solid digesta passage parameters correlated with quantitative feed intake and ingesta quality (Table 4), whereby parameters of liquid passage showed by trend stronger correlations than parameters of solid digesta passage. Ingesta CP concentration showed a positive correlation with λl and λs and a negative correlation with TT*l*, CMRT*l*, TT*s*, and CMRT*s*. Ingesta concentrations of NDF and ADF were negatively correlated with λl and λs and positively with TT*l*, CMRT*l*, TT*s*, and CMRT*s*. When excluding MER100 from the correlation analysis, only the correlation of ingesta NDF and ADF concentration with λl remained negative and that with CMRT*l* positive ($p < 0.05$). Crude protein digestibility showed a positive correlation with λl and λs and a negative correlation with TT*l*, CMRT*l*, TT*s*, and CMRT*s* (Table 4).

Tables 3, 4 near here

4 DISCUSSION

4.1 Feed intake and diet composition

Periodical scarcity and low quality of feed limit cattle production in sub-Saharan Africa. For example, in the Rift valley region of Ethiopia, Boran and Arsi cattle lost 110 g/d of LW as declined feed intake during the dry season (Bezabih et al., 2014). The sub-maintenance intake levels tested in the present experiment were chosen to mimic a progressing dry season situation. In a 35-day pre-trial period, the Boran steers were allotted to four feeding levels of estimated MER, and only Rhodes grass hay was offered. Since hay refusals at MER100 averaged 26% of hay offer in this pre-trial period, it was decided that at MER100 feeding level the animals should be offered an additional energy source to meet the MER of 0.74 MJ ME/$kg^{0.75}$ LW (NRC, 1989). The different diet composition at MER100 as compared to MER80, MER60 and MER40 has to be accounted for when interpreting the results. Furthermore, hay quality differed between the four experimental periods (Table 1), which might at least partly explain the influence of period on the dependent variables as well as the interaction of period and feeding level (Appendix, Table A3). In addition, almost all animals at MER80 and MER100 and four animals at MER60 left hay refusals, whereas no refusals occurred at MER40 across the four experimental periods. Selective feeding, together with differences in the nutritional composition of stems and leaves of Rhodes grass (higher CP and lower NDF and ADF concentrations in leaves than in stems; Jung & Allen, 1995; Mbwile & Uden, 1997; Mero & Uden, 1998) may further explain differences in ingesta composition between feeding levels below MER100.

4.2 Digesta passage and diet digestibility

Using the same marker for fiber particles and the same application procedure, the range of TT*s* in the present study (14.3 - 20.8 h) is similar to TT*s* determined for bush hay (15.6 h) and green forage (16.4 h) in *Bos indicus* cattle at *ad libitum* intake level (Schlecht, Richter, Fernández-Rivera, & Becker, 2007). The present λ*l* (7.8 - 8.8%/h) and λ*s* (2.6 - 2.8%/h) values of animals fed hay only (MER80, MER60, MER40) are lower than λ*l* (9.2%/h) and λ*s* (3.5%/h) determined in Holstein x Boran heifers fed wheat straw and Rhodes grass hay *ad libitum* (Ali et al., 2018) and the value of 3.3%/h (λ*s*) determined in cattle ingesting bush hay *ad libitum* (Schlecht et al., 2007), even though the same markers and application procedures were used. However, the present data compares well with λ*s* (2.6 - 3.0%/h) and λ*l* (5.9 - 10.0%/h) reported by Grimaud and Doreau (1995) for Holstein cows offered hay, soybean meal, and barley at 110 to 65% MER, and with λ*l* (7.8 -

10.5%/h) of *Bos indicus* cows fed rice straw and CSM at 100 and 30% MER (Grimaud, Richard, Vergeron, Guilleret, & Doreau, 1999).

4.2.1 Effects of below maintenance energy intake

The declined feed intake from MER80 to MER40 decreased CP and ADF digestibility and prolonged TT*l* and TT*s*, while λ*l* and λ*s* were not altered. That the decrease in intake from 64 g DM/kg$^{0.75}$ LW (MER80) to 40 g DM/kg$^{0.75}$ LW (MER40) did not result in changes in CMRT*s* might be due to a low rumen fill and DM content. Doreau and Diawara (2003) reported that the declined feed intake from 80 to 20 g DM/kg$^{0.75}$ LW decreased total rumen content by 35%, rumen DM content by 55% and rumen water content by 32%. Thereby the proportion of rumen water to total rumen content increased (from 91% to 93%) as intake decreased. A lower DM to water ratio in the rumen might also be the reason for the present decrease of λ*l* (by 12%) and λ*s* (by 7%) when DM intake declined by 37% from MER80 to MER40. This would moreover explain the stronger correlation between quantitative feed intake (g DM/kg$^{0.75}$ LW) and liquid than solid digesta passage parameters at feeding levels below MER. As reviewed by Doreau, Michalet-Doreau, Grimaud, Atti, and Nozière (2003), a longer particle retention time cannot prevent the decrease of (OM) digestibility at very low feed intake levels. Several explanations exist for this phenomenon, such as a high content of water or a low DM content in the rumen. Furthermore, low numbers and reduced activity of rumen microbes due to insufficient N supply and higher fecal N losses may also interfere (Doreau et al., 2004). Previous studies showed that neither the addition of protein (CSM supplementation; Grimaud & Doreau, 2003) nor of easily degradable N (urea supplementation) and ground maize (Doreau et al., 2004) could prevent this decline in digestibility of DM, OM, NDF, and ADF. However, a higher rumen N concentration provided via the rumino-hepatic cycle in a low protein diet might assure sufficient N supply for microbial growth at very low feeding levels (Michalski et al., 2012). In the present study, the decline in CP digestibility at levels below MER may also relate to a higher endogenous N losses via fecal excretion (Doreau et al., 2003). In two animals (one at MER40 in period 3 and one at MER60 in period 4), fecal N losses were 17 and 12% higher than N intake. When expressed per unit of N intake (N_I), the N_F loss increased as intake decreased (797, 867, and 897 g N_F/kg N_I at MER80, MER60, and MER40, respectively).

The linear decrease in ADF digestibility from MER80 to MER40 is consistent with results of other sub-maintenance feeding studies (Grimaud et al., 1998; Grimaud et al., 1999; Grimaud & Doreau, 2003; Doreau

et al., 2004). This decrease might be partly explained by the linear increase of fiber fractions in the diet and might indicate a lack of energy for feed degradation in the rumen. In contrast, Michalet-Doreau and Doreau (2001) reported that NDF and ADF digestibility were higher at 20% MER than at 60 and 100% MER, and Doreau and Diawara (2003) found that NDF and ADF digestibility were not affected when DM intake declined from 80 to 50 and 20 g/kg$^{0.75}$ LW.

The decreased fiber digestibility was not related to the efficiency of ruminal microbial protein synthesis, which was similar for MER80, MER60 and MER40 (11.9, 11.8, 12.7 g N/kg digestible OM intake; Wassie et al., 2019). This might indicate that rumen fermentation and microbial growth were little impaired at sub-maintenance feeding levels (Doreau et al., 2004; Wassie et al., 2019). However, apparent digestibility of DM, OM, and CP might also be affected by a decline of nutrient absorption in the rumen and lower GIT or by a reduced activity of the animal's enzymatic digestion (Ortigues & Doreau, 1995; Chilliard, Bocquier, & Doreau, 1998) due to declining blood and oxygen flow to digestive organs in situations of severe energy deficiency. Huntington and Prior (1985) reported a decreased amino acid absorption in Hereford x Angus heifers when ME intake decreased from 0.94 to 0.35 MJ/kg$^{0.75}$ LW. A lower absorption of arterial amino acids and acetate was also reported for ewes fed grassland hay at 51% as compared to 88 and 143% MER (Noziere, Remond, Bernard, & Doreau, 2000). In summary, at intake levels below maintenance energy requirements our findings confirm previous results that prolongation of digesta retention time does not improve the digestibility of all diet components.

4.2.2 Effects of (above) maintenance energy intake

At MER100, CP digestibility was higher but NDF and ADF digestibility was lower than at MER80, whereas ruminal passage rate of both liquid and solid digesta was higher at MER100. At all four feeding levels, fluid passed faster through the rumen than particles, whereby the proportional differences between liquid and solid digesta passage increased with increasing feed intake (5.1, 5.5, 5.9, and 7.2% at MER40, MER60, MER80, and MER100). Besides the higher feed intake, the more pronounced increase in λl than in λs at MER100 was probably due to the concentrate feeding which in turn might have decreased ruminal fluid volume as has been shown by Bartocci, Amici, Verna, Terramoccia, and Martillotti (1997) in buffaloes, cattle and sheep. Supply of easy-degradable carbohydrates and N through concentrate feeding is recommended for high fiber diets to improve particle breakdown and digestion (Mlay, Pereka, Weisbjerg, Hvelplund, & Madsen, 2003; Hristov et

al., 2005; Lazzarini et al., 2013; McLennan, Bolam, Kidd, Chandra, & Poppi, 2017). Higher dietary CP and lower fiber concentration at MER100 than at MER80 improved CP digestibility as well as the efficiency of ruminal microbial protein synthesis and N balance (Wassie et al., 2019). However, higher efficiency of microbial protein synthesis at MER100 than at MER80 (13.7 and 11.9 g N/kg digestible OM intake, respectively) did not improve DM and OM digestibility, and NDF and ADF digestibility were lower at MER100 than at MER80, which might be explained by the faster rumen passage of particles at MER100. This agrees with findings of previous studies at intake levels above maintenance and is likely due to a shorter time for nutrient degradation by rumen microbes (Van Soest, 1994; Janssen, 2010). Increasing feed offer to Holstein steers on a soybean hull / grass silage ration from 100 to 160% MER increased λl from 9.1 to 11.6%/h and decreased DM, OM, NDF, and ADF digestibility by 9, 9, 11, and 12%, respectively, whereas λs (3.1 and 4.2 %/h) was not affected by intake level (Mulligan et al., 2002). Okine and Mathison (1991) observed a reduction of DM, OM, and ADF digestibility and a shorter particle retention time in rumen and total GIT as intake increased from 100% to 130%, 150%, and 170% MER in non-lactating Holstein cows fed a mixture of Brome grass, timothy, and alfalfa hay (40 : 40 : 20). The higher CP digestibility at MER100 compared to MER80 is opposed to results of previous studies where CP digestibility declined when feeding levels increased above MER (Woods, Moloney, Mulligan, Kenny, & O'Mara, 1999; Mulligan et al., 2002; Gabel et al., 2003; Chaokaur et al., 2015). In the present study, CP digestibility was more strongly correlated with post ruminal laminar flow time (TT) than with rumen retention time (CMRT). The higher microbial N flow at MER100 than at MER80 (Wassie et al., 2019) and the relatively strong correlation of CP digestibility and TT point to the importance of the lower GIT for CP digestion in the present study. To summarize, by comparing our MER100 and MER80 findings with literature, the higher digestibility of NDF and ADF as declined passage rate with declining feed intake are fully confirmed. However, as indicated by the lower CP digestibility at MER80, the change in diet composition that was associated with the declining intake also influenced digestibility values.

Taken together, the present results confirm the previously reported conflicting consequences of above-/maintenance and sub-maintenance feed intake for diet digestibility, as well as for solid and liquid digesta passage. According to p and R^2 values of single and segmented regression, break point analysis (Figure 2) shows that in the current situation the breakoff point was at 52% MER, meaning that until that intake level the animal's digestive system was able to cope with decreasing energy supply by enhancing digestive efficiency,

while below this threshold a drop in digestibility was observed that could not be counterbalanced. From the paralleling N balance study of Wassie et al. (2019) it appears that only energy supply, and not the supply of CP, was the limiting factor in the present case.

Figure 2 near here

4.3 Daily live weight changes and maintenance energy requirement

Live weight changes of the animals were in the range of -1029 to 471 g/d across the four experimental periods. This is in line with the measured N retention of +5.1, -6.0, -6.4, and -8.2 g N/d for MER100, MER80, MER60 and MER40, respectively (Wassie et al., 2019). Live weight losses and a negative N balance at below MER feeding levels point to the mobilization of protein tissue (Chilliard et al., 2000) during each five-week period of adaptation and measurements. According to Chilliard et al. (1998), after a reduction of splanchnic tissues and fat mobilization, muscle tissue mobilization is the exacerbated response to medium-term energy deficiency. According to our initial ration calculations, animals at MER80, MER60 and MER40 were supposed to experience mild, moderate and severe energy deficiency. However, the regression of ME intake against average daily LW change yielded a daily MER (MJ ME/kg$^{0.75}$ LW) of 0.48 for our growing Boran steers in housed condition. This value compares well to the value for Nellore steers (0.49) fed with 60% corn or sorghum silage and 40% concentrate in Brazil (Tedeschi et al., 2002). Lower values were reported for Nellore x Red Angus crossbred steers (0.39) fed 70% corn silage and 30% concentrate in a tropical region of Brazil (Chizzotti, Valadares Filho, Tedeschi, Chizzotti, & Carstens, 2007), and for Brahman steers (0.44) fed 30% Pangola grass hay and 70% concentrate in Thailand (Chaokaur et al., 2015). Yet, also higher values were found for growing Boran (0.51) and Holstein x Boran crossbred (0.54) heifers fed 65% *Cynodon dactylon* hay and 35% wheat bran in Ethiopia (Jenet et al., 2004). Recently, McLennan et al. (2017) reported the value of 0.46 for *Bos indicus* steers fed Rhodes grass plus supplements in Northern Australia. Recalculating MER feeding levels on the basis of 0.48 MJ ME/kg$^{0.75}$ LW indicated that individual ME supply actually ranged from 47 to 133% in the current study (Appendix, Figure A1), and that the CSM and molasses mixture provided 22% of ME supply at the MER100 feeding level.

5 CONCLUSIONS

5

Liquid and solid digesta passage through the rumen and total GIT as well as the digestibility of proximate diet components were negatively affected by a decrease in feed intake from above maintenance energy supply to

severe energy deficiency. The inclusion of concentrate in the (above) maintenance diet improved DM and CP intake but reduced liquid and solid digesta retention time in the rumen and total tract as well as the digestibility of fiber fractions. At feed intake levels below maintenance energy requirements, solid and liquid digesta passage parameters were only slightly affected by feed intake, and fiber digestibility was enhanced at mild (MER80) and moderate (MER60) but depressed at severe (MER40) levels of energy deficiency. Segmented regression analysis identified an intake level of 52% MER as the breakoff point between a rather stimulating and a purely suppressive effect of declining feed intake on digesta passage and diet digestibility. It can be concluded that in the late dry season, cattle keepers in sub-Saharan farming systems can tolerate energy deficiency of their animals until that level but must offer supplement feeds if intake levels drop below this threshold.

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TABLE 1 Dry matter (DM), organic matter (OM), crude protein (CP), neutral detergent fiber (NDF), acid detergent fiber (ADF), and metabolizable energy (ME) concentrations of Rhodes grass hay, cotton seed meal, and sugarcane molasses offered to Boran steers, as well as average ambient air temperature and humidity during four experimental periods[1]

Feedstuff	Period[1]	n	DM	OM	CP	NDF	ADF	ME	Temperature	Humidity
			g/kg FM	g/kg DM				MJ/kg DM	°C	%
Rhodes grass hay	1	2	924	917	31	759	490	6.6	18	66
	2	2	910	916	37	780	493	6.0	20	59
	3	2	893	923	30	777	510	6.3	19	69
	4	2	935	908	34	761	483	6.4	20	55
	SEM		9.7	1.4	0.8	5.3	5.7	0.13	0.1	0.8
Cotton seed meal	1	1	928	949	299	500	359	8.5		
	2	1	925	951	303	490	361	8.4		
	3	1	920	947	294	525	368	8.4		
	4	1	923	948	293	517	358	7.8		
	SEM		1.6	0.8	2.3	7.8	2.2	0.16		
Molasses	1,2 & 3,4	2	699	882	26	n.a.	n.a.	10.8		
	SEM		0.0	0.3	1.4					

SEM: Standard error of the mean; n.a.: not available.

[1] Periods: 1= August 25 – September 11, 2016; 2= September 12 – October 30, 2016; 3= October 31 – December 18, 2016; 4= December 19 – January 23, 2017.

TABLE 2 Intake of dry matter (DM), organic matter (OM), crude protein (CP), neutral detergent fiber (NDF), acid detergent fiber (ADF), and metabolizable energy (ME) by Boran steers at four feeding levels of maintenance energy requirements (MER), as well as average daily live weight (LW) change, ingesta composition, and digestibility of proximate diet components

	Feeding level				Period					Significance				
Variable	**MER100**	**MER80**	**MER60**	**MER40**	**1**	**2**	**3**	**4**	**SEM**	**F[1]**	**P[1]**	**F*P[1]**	**Lnr[2]**	**Qtc[2]**
Intake (g/kg$^{0.75}$ LW)														
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	***	***	**	***	***
ME (MJ/kg$^{0.75}$ LW)	0.56^{d}	0.41^{c}	0.36^{b}	0.25^{a}	0.45^{c}	0.36^{a}	0.36^{a}	0.41^{b}	0.017	***	***	**	***	***
LW change (kg/d)	0.20^{d}	-0.07^{c}	-0.32^{b}	-0.71^{a}	-0.15^{b}	-0.05^{b}	-0.32^{a}	-0.39^{a}	0.056	***	***	(*)	***	(*)
Ingesta composition (g/kg DM)														
OM	914^{b}	912^{a}	915^{b}	916^{b}	917^{c}	913^{b}	920^{d}	907^{a}	0.8	***	***		***	(*)
CP	68^{c}	35^{b}	33^{a}	33^{a}	39^{a}	47^{d}	40^{ab}	43^{c}	2.2	***	***		***	*
NDF	689^{a}	765^{b}	769^{c}	769^{c}	740^{a}	759^{c}	753^{b}	741^{a}	5.1	***	***		***	*
ADF	445^{a}	491^{b}	493^{bc}	494^{c}	478^{b}	479^{b}	496^{c}	470^{a}	3.4	***	***	*	**	
ME (MJ/kg DM)	6.9^{c}	6.4^{b}	6.3^{a}	6.3^{a}	6.7^{d}	6.2^{a}	6.5^{b}	6.6^{c}	0.04	***	***	(*)	***	*
Digestibility (g/kg)														
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	***	**		**	

SEM: Standard error of the mean; n = 12.

Periods: 1 = August 25 – September 11, 2016; 2= September 12 – October 30, 2016; 3= October 31 – December 18, 2016; 4= December 19 – January 23, 2017.

[1] Statistical significance: (*) $p \leq 0.10$; *$p \leq 0.05$; **$p \leq 0.01$; ***$p \leq 0.001$ of feeding level (F), period (P), and level x period interaction (F*P). An empty cell indicates non-significant effects; Within rows, means with different superscripts differ at $p < 0.05$ (Tukey post-hoc test).

[2] Linear (Lnr) and quadratic (Qtc) effect test for pure Rhodes grass feeding (MER80, MER60, MER40).

TABLE 3 Liquid (*l*) and solid (*s*) digesta ruminal passage rate (λ), post ruminal transit time (TT), half time of digesta in the rumen (T_{50}), retention time in the rumen (CMRT), and retention time in the total gastrointestinal tract (TMRT) as determined in Boran steers at four feeding levels of maintenance energy requirements (MER)

	Feeding level				Period				SEM	Significance			
Variable	**MER100**	**MER80**	**MER60**	**MER40**	**1**	**2**	**3**	**4**		**F[1]**	**P[1]**	**F*P[1]**	**Lnr[2]**
Liquid digesta passage													
λ*l* (%/h)	10.6 ^{b}	8.8 ^{a}	8.2 ^{a}	7.8 ^{a}	8.5 ^{a}	8.8 ^{ab}	8.2 ^{a}	9.8 ^{b}	0.32	***	**		*
TT*l* (h)	7.0 ^{a}	7.9 ^{ab}	9.1 ^{b}	11.0 ^{c}	7.6 ^{a}	8.0 ^{ab}	9.3 ^{bc}	10.1 ^{c}	0.34	***	***		***
T_{50}*l* (h)	16.0 ^{a}	19.5 ^{b}	21.5 ^{b}	22.0 ^{b}	19.9 ^{ab}	19.7 ^{ab}	21.6 ^{b}	17.8 ^{a}	0.64	***	*		*
CMRT*l* (h)	19.1 ^{a}	23.3 ^{b}	25.6 ^{b}	26.2 ^{b}	23.7 ^{ab}	23.5 ^{ab}	25.7 ^{b}	21.3 ^{a}	0.77	***	*		*
TMRT*l* (h)	26.1 ^{a}	31.2 ^{b}	34.7 ^{bc}	37.2 ^{c}	31.3 ^{a}	31.6 ^{a}	35.0 ^{b}	31.4 ^{a}	0.88	***	*		***
Solid digesta passage													
λ*s* (%/h)	3.5 ^{b}	2.8 ^{a}	2.8 ^{a}	2.6 ^{a}	2.9	3.1	2.9	2.9	0.09	***		(*)	
TT*s* (h)	14.3 ^{a}	15.5 ^{ab}	17.5 ^{b}	20.8 ^{c}	16.3	16.0	18.1	17.6	0.60	***	(*)		***
T_{50}*s* (h)	49.8 ^{a}	60.5 ^{b}	61.7 ^{b}	66.2 ^{b}	58.7	56.4	61.5	61.5	1.83	***			
CMRT*s* (h)	59.4 ^{a}	72.1 ^{b}	73.6 ^{b}	78.9 ^{b}	70.0	67.2	73.3	73.3	2.18	***			
TMRT*s* (h)	73.6 ^{a}	87.6 ^{b}	91.1 ^{b}	99.6 ^{b}	86.3	83.2	91.4	91.0	2.42	***	*		**

SEM: Standard error of the mean; n = 12.

Periods: 1= August 25 – September 11, 2016; 2= September 12 – October 30, 2016; 3= October 31 – December 18, 2016; 4= December 19 – January 23, 2017.

[1] Statistical significance: (*) $p \leq 0.10$; *$p \leq 0.05$; **$p \leq 0.01$; ***$p \leq 0.001$ of feeding level (F), period (P), and level x period interaction (F*P). An empty cell indicates non-significant effects. Within rows, means with different superscripts differ at $p < 0.05$ (Tukey post-hoc test).

[2] Linear (Lnr) effect test for pure Rhodes grass feeding (MER80, MER60, MER40).

TABLE 4 Spearman correlation coefficients (r_s) and significance levels[1] of the individual relationships between ingesta composition, quantitative intake, and apparent total tract digestibility of dry matter (DM), organic matter (OM), crude protein (CP), neutral detergent fiber (NDF), and acid detergent fiber (ADF) with liquid (*l*) and solid (*s*) digesta ruminal passage rate (λ), post ruminal transit time (TT), and rumen retention time (CMRT) in Boran steers at four feeding levels of maintenance energy requirements

	Liquid digesta passage			**Solid digesta passage**		
Variable	**λ*l*** (%/h)	**TT*l*** (h)	**CMRT*l*** (h)	**λ*s*** (%/h)	**TT*s*** (h)	**CMRT*s*** (h)
Intake (g/kg$^{-0.75}$ LW)						
DM	0.57 ***	-0.64 ***	-0.57 ***	0.48 ***	-0.52 ***	-0.48 ***
OM	0.56 ***	-0.65 ***	-0.56 ***	0.48 ***	-0.51 ***	-0.48 ***
CP	0.56 ***	-0.59 ***	-0.56 ***	0.48 ***	-0.55 ***	-0.48 ***
NDF	0.56 ***	-0.64 ***	-0.56 ***	0.45 **	-0.53 ***	-0.45 **
ADF	0.53 ***	-0.65 ***	-0.53 ***	0.44 **	-0.50 ***	-0.44 **
Ingesta composition (g/kg DM)						
OM	-0.27 (*)	-0.03	0.27 (*)	-0.03	0.16	0.03
CP	0.41 **	-0.38 **	-0.41 **	0.42 **	-0.40 **	-0.42 **
NDF	-0.52 ***	0.35 *	0.52 ***	-0.42 **	0.26 (*)	0.42 **
ADF	-0.53 ***	0.31 *	0.53 ***	-0.42 **	0.30 *	0.42 **
Digestibility (g/kg)						
DM	0.09	-0.18	-0.09	0.05	-0.12	-0.05
OM	0.03	-0.17	-0.03	-0.02	-0.10	0.02
CP	0.31 *	-0.47 ***	-0.31 *	0.34 *	-0.45 **	-0.34 *
NDF	-0.16	0.06	0.16	-0.19	0.06	0.19
ADF	-0.11	0.00	0.11	-0.18	0.03	0.18

LW: Live weight; n = 48.
[1]Significance levels: (*) $p \leq 0.10$, *$p \leq 0.05$, **$p \leq 0.01$, ***$p \leq 0.001$; an empty cell indicates non-significant effects.

Figure captions:

FIGURE 1 Relationship between the daily metabolizable energy intake (MEI; left hand) and daily dry matter intake (DMI; right hand) on average daily live weight (LW) change in Boran steers (n = 48) at four feeding levels

FIGURE 2 Segmented regression of metabolizable energy intake (IME, in % of maintenance energy requirements, MER) against digestibility of a) dry matter (DMD), b) organic matter (OMD), c) neutral detergent fiber (NDFD), and d) acid detergent fiber (ADFD) using data of hay-fed animals only (diets MER80, MER60 and MER40; n=34). Response values show a slight (○) and steep (▲) decline with declining MER intake. The breakoff point (intersection of the two regressions) is at 52% MER for DMD ($p = 0.04$, $R^2 = 0.49$), OMD ($p = 0.06$, $R^2 = 0.47$), and ADFD ($p = 0.04$, $R^2 = 0.54$) and at 53% MER for NDFD ($p = 0.21$, $R^2 = 0.37$)

digesta passage

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