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

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Abstract

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 comprised three weeks of adaptation, two weeks of data collection and two weeks of recovery. 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 ($p < .001$) 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. Digestibility of neutral and acid detergent fibre (NDF, ADF) was highest at MER80, whereas rumen retention time of liquid and solid digesta was longest at MER40. The correlation of rumen retention time of liquid and solid digesta with the digestibility of proximate diet components was weak but positive, whereas the correlation of liquid and solid rumen retention time with quantitative feed and nutrient intake was strong ($p < .01$) and negative. Our results suggest that tropical cattle are able to buffer a moderate energy deficit by prolonging rumen retention time of digesta and hence improve 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 fibre (NDF, ADF) concentrations during the long dry season (Angassa & Beyene, 2003; Bezabih, Pellikaan, Tolera, Khan, & Hendriks, 2014; Debele, Guru, Hundessa, & Duguma, 2013). At feeding levels above or close to maintenance energy requirements (MER), 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). 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

in the digestibility of dry matter (DM), organic matter (OM), CP, NDF and ADF as feed intake decreased from 160% to 100% 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 particle retention time in the rumen and total gastrointestinal tract (GIT) and an increase in DM, OM and ADF digestibility as intake of a hay ration decreased from 170% to 100% MER. An increase in 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). Improved 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: 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 were 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).

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 (Abdou, Nsahlai, & Chimonyo, 2011; Savadogo, Zemmelink, Nianogo, & Van Keulen, 2000), the current study aimed at reexamining these conflicting consequences of above-maintenance/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 (a) would consistently result in a longer rumen and total tract retention time of liquid and solid digesta, which (b) would improve digestibility of proximate diet components. Furthermore, the collected data were 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 (ILRI), 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, Nairobi, Kenya) and ticks (Flumethrin 1 g/L, 30 ml/animal pour-on; Bayer New Zealand, 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 measurement weeks including one week of digesta passage and digestibility measurements when feed intake and faecal 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*). 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 × 2.8 m) in an open barn during adaptation and recovery weeks, and in individual pens (1.1 m × 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$^{0.75}$

TABLE 1 Dry matter (DM), organic matter (OM), crude protein (CP), neutral detergent fibre (NDF), acid detergent fibre (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

			DM	OM	CP	NDF	ADF	ME	Temperature	Humidity
Feedstuff	Period	*n*	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					

Abbreviations: n.a, not available; *SEM*, Standard error of the mean.
[a]Periods: 1 = 25 August–11 September 2016; 2 = 12 September–30 October 2016; 3 = 31 October–18 December 2016; 4 = 19 December–23 January 2017.

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 approximately 5 cm particle length. The Rhodes grass hay used in the experiment was purchased from a commercial farm but consisted of different batches. 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, each animal was offered good-quality Rhodes grass hay ad libitum, 2 kg/d of CSM, 1 kg/d of molasses and approximately 100 g/d of Brachiaria grass (*Brachiaria decumbens* Stapf.) (all weights as fed) to regain LW before the start of 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, New York, USA; capacity 6,000 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 measurement week, pooled per animal, thoroughly homogenized and sampled (100 g FM). Samples of offered and refused feed were dried at 50°C for 72 hr (Genlab forced-air oven SDO/425/DIG, Genlab, Widnes, UK) and reweighed to determine dry weight.

As soon as an animal defecated, total faecal mass was collected directly from the clean pen floor throughout the week of digestibility determination. For each animal, all faeces were collected into a 10-litre bucket and weighed (Citizen CTG6H scale, Citizen Scales, New York, USA; capacity 6,000 g, accuracy 0.1 g) once every 24 hr (at 8:00 a.m.). Afterwards, faeces were thoroughly mixed by hand and a subsample of 300 g FM was dried at 50°C for 72 hr (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 faeces were stored in airtight 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 faeces was kept for analysis. Frozen faecal samples were thawed, pooled per animal and period (proportionally to the daily amount of air dry faeces 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 fibre particles and cobalt (Co)-EDTA (ethylenediaminetetraacetic acid). To prepare Yb-marked fibre, 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 hr and then rinsed repeatedly with tap water. Washed fibre particles were dried at 70°C and thereafter soaked for 24 hr in 12.4 mmol/L aqueous solution of Yb (III) acetate hydrate. Afterwards, the fibre was again rinsed with tap water. To remove excess Yb, the marked particles were soaked for 6 hr 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 fibre 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) was added, and 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 airtight bag.

On the first day of the digestibility measurements, each animal was offered a single pulse dose of Yb-marked fibre (560 mg/kg LW; Richter & Schlecht, 2006) mixed with 20 g molasses before morning feeding. After the marked fibre 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 faeces, gentle anal stimulation and grab sampling of fresh faeces 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 hr post-dosing. The fresh faeces were weighed and homogenized, and 60 g of FM was kept for marker determination. The residual material was collected into the 10-L bucket of daily faecal sampling (see above). Faecal samples collected for marker determination were dried at 50°C for 72 hr, reweighed, ground to pass a 1-mm mesh (see above) and stored in airtight polyethylene bags until analysis.

2.4 | Chemical analysis of samples

Ground samples of hay, CSM, sugarcane molasses, hay refusals and faeces (hourly samples for Yb and Co concentrations, and weekly pooled samples) were analysed 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 including residual ash (VDLUFA, 1976; methods 6.5.1 and 6.5.2). The N concentration in feedstuffs offered, hay refusals and thawed faeces was determined by the Kjeldahl procedure (AOAC, 1990; method 984.13) using a Tecator 1,028 distilling unit (Tecator GmbH; Hagen, Germany). The CP concentration was calculated by multiplying N concentration with factor 6.25. Crude lipid concentrations in feedstuffs offered were analysed according to AOAC (1990; method 920.29), and their ME concentration was estimated from 24-hr 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 fibre and of dried faeces 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) was 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, and the bottle was tightly sealed and placed in an oven (Genlab SDO/425/DIG, Genlab, 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 faecal 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) was calculated by subtracting the amount excreted via faeces from the

TABLE 2 Intake of dry matter (DM), organic matter (OM), crude protein (CP), neutral detergent fibre (NDF), acid detergent fibre (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	***	**		**	

Abbreviation: *SEM*, Standard error of the mean; $n = 12$.

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

[1]Statistical significance: (*) $p \leq .10$; *$p \leq .05$; **$p \leq .01$; ***$p \leq .001$ 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 $p < .05$ (Tukey post hoc test).

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

respective amount ingested (i.e. the ingesta) and dividing the difference by the ingested amount. The cumulative quantity of Yb and Co excreted during a measurement week was calculated from the elements' concentration in individual faecal samples multiplied by the respective total faecal 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 faeces (TT; equivalent to post-ruminal laminar flow), ruminal passage rate (λ), half-time in the mixing compartment (T_{50}: $0.8392 \times 2\lambda^{-1}$), 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 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 analysed with the following model:

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

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_{ijkl} is the random residual error. Significance was declared at $p \leq .05$. Differences between treatments at $.05 > p \leq .10$ 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 analysed 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 measurement 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 was reduced ($p < .001$) with decreasing feeding level (140, 16 and 0 g/kg DM offer for MER80, MER60 and MER40 vs. 77 g/kg DM offer for MER100). Feed intake varied between experimental periods (Table 2) and was lowest in period 3. 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 composition as well as CP, NDF and ADF digestibility were affected by feeding level (Table 2), while digestibility of DM ($p = .07$) and OM ($p = .09$) was 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 ($p = .001$). Yet, NDF as well as ADF digestibility were similar for MER40 and MER100 ($p > .05$) but differed from MER80 ($p < .001$). Nutrient digestibility also varied between experimental periods, with highest values

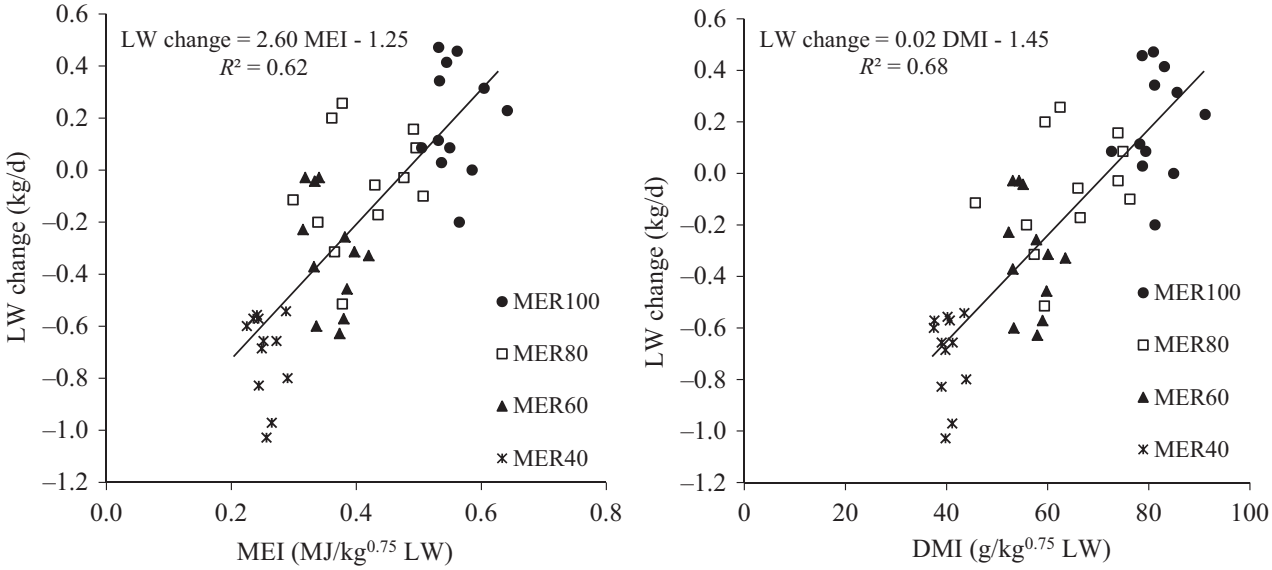

FIGURE 1 Relationship between the daily metabolizable energy intake (MEI; left hand) and daily dry matter intake (DMI; right hand) on average daily live weight (LW) change in Boran steers ($n = 48$) at four feeding levels

for DM, OM, NDF and ADF digestibility observed in period 1 (Table 2). The Spearman correlation was negative for the relationship between ingesta NDF concentration and the digestibility of DM (r_s = −.41, p < .01), OM (r_s = −.38, p < .01) and CP (r_s = −.43, p < .01). Similarly, ingesta ADF concentration showed negative correlation with the digestibility of DM (r_s = −.32, p < .05) and CP (r_s = −.63, p < .001), whereas ingesta CP concentration only correlated with CP digestibility (r_s = .87, p < .001).

Decreased feeding levels introduced LW losses and only animals at MER100 gained LW (Table 2). Linear regression analysis (Figure 1) showed that LW change correlated (p < .001) with ME and DM intake (ME intake: R^2 = .62; DM intake: R^2 = .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.

3.2 | Digesta passage

Feeding level influenced liquid (*l*) and solid (*s*) digesta passage parameters (Table 3). The hourly outflow rates from the rumen, λ*l* and λ*s*, 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 fibre particles (TT*s*) and liquid digesta (TT*l*) through the lower GIT was slowest at MER40 (p < .05), whereas half-time of liquid and solid digesta in the rumen ($T_{50}l$ and $T_{50}s$) was similar among feeding levels below MER and >18% longer than at MER100 (p < .05). All liquid digesta passage parameters fluctuated between experimental periods, with λ*l* being highest in period 4 (p < .05). As a result, liquid retention time in the rumen (CMRT*l*) as well as in the total GIT (TMRT*l*) was shortest (p < .05) in this period. For animals fed hay only (MER80, MER60 and MER40), the parameters λ*l* and λ*s*, $T_{50}l$ and $T_{50}s$, CMRT*l* and CMRT*s*, as well as TMRT*s* were similar among feeding levels (p > .05), whereas TT*l*, TT*s* and TMRT*l* were highest in MER40 (p < .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 λ*l* and λ*s* and a negative correlation with TT*l*, CMRT*l*, TT*s* and CMRT*s*. Ingesta concentrations of NDF and ADF were negatively correlated with λ*l* and λ*s* and positively with TT*l*, CMRT*l*, TT*s* and CMRT*s*. When excluding MER100 from the analysis, only the correlation of ingesta NDF and ADF concentration with λ*l* remained negative and that with CMRT*l* positive (p < .05). Crude protein digestibility showed a positive correlation with λ*l* and λ*s* and a negative correlation with TT*l*, CMRT*l*, TT*s* and CMRT*s* (Table 4).

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 feed intake declined during the dry season (Bezabih et al., 2014). The submaintenance 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 resulting difference in the composition of diet MER100 (hay and supplement) versus diets MER80, MER60 and MER40 (hay only) must be considered when interpreting the present findings. 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. In addition, hay quality differed between the four experimental periods (Table 1), which seemed to be the major reason for the influence of period on the dependent variables as well as the interaction of period and feeding level (Appendix, Table A3). Even though animals subjected to MER40 and MER60 showed higher LW gain in the recovery weeks than animals subjected to MER80 and MER100, maximum absolute LW differences between the four groups were always very close to 20 kg at the end of the first week of adaptation. Therefore, carry-over effects of reduced feed and energy intake on digestive physiology and energy metabolism (Philp, Komarek, Pain, & Bellotti, 2016) might not have completely disappeared until the start of measurements in subsequent experimental periods, but were assumed to be of similar magnitude across periods 2 to 4.

4.2 | Digesta passage and diet digestibility

Using the same marker for fibre particles and the same application procedure, the range of TT*s* in the present study (14.3–20.8 hr) is similar to TT*s* determined for bush hay (15.6 hr) and green forage (16.4 hr) 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 values are in accordance with λ*s* (2.6%–3.0%/h) and λ*l* (5.9%–10.0%/h) reported for Holstein cows offered hay, soybean meal and barley at 110 to 65% MER (Grimaud & Doreau, 1995), 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 TTs, while λ*l* and λ*s* were not altered. That the decline 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 CMRTs might be due to a low rumen fill and DM content. Doreau and Diawara (2003) reported that 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 faecal 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 loss via faecal excretion (Doreau et al., 2003). In two animals (one at MER40 in period 3 and one at MER60 in period 4), faecal N losses were 17 and 12% higher than N intake. When expressed per unit of N intake (N_I), faecal N loss (N_F) 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 (Doreau et al., 2004; Grimaud & Doreau, 2003; Grimaud, Richard, Kanwé, Durier, & Doreau, 1998; Grimaud et al., 1999). It might be partly explained by the linear increase in the concentration of fibre fractions in ingesta from MER80 to MER40 and the concomitantly reduced energy intake that impeded fibre degradation in the rumen. The latter occurred despite prolonged rumen retention time of solid digesta and was probably partly affected by the prolonged retention time of liquid digesta that led to an increased rumen water pool (see above), which presumably entailed a (further) lack of energy for rumen microbial degradation of fibre. 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

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					Significance			
Variable	MER100	MER80	MER60	MER40	1	2	3	4	*SEM*	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	***	*		**

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

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

[1]Statistical significance: (*) $p \le .10$; *$p \le .05$; **$p \le .01$; ***$p \le .001$ 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 $p < .05$ (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 fibre (NDF), and acid detergent fibre (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

Abbreviation: LW: Live weight; n = 48.
[1]Significance levels: (*) $p \le .10$, *$p \le .05$, **$p \le .01$, ***$p \le .001$; an empty cell indicates non-significant effects.

affected when DM intake declined from 80 to 50 and 20 g/kg$^{0.75}$ LW.

The decreased fibre 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 (Chilliard, Bocquier, & Doreau, 1998; Ortigues & Doreau, 1995) 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). For intake levels below maintenance energy requirements, our results show a consistent prolongation of liquid and solid digesta retention time in the rumen and total GIT, which confirms our first hypothesis. However, prorogued digesta retention did not improve diet digestibility, which is in agreement with some of the previous studies on deficient feed and energy intake (Doreau et al., 2004; Grimaud & Doreau, 1995) but contradicts our second hypothesis, even though we had expected that the environmentally well-adapted Boran breed that originates from southern Ethiopia would be able to better cope with undernutrition than imported Holstein or Jersey breeds that are widely used in (East) African smallholder dairy systems (Bebe, Udo, Rowlands, & Thorpe, 2003).

4.2.2 | Effects of (above-) maintenance energy intake

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 λ*l* than in λ*s* 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 fibre diets to improve particle breakdown and digestion (Hristov et al., 2005; Lazzarini et al., 2013; McLennan, Bolam, Kidd, Chandra, & Poppi, 2017; Mlay, Pereka, Weisbjerg, Hvelplund, & Madsen, 2003). Higher dietary CP and lower fibre 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 (Janssen, 2010; Van Soest, 1994). 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 disagreed with results of previous studies where CP digestibility declined when feeding levels increased above MER (Chaokaur et al., 2015; Gabel et al., 2003; Mulligan et al., 2002; Woods, Moloney, Mulligan, Kenny, & O'Mara, 1999). 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 underlined 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 passage rate prolonged while feed intake declined are fully confirmed. However, as indicated by the lower CP digestibility at MER80, the change in diet composition that was associated with the declined intake also influenced digestibility values.

Taken together, the present results confirmed the previously reported conflicting consequences of above-maintenance/maintenance and sub-maintenance feed intake for diet digestibility, as well as for solid and liquid digesta passage. To determine the breakoff point where diet digestibility is reversed from improvement to decline, we first recalculated the animals' MER on the basis of the maintenance ME requirement value of 0.48 MJ/kg$^{0.75}$ LW that was determined across the experiment (section 3.13.1). We then run simple linear, third-order polynomial and segmented regression analysis on intake (recalculated MER, %) against digestibility of DM, OM, NDF and ADF. For the segmented regression analysis, we used the function SEGMENTED in the R package (R Core Team, 2017). For the four simple linear regressions, R^2 values were 0.30 (dNDF), 0.36 (dDM), 0.37 (dOM) and 0.44 (dADF), while the third-order polynomial regression yielded R^2 values of 0.40 (dNDF), .47 (dDM, dOM) and .55 (dADF). Yet, with third-order polynomial regression, an infinite improvement of digestibility with increasing feed intake is suggested which contradicts physiology (Appendix, Figure A2). Therefore, we accepted the segmented regression as an approximation of the third-order polynomial regression (Figure 2). The results of the segmented regression showed that in the current situation, the breakoff point between a stagnant or relatively slow decline in digestibility values and a steep drop occurred at 52% MER. This indicates that until an intake level of 52% MER, the animal's digestive system was able to cope with decreasing energy supply by enhancing or at least maintaining digestive efficiency, while below this threshold, the drop in digestibility 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.

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 is similar 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). Higher values were reported from Ethiopia for growing Boran (0.51) and Holstein x Boran heifers (0.54) fed 65% *Cynodon dactylon* hay and 35% wheat bran (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

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 decreased 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

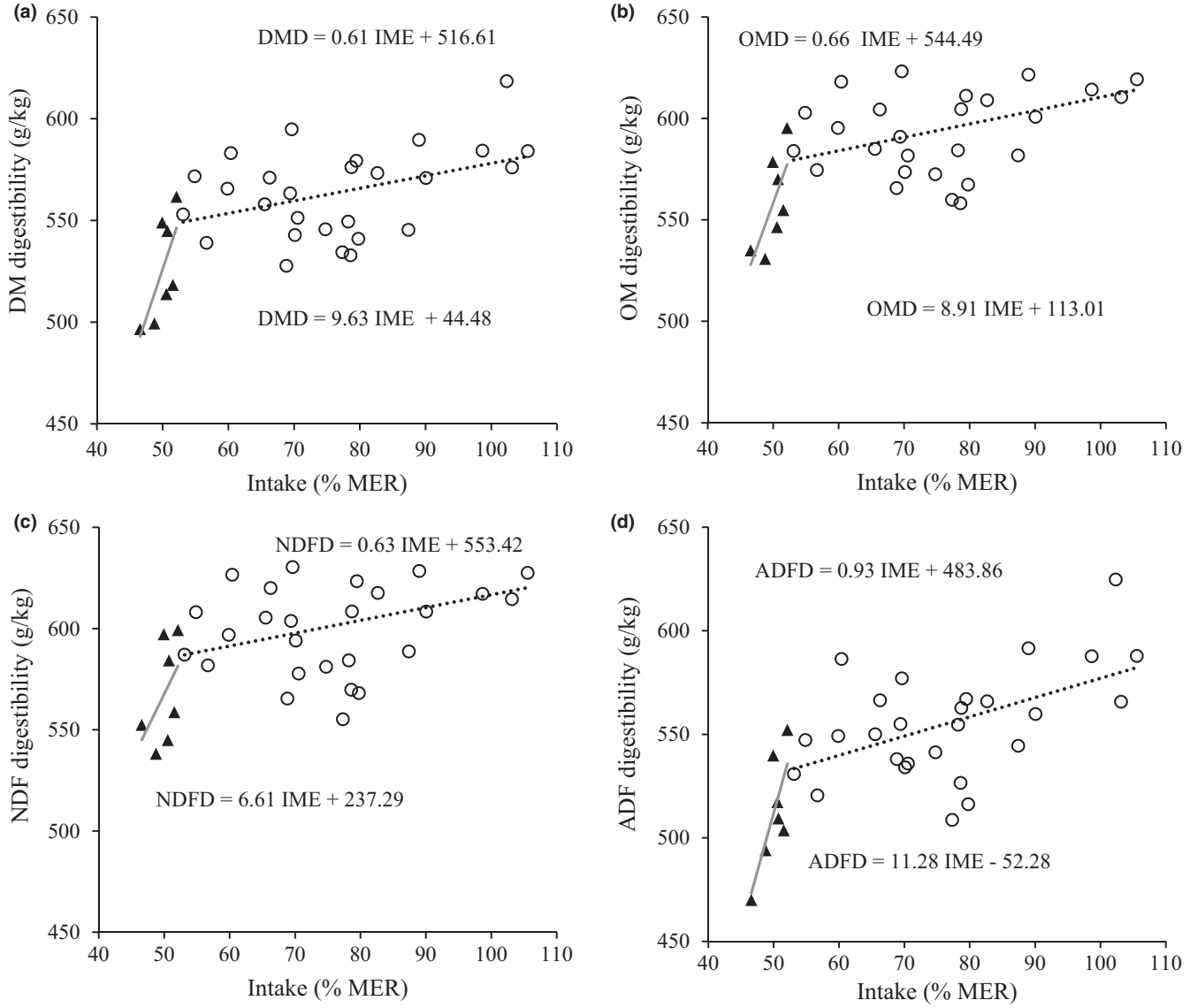

FIGURE 2 Segmented regression of metabolizable energy intake (IME, in % of maintenance energy requirements, MER) against digestibility of a) dry matter (DMD), b) organic matter (OMD), c) neutral detergent fibre (NDFD), and d) acid detergent fibre (ADFD) using data of hay-fed animals only (diets MER80, MER60 and MER40; $n = 34$). Response values show a slight (o) and steep (▲) decline with declining MER intake. The breakoff point (intersection of the two regressions) is at 52% MER for DMD ($p = .04$, $R^2 = .49$), OMD ($p = .06$, $R^2 = .47$), and ADFD ($p = .04$, $R^2 = .54$) and at 53% MER for NDFD ($p = .21$, $R^2 = .37$)

rumen and total tract as well as the digestibility of fibre fractions. At feed intake levels below maintenance energy requirements, solid and liquid digesta passage parameters were only slightly affected by feed intake, and fibre digestibility was slightly 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 decreases below this threshold.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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