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Feed efficiency and enteric methane production of Nellore cattle in the feedlot and on pasture

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Abstract. The objective of the present study was to assess the relationship between residual feed intake (RFI) evaluated in a feedlot-performance test and on pasture, and to determine the effect of feedlot RFI classification on enteric methane (CH_4) production in the feedlot and on pasture. Seventy-three animals (25 with a low RFI, 24 with a medium RFI and 24 with a high RFI) classified in a feedlot performance test were subjected to performance testing on *Brachiaria brizantha* cv. Marandu pasture. Enteric CH_4 was measured in a sample of these animals ($n = 47$, with high and low RFI) by the sulfur hexafluoride tracer-gas technique after the feedlot-performance test and during the performance test on pasture. In the feedlot-performance test, dry-matter intake (DMI) of low-RFI animals was 9.4% and 19.7% lower ($P < 0.05$) than that of medium- and high-RFI animals respectively. However, there was no difference in DMI and, consequently, in RFI on pasture among animals classified as low, medium and high RFI. Accordingly, there is evidence of re-ranking of animals for RFI performance tested in the feedlot after weaning and, subsequently, on pasture. During the period of enteric CH_4 measurement in the feedlot and on pasture, the DMI, neutral detergent-fibre intake and gross-energy intake of low-RFI animals were lower than those of high-RFI animals, and low-RFI animals exhibited greater DM and neutral detergent fibre digestibility only in the feedlot. Enteric CH_4 production did not differ between low- and high-RFI animals either in the feedlot (101 and 107 g CH_4/day) or on pasture (101 and 95.9 g CH_4/day). A significant difference in CH_4 yield (CH_4/kg DMI) was observed on pasture between animals with low and high RFI (17.6 and 13.7 g CH_4/kg DMI respectively). The results did not support the hypothesis that an increase in feed efficiency, evaluated in growing animals in feedlot-performance tests, decreases enteric CH_4 production (g/day) proportionally to the lower DMI.

Additional keywords: dry matter intake, performance test, residual feed intake.

Introduction

The rising global demand for food stimulates livestock production, but also increases the emission of greenhouse gases. For livestock production systems, nitrous oxide, methane (CH_4) and carbon dioxide emissions, which are the three main greenhouse gases emitted by the sector, are losses of nitrogen (N), energy and organic matter that undermine efficiency and productivity (Gerber *et al.* 2013). Enteric CH_4 emitted by ruminant animals, as part of their digestive process, is an important greenhouse gas (IPCC 2006). Mitigation of CH_4 emission from cattle herds needs to consider feeding systems, which should be adopted without compromising farming costs and animal productivity. Increased animal productivity is a very effective strategy for reducing CH_4 emissions per unit of livestock product.

Residual feed intake (RFI) has been used as a selection criterion for beef cattle to increase individual feed efficiency (Grion *et al.* 2014). Efficient or low-RFI animals have a significant economic advantage since they consume less feed than expected for their weight and rate of gain than do their more inefficient or high-RFI counterparts (Carberry *et al.* 2012). The selection of low-RFI animals has the potential to significantly reduce feed costs for meat production and the lower consumption can result in less production of enteric CH_4 (Hegarty *et al.* 2007; Fitzsimons *et al.* 2013). However, Jones *et al.* (2011) reported that low-RFI animals contribute to reducing CH_4 production in grazing systems only when the pasture has a high nutritional value. Freetly and Brown-Brandl (2013) suggested that selection of cattle for increased feed efficiency

will not necessarily reduce enteric CH_4 emission and that CH_4 emission may even increase with increasing feed efficiency.

Feed efficiency is usually assessed post-weaning; however, its evaluation in other phases of the production cycle and with different diets is not well established. Studies have shown that crossbred steers fed a grower and finisher diet changed their RFI rankings from one feeding period to another (Durunna *et al.* 2011), and there is evidence of RFI re-ranking in replacement heifers, using data collected from two feeding trials conducted on a single diet (Durunna *et al.* 2012).

The objective of the present study was to assess the relationship between RFI evaluated in a feedlot-performance test and that evaluated on pasture, and to determine the effect of feedlot RFI classification on enteric CH_4 production in the feedlot and on pasture in growing Nellore beef cattle.

Materials and methods

The study was approved by the Animal Ethics Committee of Instituto de Zootecnia, Nova Odessa, SP, Brazil, and was conducted in accordance with Guidelines for Animal Welfare and Humane Slaughter (São Paulo State, Law Number 11.977). The study was conducted at Centro APTA Bovinos de Corte, Instituto de Zootecnia, Sertãozinho, São Paulo, Brazil. The climate of the region is tropical humid, with an average annual temperature and rainfall of 24°C and 1312 mm respectively. The experiment included 73 Nellore cattle born in 2011, which were subjected to performance testing in the feedlot (June to November 2012) and on pasture (January to April 2013). Enteric CH_4 production was measured in a sample of these animals ($n = 47$).

RFI in the feedlot

Seventy-three animals (12 males and 13 females with low RFI; 12 males and 12 females with medium RFI; and 12 males and 12 females with high RFI) were sampled from 108 uncastrated males (starting at 272 ± 22 days of age and 242 ± 39 kg of bodyweight (BW)) and 51 females (starting at 324 ± 25 days of age and 259 ± 29 kg of BW) subjected to a feedlot-performance test and classified within sex as low RFI (RFI < –0.5 standard deviation (s.d.) below the mean), medium RFI (RFI ± 0.5 s.d. below and above the mean) and high RFI (RFI > 0.5 s.d. above the mean). The s.d. of RFI was 0.741 kg and 0.437 kg for males and females respectively. Males remained in the test for 91 days and females for 86 days. The animals were distributed randomly to the facilities. Eighty-five males were housed in collective pens (only males) equipped with 10 feeders of the GrowSafe® automatic feeding system (GrowSafe Systems, Airdrie, Alberta, Canada), and 23 males and all females were housed in individual pens (two facilities), with *ad libitum* access to water and ration.

The diet in the performance tests consisted of corn silage, *Brachiaria brizantha* cv. Marandu, hay and concentrate containing ground corn, soybean meal, urea, mineral salt and ammonium sulfate (Table 1) and was offered twice a day (0800 hours and 1500 hours). Diet samples were collected at intervals of 28 days for the determination of dry matter (DM). In the individual pens, daily intake was calculated as the difference between the amount of feed offered and leftovers. In the collective

Table 1. Percentage of ingredients and chemical composition of the diets used in the feedlot-and pasture-performance tests

DM, dry matter; OM, organic matter; CP, crude protein; NDIN, neutral detergent insoluble nitrogen; ADIN, acid detergent insoluble nitrogen; NDF, neutral detergent fibre; apNDF, NDF corrected for ash and protein; ADF, acid detergent fibre; ADL, acid detergent lignin; iNDF, indigestible NDF; TDN, total digestible nutrients; GE, gross energy; ME, metabolisable energy

Ingredient (% DM)	Feedlot Whole diet	Pasture Forage	Supplement
Corn silage	53.6	–	–
Ground corn	21.7	–	59.5
Soybean meal	11.6	–	–
Grass hay	10.1	–	–
Cottonseed cake	–	–	25.2
Mineral salt[A]	2.28	–	5.11
Ammonium sulfate	0.072	–	–
Urea	0.648	–	10.2
Forage mass (t/ha)	–	8.17	–
Chemical composition of the diet			
DM (%)	54.4	23.5	95.4
OM (%DM)	95.3	89.9	98.3
CP (%DM)	13.9	11.2	38.9
NDIN (%DM)	0.53	0.58	1.03
ADIN (%DM)	0.54	0.20	0.94
Ether extract (%DM)	1.90	2.29	4.52
NDF (%DM)	50.2	64.8	36.1
apNDF (%DM)	45.1	57.8	31.4
ADF (%DM)	22.9	33.2	12.3
Cellulose (%DM)	19.1	30.4	7.40
Hemicellulose (%DM)	27.2	31.0	23.8
ADL (%DM)	3.80	2.21	4.93
iNDF (%DM)	13.8	16.9	6.96
TDN (%)[B]	70.2	68.3	68.6
GE (Mcal/kg)	4.16	4.40	3.64
ME (Mcal/kg)[C]	2.54	2.44	2.43

[A]Composition/kg: phosphorus, 8%; calcium, 15%; sodium, 14.5%; sulfur, 1.2%; nickel, 1.1%; zinc, 0.25%; copper, 0.16%; manganese, 0.16%; cobalt, 0.0011%; iodine, 0.0023%; selenium, 0.0027%, fluoride, 0.08%.
[B]TDN estimated according to Detmann *et al.* (2010).
[C]ME estimated by digestible energy× 0.82.

pens, feed intake was recorded automatically by the GrowSafe® (GrowSafe Systems, Airdrie, AB, Canada). Feed intake was multiplied by DM content and the DM intake (DMI) of each animal was calculated on the basis of the average of all test days.

The animals were weighed weekly in the morning without fasting (males) or at the beginning and end of the test after a 16-h fast (females). The average daily gain (ADG) of each animal was calculated as the linear regression coefficient of weights on the test days (males) or as the difference between final and initial weights on the test days (females).

Residual feed intake was calculated as the difference between the observed DMI and DMI estimated (eDMI) by the regression of DMI on ADG and mid-test metabolic bodyweight ($BW^{0.75}$) for each group tested (sex and facility, $n = 4$), as follows:

$$\text{DMI} = \beta_{\text{ADG}} \times \text{ADG} + \beta_{\text{BW}^{0.75}} \times \text{BW}^{0.75} + \varepsilon(\text{i.e. RFI}),$$

where β_{ADG} and $\beta_{BW}^{0.75}$ are regression coefficients of the ADG and $BW^{0.75}$ respectively, and ε is the residual of the equation (i.e. RFI). The intercept was non-significant for DMI in each group tested and no intercept term was fitted; therefore, R^2 was not corrected for the mean.

The equations were as follows: eDMI = α + 1.170 (± 0.504) $\times$ ADG + 0.070 (± 0.009) $\times$ $BW^{0.75}$ ($R^2 = 0.997$) and eDMI = α + 1.963 (± 0.609) $\times$ ADG + 0.063 (± 0.010) $\times$ $BW^{0.75}$ ($R^2 = 0.986$) for males tested in individual and collective pens respectively, and eDMI = α + 1.843 (± 0.805) $\times$ ADG + 0.076 (± 0.012) $\times$ $BW^{0.75}$ ($R^2 = 0.996$) and eDMI = α + 1.463 (± 0.529) $\times$ ADG + 0.081 (± 0.007) $\times$ $BW^{0.75}$ ($R^2 = 0.997$) for females tested in two facilities with individual pens respectively. In the equations, α is the mean DMI of each group tested.

RFI on pasture

The 73 animals classified regarding RFI in the feedlot-performance test remained for 78 days (males) and 85 days (females) on pasture after an adaptation period of 28 days. Male animals ($n = 36$) were allocated to nine paddocks of 2 ha (3 paddocks/RFI class; 4 animals/paddock). Female animals ($n = 37$) were allocated to nine paddocks of 1 ha (3 paddocks/RFI class; 4 animals/paddock, except for one paddock with 5 animals). The pasture consisted of *Brachiaria brizantha* (Hochst. ex A.Rich.) Stapf cv. Marandu, and the paddocks were equipped with collective feeders for the supply of supplement, drinkers and a covered area of 36 m^2.

The grazing method was continuous put-and-take stocking (Allen *et al.* 2011), and the grazing heights were 30 cm. Nellore animals of the same age, BW and sex were used. Forage quality was evaluated every 28 days by using a hand-plucked technique designed to simulate removal of representative forage (Sollenberger and Cherney 1995). Forage mass was measured every 28 days using two samples collected at ground level by using metal squares (1 m^2) from the sites at medium height per paddock. A multiple supplement was offered daily to the animals (0.5 kg/animal.day), which consisted of ground corn, cottonseed cake, soybean meal, urea and mineral salt (Table 1). The supplement was formulated to meet the nutritional requirements of male and female Nellore animals for an ADG of 0.8 kg/day.

Faecal output was estimated using Cr_2O_3 as the external marker and TiO_2 (Titgemeyer *et al.* 2001) to estimate individual-supplement intake, both at 10 g/animal.day, for 9 days. Days 1–7 were used for adaptation and faecal samples were collected from Day 8 to Day 10 at previously defined time points (1500 hours, 1100 hours and 0700 hours). Cr_2O_3 was stored in paper cartridges and introduced directly into the oesophagus of the animals at 1200 hours with the aid of a polyvinyl chloride applicator, while TiO_2 was homogenised into the supplement. Samples of faeces corresponding to the different collection times composed a sample for each animal. DMI was obtained with the equation proposed by Detmann *et al*. (2001) using indigestible neutral detergent fibre (iNDF) as the internal marker. The apparent DM digestibility coefficients of pasture-fed animals were calculated as described by Berchielli *et al*. (2011).

The animals were weighed at intervals of 15 days without previous fasting. The ADG of each animal was calculated as the linear regression coefficient of weights on the test days, and RFI was again calculated as the difference between the observed mean DMI and eDMI with the regression equation of DMI on ADG and $BW^{0.75}$ within sex. The intercept was non-significant for DMI. The equations were as follows: eDMI = α + 0.154 (± 0.910) $\times$ ADG + 0.077 (± 0.005) $\times$ $BW^{0.75}$ for males, and eDMI = α + 0.962 (± 1.684) $\times$ ADG + 0.051 (± 0.008) $\times$ $BW^{0.75}$ for females, where α is the mean DMI of each sex. No intercept term was used and R^2 (0.52) was, therefore, not corrected for the mean.

Enteric CH_4 production

After the feedlot-performance test, enteric CH_4 production was measured in low-RFI ($n = 25$) and high-RFI ($n = 22$) animals after a 14-day period of adaptation to the collection devices. Faecal samples were collected once a day for three consecutive days and faecal DM excretion of the animals was estimated using iNDF as the internal marker (Cochran *et al.* 1986). The apparent DM digestibility of the animals in the feedlot performance test was calculated as described by Cochran and Galyean (1994).

Enteric CH_4 production on pasture was determined after adaptation of the animals for 28 days. CH_4 production was measured by the SF_6 tracer-gas technique as described by Johnson and Johnson (1995). Expired and eructated gas samples were stored in collection canisters and replaced at intervals of 24 h over six consecutive days (continuous sampling for 144 h), for a total of six canisters per animal. To correct for atmospheric CH_4 concentrations, ambient air samples were collected with two collection canisters per day (basal). At the end of the sampling period, SF_6 and CH_4 concentrations were determined with an HP6890 gas chromatograph (Agilent, San Jose, CA, USA). The emission of CH_4 by the animal was calculated in relation to the known rate of SF_6 release in the rumen, subtracting basal CH_4 concentrations (Westberg *et al.* 1998) as follows:

$$Q_{CH_4} = Q_{SF_6}([CH_4]_y - [CH_4]_b)/[SF_6],$$

where Q_{CH_4} = emission rate of CH_4 by the animal; Q_{SF_6} = known emission rate of SF_6; $[CH_4]_y$ = CH_4 concentration in the canister; $[CH_4]_b$ = basal CH_4 concentration, and $[SF_6]$ = SF_6 concentration in the canister.

Chemical analyses

The forage samples, silage samples, concentrate ingredients, leftovers and faecal samples were weighed and dried in a forced-ventilation oven at 60 $\pm$ 5°C for 72 h, ground in a Willey mill (Thomas Scientific, Swedesboro, NJ, USA) to pass through a 1-mm screen, and analysed for the determination of DM (Method 934.01), mineral matter (Method 942.05) and ether extract (Method 920.39) according to the AOAC (1990). Crude energy was determined with an automated IKA® calorimeter Model 2000 (IKA WORKS Inc., Staufen, Breisgau, Germany). N was determined by the Dumas method (Etheridge *et al.* 1998), which is based on the release of N by combustion at high temperature in pure oxygen in a LECO FP-528 nitrogen analyser (LECO Corporation, St Joseph, MI, USA). NDF and

Table 2.   Performance and efficiency traits of Nellore cattle classified for residual feed intake (RFI) in the feedlot- and pasture-performance tests
Means in the same row followed by different lowercase letters differ significantly ($P < 0.05$). $BW^{0.75}$, metabolic bodyweight; DMI, dry-matter intake; ADG, average daily gain; RFI, residual-feed intake

Trait	Feedlot RFI			s.e.m.	*P*-value	Pasture RFI			s.e.m.	*P*-value
	Low ($n = 25$)	Medium ($n = 24$)	High ($n = 24$)			Low ($n = 25$)	Medium ($n = 24$)	High ($n = 24$)		
Age (day)	295	302	295	4.84	0.508	470	477	470	4.84	0.510
Initial BW (kg)	246	258	244	6.68	0.329	377	374	369	6.72	0.734
Final BW (kg)	343	351	341	7.52	0.619	402	399	391	6.36	0.450
$BW^{0.75}$ (kg)	71.2	73.2	70.8	1.31	0.402	88.5	88.0	86.8	1.09	0.558
DMI (kg/day)	6.31c	7.12b	7.86a	0.148	<0.001	6.07	5.88	5.85	0.262	0.808
ADG (kg/day)	1.11	1.11	1.12	0.032	0.990	0.463	0.467	0.411	0.037	0.492
RFI (kg DM/day)	–0.683c	–0.022b	0.787a	0.058	<0.001	0.076	–0.078	–0.003	0.251	0.910

ADF analyses were based on procedures described by Mertens (2002), both adapted to the Ankom200 Fibre Analyzer (Ankom Technology, Fairport, NY, USA) and revised to ash and protein, according to Licitra *et al*. (1996).

The digestion assays for the recovery of TiO_2 from faecal samples were performed as described by Myers *et al*. (2004), and for the recovery of Cr_2O_3 by the wet method as described by Kimura and Miller (1957). The content of iNDF in the feed, leftover and faecal samples was determined after *in situ* incubation for 288 h (Casali *et al*. 2008).

Statistical analyses

Least-square means were calculated to compare the variables between RFI classes (low, medium and high, and only low and high for the period of measurement of enteric CH_4 production) using the general linear model procedure (SAS Institute Inc., Cary, NC, USA). The statistical model included the effects of RFI class, sex (male or female), and the interaction between RFI class and sex. Means were compared by the Tukey test and significance was considered when $P < 0.05$. Pearson correlations were estimated for BW, $BW^{0.75}$, DMI, ADG and RFI obtained in the feedlot-and pasture-performance tests, and for BW, DMI, NDFI, GEI, DM digestibility (DMD), NDF digestibility (NDFD), gross-energy digestibility (GED) and CH_4 (g/day) determined during the period of CH_4 measurement in the feedlot and on pasture. Pearson correlations were also estimated between RFI and CH_4, DMD and CH_4, and RFI and DMD within each testing environment.

Results

Residual feed intake

In the feedlot- and pasture-performance tests, no significant differences in the initial BW, final BW, $BW^{0.75}$ or ADG were observed among animals classified as low, medium and high RFI in the feedlot test (Table 2). In the feedlot-performance test, DMI of low-RFI animals was 9.4% and 19.7% lower ($P < 0.05$) than that of medium- and high-RFI animals respectively. The mean RFI was –0.683, –0.022 and 0.787 kg DM/day for the low-, medium- and high-RFI class, with a mean difference in RFI of 1.47 kg DM/day between greater- and lower-efficient animals. On pasture, there was no difference in DMI and, consequently, in RFI among animals classified as low-, medium- and high-feedlot

RFI. The effect of sex was significant for age, initial and final BW, $BW^{0.75}$, and DMI in feedlot and pasture, and the interaction RFI class × sex was significant only for DMI and RFI obtained in the feedlot test.

Pearson correlations between DMI, ADG and RFI obtained in the feedlot and on pasture were low, except for BW and $BW^{0.75}$, which showed a significant ($P < 0.001$) correlation of medium to high magnitude (Table 3).

CH_4 production

During the period of enteric CH_4 measurement in the feedlot or pasture, no significant difference was observed in BW or $BW^{0.75}$ between animals classified as low and those classified as high RFI (feedlot-performance test; Table 4). Faecal excretion of low-RFI animals was 9.5% and 12.7% lower than that of high-RFI animals during the period of enteric CH_4 measurement in the feedlot and on pasture respectively. Low-RFI animals had lower DMI, NDFI and GEI than high-RFI animals during both periods of enteric CH_4 measurement ($P < 0.05$). Low-RFI animals exhibited higher DMD and NDFD than did high-RFI animals during the period of enteric CH_4 measurement in the feedlot, but a similar GED ($P > 0.05$). In contrast, no significant difference in DMD, NDFD or GED was observed between low- and high-RFI animals during the period of measurement on pasture.

The production of enteric CH_4, in both periods of measurement, expressed as g/day and kg/year did not differ between low- and high-RFI animals ($P > 0.05$), while methane production expressed as g/BW and $g/BW^{0.75}$ differed between low- and high-RFI animals during the feedlot period ($P < 0.05$). The production of CH_4 expressed as g/kg DMI, g/kg NDFI and % GEI did not differ between low- and high-RFI animal during the feedlot period ($P > 0.05$), but significant differences were observed between these animals during the period of enteric CH_4 measurement on pasture. The effect of sex was significant for BW, CH_4 and for the variables related to DMI, and the interaction between RFI class × sex was significant only for DMI-related variables.

Low correlations were estimated between the traits (DMI, NDFI, GEI, DMD, NDFD and GED) obtained during the period of CH_4 measurement in the feedlot and on pasture ($n = 47$). However, a moderate correlation (0.411) was observed in enteric CH_4 production (g/day) between the feedlot and on pasture and a

high correlation (0.883) was observed in BW (Table 3). The correlations between RFI vs CH_4 (0.068 and –0.117; $P = 0.652$ and $P = 0.433$) and DMD vs CH_4 (–0.176 and 0.010; $P = 0.237$ and $P = 0.947$) were not significant both in the feedlot and on pasture respectively. A moderate correlation was observed between RFI vs DMD (–0.410 and 0.381, $P = 0.004$ and $P = 0.008$, in the feedlot and on pasture respectively; Fig. 1) and RFI vs NDFD (–0.366, $P = 0.011$, in the feedlot).

Discussion

The ranking and selection of animals that will remain efficient during different growth phases and in different production systems, while keeping enteric CH_4 emissions low, are important challenges for beef-cattle producers worldwide. Although a considerable proportion of the global beef cattle herd is raised on pasture, available studies are restricted to the assessment of RFI in feedlot animals, without subsequent reranking on pasture. Here, we address this limitation of current knowledge, taking into consideration the effects on enteric CH_4 emissions.

Average daily gain did not differ among the RFI classes (Table 2), since RFI is an efficiency measure that is independent of growth rate or animal performance (Koch *et al.* 1963). As also reported in recent studies (Sobrinho *et al.* 2011; Fitzsimons *et al.* 2013), lower DMI (kg/day) was attributed to low-RFI animals in the feedlot (Table 2). On pasture, DMI was similar in low-, medium- and high-feedlot RFI animals. Studies also reported similar DMI on pasture for low- and high-RFI animals previously evaluated in a post-weaning feedlot-performance test (Herd *et al.* 1998) or on pasture (Jones *et al.* 2011). These results can be probably due to intrinsic errors of the methods used to estimate the DMI of animals on pasture, impairing a very accurate individual estimate of DMI for the calculation of RFI, although the average DMI estimated

on pasture is consistent with that of grazing animals (Canesin *et al.* 2014). However, using the same method (n-alkanes) as used by Herd *et al.* (1998) for the estimation of DMI on pasture, Manafiazar *et al.* (2015) observed that beef heifers classified as low RFI during the pos-tweaning feedlot period had a lower DMI as heifers grazing pasture than did their high-RFI herd mates.

The correlations showed changes in RFI calculated in the feedlot and then on pasture, when the animals were already in another growth phase, as shown in Table 3. The low or null correlations between the two performance tests indicated that most animals were reranked and that the feed efficiency identified in animals may not correspond to the efficiency of these animals when subsequently tested on pasture.

Some studies have evaluated the feed efficiency of animals during different periods and using different diets and, indeed, observed low to medium rank correlations between animals (Durunna *et al.* 2011, 2012; Magnani *et al.* 2013b), implying that the period of evaluation and diet affect the RFI of animals.

Low to medium correlations between ADG obtained in different tests are expected (Mercadante *et al.* 2015), since this trait is the most variable among the three RFI components (Wang *et al.* 2006). However, the low correlations close to zero between DMI and RFI obtained in the feedlot- and pasture-performance tests were not expected (Durunna *et al.* 2011, 2012; Magnani *et al.* 2013b; Mercadante *et al.* 2015). Despite advances in the experimental and analytical procedures over time, the estimation of feed intake in pasture-raised animals continues to be costly and of low accuracy.

During the period of enteric CH_4 measurement (Table 4), lower NDFI and GEI (kcal/day) were observed in low-RFI animals than in high-RFI animals because of the lower DMI, both in the feedlot and on pasture. In feedlot, higher DMD and NDFD were measured in low-RFI animals (Table 4) and a negative relationships between RFI and DMD (Fig. 1) and NDFD of the diet during the period of enteric CH_4 measurement were observed. These differences among RFI classes are consistent with the results of Nkrumah *et al.* (2006) and Magnani *et al.*

Table 3. Pearson's correlation coefficient between traits obtained in the feedlot and those obtained on pasture

$BW^{0.75}$, metabolic bodyweight; DMI, dry-matter intake; ADG, average daily gain; RFI, residual-feed intake; NDFI, neutral detergent-fibre intake; GEI, gross-energy intake; DMD, dry-matter digestibility; NDFD, neutral detergent-fibre digestibility; GED, gross-energy digestibility; CH_4 (g/day)

Trait	Correlation coefficient	*P*-value
Performance-test period (n = 73)		
BW	0.731	<0.001
$BW^{0.75}$	0.607	<0.001
DMI	–0.097	0.414
ADG	0.113	0.340
RFI	–0.033	0.783
Measurement of enteric CH_4 period (n = 47)		
BW	0.880	<0.001
DMI	0.108	0.472
NDFI	0.077	0.608
GEI	0.136	0.362
DMD	0.171	0.249
NDFD	0.187	0.208
GED	0.160	0.282
CH_4	0.411	0.004
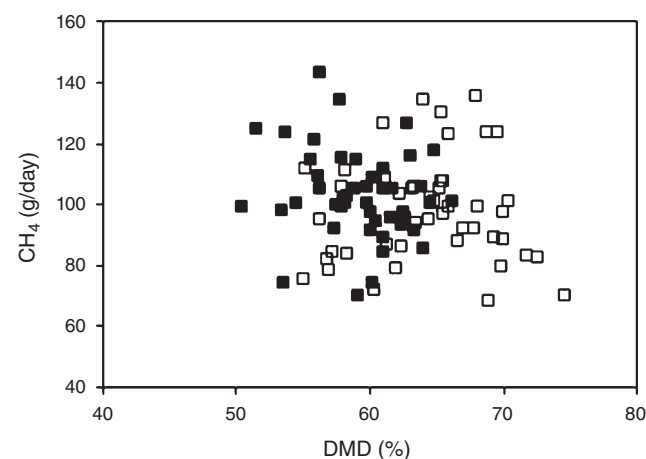
Fig. 1. Enteric methane (CH_4) production and dry matter digestibility (DMD) obtained in the feedlot (solid symbols) and on pasture (open symbols).

Table 4. Enteric methane production during the feedlot and pasture periods of Nellore cattle classified as low and high residual feed intake (RFI) in the feedlot

$BW^{0.75}$, metabolic bodyweight; FE, faecal excretion; DMI, dry-matter intake; NDFI, neutral detergent-fibre intake; GEI, gross-energy intake; DMD, dry-matter digestibility; NDFD, neutral detergent-fibre digestibility; GED, gross-energy digestibility

	Feedlot RFI		s.e.m.	*P*-value	Pasture RFI		s.e.m.	*P*-value
	Low (*n* = 25)	High (*n* = 22)			Low (*n* = 25)	High (*n* = 22)		
Trait[A]								
BW (kg)	357	355	7.71	0.852	377	368	7.25	0.356
$BW^{0.75}$ (kg)	82.0	81.6	1.33	0.832	85.5	83.9	1.24	0.365
FE (kg/day)	3.92	4.33	0.085	0.001	2.20	2.52	0.104	0.036
DMI (kg/day)	8.57	9.43	0.202	0.004	5.98	7.42	0.362	0.007
NDFI (kg/day)	4.34	4.79	0.105	0.005	3.63	4.43	0.214	0.012
GEI (kcal/day)	35.8	39.3	0.840	0.005	22.2	27.2	1.31	0.009
DMD (%)	60.9	57.0	0.564	<0.001	63.1	65.5	1.04	0.116
NDFD (%)	57.5	54.6	0.592	0.001	62.7	63.4	1.11	0.651
GED (%)	59.6	57.0	1.25	0.150	62.5	64.9	1.21	0.182
Enteric CH_4 production								
CH_4 (g/day)	101	107	2.75	0.152	101	95.9	3.26	0.279
CH_4 (kg/year)	37.0	39.1	1.01	0.152	36.9	35.0	1.19	0.279
CH_4 (kg/BW)	0.28	0.30	0.007	0.053	0.27	0.26	0.008	0.627
CH_4 (g/kg $BW^{0.75}$)	1.23	1.32	0.029	0.054	1.18	1.15	0.36	0.510
CH_4 (g/kg DMI)	11.9	11.4	0.254	0.166	17.6	13.7	0.786	0.001
CH_4 (g/kg NDFI)	23.4	22.5	0.492	0.187	29.1	22.9	1.28	0.001
CH_4 (% GEI)	2.85	2.71	0.062	0.120	4.85	3.71	0.206	<0.001

[A]Traits determined during the period of measurement of enteric CH_4 in the feedlot and on pasture.

(2013*a*), who observed greater DMD and NDFD in low-RFI animals. On feedlot, the results of the present study supported the hypothesis that the greater efficiency in low-RFI cattle could be partially explained by an enhanced capacity to digest ingested feed (Richardson and Herd 2004). In contrast, no difference in nutrient digestibility among the RFI classes was observed when the animals were measured on pasture. The variation in diet digestibility between animals is due to factors such as the mechanism of digestion and absorption, rumen retention time and ingestive behaviour (Russell and Gahr 2000). On pasture, the animals have 40.1% more feeding time and ~14.2% more time on rumination activity than on feedlot, and the greatest chewing stimulation promotes increased saliva production, which improves the conditions of ruminal pH and development of microbes responsible for greater digestion of fibre (Segabinazzi *et al.* 2014). This fact corroborates with the results of Cota *et al.* (2014), who observed a lower nutrient intake and greater digestibility in Nellore cattle on pasture than on feedlot.

In the present study, enteric CH_4 production (g/day and kg/year) measured in both periods was similar in low- and high-RFI animals. Since animals that are more efficient have a lower DMI adjusted for ADG and $BW^{0.75}$, the hypothesis can be raised that these animals produce smaller amounts of enteric CH_4 than do their less efficient counterparts. Indeed, some studies have shown that more efficient animals produce less enteric CH_4 than less efficient animals, especially when these animals are fed a high-concentrate diet (Hegarty *et al.* 2007). However, the results reported by Freetly and Brown-Brandl (2013) and Mercadante *et al.* (2015) did not support the hypothesis that an increase in feed efficiency decreases CH_4 production. The authors, respectively,

found a positive correlation between ADG : DMI and CH_4 and similar CH_4 production in low- and high-RFI animals receiving a diet that contained more than 50% roughage. Freetly and Brown-Brandl (2013) suggested the increase in CH_4 production rates with increasing feed efficiency (ADG : DMI) to be the result of higher feed fermentation, increasing the availability of nutrients and enteric CH_4 production. Similarly, Jones *et al.* (2011) found no difference in enteric CH_4 production (g/kg BW; g/kg $BW^{0.75}$) of cows with different RFI maintained on pasture. According to de Haas *et al.* (2011), the limited evidence available indicates that an increase in feed efficiency is partially or completely related to a higher level of fermentation and digestion of the ingested feed and, consequently, to higher enteric CH_4 production per unit feed and greater %GEI lost as CH_4. These results support the higher digestibility of DM and NDF (in the feedlot), similar CH_4 production expressed as g/day (in the feedlot and on pasture), and higher CH_4 production expressed as g/kg DMI, g/kg NDFI and %GEI (on pasture) of low-RFI animals when compared with high-RFI animals. During the period of enteric CH_4 measurement on pasture, the reduced rumen retention time in high-RFI animals, associated with a higher feed intake, probably tends to lower CH_4 yield per unit DMI.

The production of CH_4 expressed as g/day observed in the present study was lower than the 147 g CH_4/day estimated by Fiorentini *et al.* (2014) for Nellore cattle fed a high-roughage diet (60% corn silage), and the value reported by the IPCC (2006) which estimated a mean emission of 49 kg CH_4/year for young cattle (230 kg BW) in Latin America. The percentage of gross energy lost as enteric CH_4 (%GEI) was lower than the values reported by Fiorentini *et al.* (2014; 4.81%) and those observed for continental crossbred steers fed corn silage-based diets

(7.3–8.4%; McGeough *et al.* 2010). Importantly, the values in the present study were lower than those estimated by the models developed by IPCC (2006) of 6.5% for cattle raised under tropical conditions.

Conclusions

In conclusion, it is not possible to affirm that animals with a lower DMI and the same performance emit less enteric CH_4 than do animals with a higher intake. Under the conditions of the present study, there is evidence of re-ranking of animals for RFI tested in the feedlot after weaning and, subsequently, on pasture.

Acknowledgements

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