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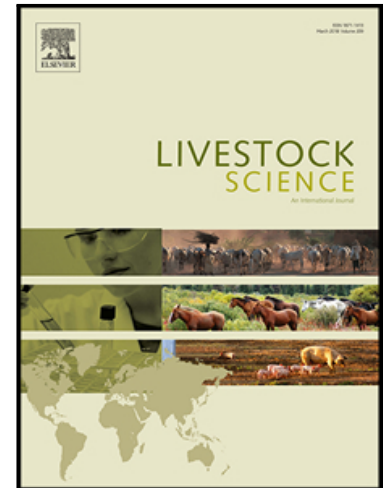
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Journal Pre-proof

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Highlights

- Voluntary forage intake is positively associated with neutral detergent fibre digestibility
- Increasing neutral detergent fibre digestibility increases ruminal microbial nitrogen production
- There is a positive correlation between neutral detergent fibre digestibility and weight gain in cattle

Journal Pre-proof

What is the impact of neutral detergent fibre digestibility on productive performance of beef cattle fed tropical forages?

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Abbreviations: ADG, average daily gain; BW, body weight; CP, crude protein; DM, dry matter; DOM, digested organic matter; EBWeq, equivalent empty body weight; EBWG, empty body weight gain; iNDF, indigestible neutral detergent fibre; NB, nitrogen balance; NDF, neutral detergent fibre; NDFD, total neutral detergent fibre digestibility; NFC, non-fibrous carbohydrates; NDI, nitrogen digested in the intestines; NMIC, rumen microbial nitrogen production; NPg, net protein of gain; OM, organic matter; pdNDF, potentially digestible neutral detergent fibre; Δ NB, net N accretion rate in animal's body.

ABSTRACT

Our objective was to quantify the relationship between total neutral detergent fibre (NDF) digestibility and nutritional and productive characteristics in cattle fed tropical forages using a meta-analytical approach. The dataset used to develop this work was compiled from 24 experiments carried out with beef cattle in Brazil, published between 2005 and 2020, and totalising 115 treatment means. All the experiments were carried out using change-over designs and included a control treatment (i.e., only forage). There was a linear and positive relationship ($P < 0.01$) between total NDF digestibility and voluntary forage intake. We estimated a 0.17 g/kg body weight increase in forage intake for each percentage point (i.e., 0.01 g/g) of improvement in NDF digestibility. On average, increasing total NDF digestibility caused a linear improvement ($P < 0.01$) in rumen microbial nitrogen production (NMIC) and in dietary digested organic matter (DOM). The total NDF digestibility was linear and positively associated with nitrogen balance (NB, $P < 0.01$). However, the increment in NB as a response to total NDF digestibility was more prominent as dietary NDF decreased ($P < 0.01$). In summary, we concluded that increasing NDF digestibility in cattle fed tropical forage-based diets improves the voluntary forage intake and the supply of energy and metabolisable protein. This simultaneous effect causes an increase in the animal's nitrogen accretion and weight gain, but this effect will be more prominent as the dietary content of neutral detergent fibre decreases.

Keywords: forage intake, nitrogen balance, microbial nitrogen, weight gain.

1. Introduction

The insoluble fibre in ruminant diets is mainly composed by the carbohydrates and phenolic compounds contained in primary and secondary plant cell wall. Its carbohydrate portion is polymerised basically through β -glycosidic linkages, which makes it inaccessible to mammalian intestinal enzymes. Therefore, the insoluble fibre utilisation for energy purposes in biological systems occur through microbial fermentative processes, such as that which occurs in the rumen. Considering that plant cell wall is the greatest reservoir of chemical energy in biosphere (Haynie, 2008), the ruminal fermentation of its carbohydrates turns the domestic ruminants into transformation agents of this energy, which insets them as important players in the biogenic carbon cycle and human food security worldwide.

The insoluble fibre is a multi-dimensional nutritional entity in ruminant nutrition (Tedeschi et al., 2023). Nevertheless, to be adequately prospected in ruminant production systems, an adequate chemical approach is necessary in order to allow its adequate quantification. In this sense, the insoluble neutral detergent fibre (NDF) has been proposed as a chemical approach of insoluble fibre (Van Soest, 2015). Indeed, it is feasible to be quantified in laboratories and constitutes the best chemical approach of insoluble fibre for ruminant nutrition and feeding we have nowadays.

Even though the characteristic NDF insolubility in neutral and aqueous mediums allows us to relate it to the dietary capacity of occupying physical space inside rumen, its rumen fill effect also depends on its degradation and transit dynamics (Waldo et al., 1972; Vieira et al., 1997; Detmann et al., 2014a). Those dynamic events can be integrated statically to produce the NDF digestibility coefficient. Despite of being less informative than the complete set of rumen dynamic parameters, the digestibility coefficient makes it possible to more simply link the intake potential and energy availability from fibre in the

gastrointestinal tract of ruminant animals (Detmann et al., 2014a). Therefore, NDF digestibility can be seen as one of the main indicators of available energy from cellulose and hemicellulose for rumen microbial growth and for supplying the maintenance and production requirements of the host animal.

When cattle are fed tropical forages, especially in grazing systems, supplements are offered with the aim of balancing the diet and improving energy extraction from fibrous carbohydrates (Detmann et al., 2009; 2014b). Normally, the supplementation programs for grazing cattle in the tropics prioritize protein or nitrogen (N) compounds, as the tropical forages tends to have low N content, which can compromise the ruminal degradation of fibre and also the efficiency of utilisation of metabolisable protein and energy by the animal (Detmann et al., 2020). Therefore, achieving improvements in NDF digestibility is used as one of the main arguments to support protein supplements utilisation for grazing cattle in the tropics. However, to the best of our knowledge, quantitative estimates of the impact of NDF digestibility improvements or variation in animal performance and nutritional characteristics are not available in tropical regions.

Therefore, our objective was to quantify the relationship between total NDF digestibility and nutritional and productive characteristics in cattle fed tropical forages using a meta-analytical approach.

2. Material and Methods

This study used data from previously published papers and did not require an approval from the Animal Care and Use Committee of the Universidade Federal de Viçosa.

2.1. Data acquisition

The dataset used to develop this work was compiled from 24 experiments carried out with beef cattle in Brazil, published between 2005 and 2020, and totalising 115 treatment means from 570 experimental units (Table 1). All the experiments were carried out using change-over designs (i.e., Latin squares) and included a control treatment (i.e., only forage, without supplementation). Several types of supplements were provided to the animals: protein supplements [crude protein (CP) content higher than 300 g/kg], protein-energy supplements (200-300 g CP/kg), energy supplements (<200 g CP/kg), and nitrogen-salt supplements (a mix of complete mineral mixture and urea). Some experiments were carried out on pasture, whereas part of them were carried out with housed animals being fed hays.

The dataset comprised the following variables: forage NDF and CP contents, dietary NDF and CP contents, forage and NDF intakes, total and ruminal NDF digestibility, potentially digestible NDF digestibility, dietary digested organic matter (DOM) content, rumen microbial N production (NMIC), N compounds digested in the intestines (NDI), and N balance (NB) in the animal's body (Table 2).

The data was analysed using meta-analysis techniques (St-Pierre, 2001; Van Houwelingen et al., 2002) through the MIXED procedures of SAS 9.4 (Littell et al., 2006). The basic model structure was used (St-Pierre, 2001; Sauvant et al., 2008):

$$Y_{ij} = \beta_0 + b_0 + \beta_1 \times X_{1ij} + b_1 \times X_{1ij} + \dots + \beta_n \times X_{nij} + b_n \times X_{nij} + \varepsilon_{ij} \quad (1),$$

where Y_{ij} is the dependent variable measured in the experiment i and in the observation j ; β_0 is the intercept; b_0 is the random effect of the experiment i ; X_{1ij}, \dots, X_{nij} are the values of the continuous predictor variables; β_1, \dots, β_n are the overall regression coefficients; b_1, \dots, b_n are the random effects of experiments on the regression coefficients; and ε_{ij} is the random error.

The number of replicates for each treatment mean was used as weighing criterion during the model adjustment. The adequacy of the models, which includes the best (co)variance matrix structure, was evaluated through the Akaike's information criterion with correction and the dispersion pattern of studentized residues. The variance components were estimated using the restricted maximum likelihood method. The coefficients of determination (R^2) of the fitted models were calculated as the square of correlation between predicted and observed values. All statistical evaluations were performed using 0.05 as the critical level for the occurrence of type I error.

Overall, the linear regression models were not fitted in accordance to the influence of the class variables sex and genetic group of the animals, and forage species. This decision was influenced by the fact that most of the information was obtained using *Urochloa* sp. On the other hand, differences regarding sex and genetic group are not expected to be prominent concerning NDF digestibility. Furthermore, sex, genetic group, and forage species did not present an adequate distribution across experiments and were not considered in the analyses to avoid biases in the estimates.

The estimates of average daily gain (ADG) were based on the relationship between NDF digestibility (g/g) and NB (g/d). The NB variation rate was defined as its partial derivative as a function of NDF digestibility (for more details, see Results and Discussion):

$$\Delta NB = \frac{\partial NB}{\partial NDFD} \quad (2),$$

where ΔNB is the variation rate in body N balance as a function of total NDF digestibility (g/d), NB is the N balance in the animal's body (g/d), and NDFD is the total NDF digestibility (g/g).

Considering that ΔNB represents the net N accretion rate in animal's body, we converted it into net protein for weight gain (i.e., growth) as follows:

$$NPg = \Delta NB \times 6.25 \quad (3),$$

where NPg is the net protein for body weight gain (g/d).

The NPg estimate was used to calculate the expected variation in the ADG according to the equation (Silva et al., 2023):

$$NPg = 176.01 \times EBWG - 0.381 \times EBWeq^{0.75} \times EBWG^{1.035} \quad (4),$$

where EBWG is the empty body weight gain (kd/d), and EBWeq is the equivalent empty body weight (kg).

Due to the presence of the EBWG in the equation (4) with two different exponents, this equation was solved using an iterative procedure through the Microsoft Excel solver tool. All the conversions of EBWeq and EBWG into body weight (BW) and ADG followed the equations described in the BR-CORTE nutritional system (Silva et al., 2023). For the calculations, we considered the projection of results for a Zebu animal under grazing with different sexes and BW ranges.

3. Results and Discussion

3.1. Supporting the utilisation of total NDF digestibility as an indicator of energy availability in the rumen

Even though the total NDF digestibility is positively associated with energy availability from cell-wall carbohydrates, this characteristic presents some intrinsic restrictions. First, the greatest utilisation efficiency of energy from fibre is achieved when it is degraded in the rumen, which propitiates the pre-intestinal absorption of volatile fatty acids and directs part of energy towards microbial growth. The microbial protein produced from fibre energy is the most important source of metabolisable protein for animals fed tropical forage-based diets.

In this sense, the total NDF digestibility is not capable of providing information regarding the partition of fibre degradation between the rumen and the large intestine. Overall, the NDF degradation in the large intestine is an opportunistic event, as the greater the escape of potentially degradable NDF from rumen, the greater the amount of NDF degraded in the large intestine (Dixon and Stockdale, 1999; Oliveira et al., 2020). Therefore, studies that aim to correlate NDF digestion and nutritional strategies would be more informative if they focused on ruminal NDF digestibility. Nonetheless, the number of studies where ruminal digestion is quantified is much lower when compared to studies where total digestibility is measured. A similar pattern also occurred in our dataset (Table 2).

Thus, in order to allow us using the full dataset, we first verified the relationship between ruminal and total NDF digestibility. We found this relationship is strong ($r = 0.98$, $P < 0.01$) and that ruminal digestibility corresponded to approximately 94% of the NDF digested throughout the gastrointestinal tract (Figure 1). This estimate approaches the average NDF digestion partition values obtained in tropical (89%; Silva et al., 2018) and non-tropical (95%; Huhtanen et al., 2010) conditions. Therefore, it can be understood that any variation in ruminal NDF digestibility corresponds to a directly proportional variation in total NDF digestibility. This ensures the adequate utilisation of total NDF digestibility as an indicator of fibre energy availability in the rumen.

An additional constraint associated with the utilisation of total NDF digestibility relies on the fact that NDF presents two distinct pools: potentially digestible or degradable NDF (pdNDF) and indigestible or undegradable NDF (iNDF). In practical terms, iNDF cannot be degraded in the ruminant gastrointestinal tract. Thus, all and every digestion/degradation event can only occur on pdNDF (Mertens and Grant, 2020). Consequently, the totally informative digestibility coefficient regarding fibre utilization

would be the one calculated using the NDF fraction with true degradation potential (Detmann, 2023). Though, as previously discussed for ruminal NDF digestibility, there is a low proportion of studies where pdNDF digestibility is evaluated, a pattern also observed in our dataset. Nevertheless, the correlation between NDF and pdNDF total digestibilities was strong ($r = 0.98$; $P < 0.01$) in our dataset. The estimate of the slope for the fitted model approaches the unity (1.056, Figure 2), which indicated a numerical similarity when the variations in NDF and pdNDF total digestibilities are jointly evaluated. It can be observed in Figure 2 that some total pdNDF digestibilities were greater than 1, which would be a nutritional inconsistency. However, no treatment mean used in the dataset was greater than 1 (Table 2). The appearance of pdNDF digestibilities greater than 1 is an artifact created by the adjustment of average values regarding random effects of experiments. This is a necessary feature and one of the main benefits of a meta-analytical approach. Although some adjusted means may exhibit minor nutritional inconsistencies, the pattern observed in the fitted model is considered accurate and appropriate for discussion and inference.

In this sense, the pattern of the fitted models presented in Figures 1 and 2 provides an adequate support for using total NDF digestibility as the main independent variable for the remaining relationships to be studied herein.

3.2. Relationships between total NDF digestibility and nutritional and productive performance characteristics

There was a linear and positive relationship ($P < 0.01$) between voluntary forage intake and total NDF digestibility (Figure 3). We estimated a 0.17 g/kg BW increase in forage intake for each percentage point (i.e., 0.01 g/g) of improvement in NDF

digestibility. No direct nor interactive effects were observed ($P>0.05$) when dietary NDF content was included in the model.

In fact, we detected no association between forage intake and dietary NDF content ($P>0.59$; Figure 4). This pattern corroborated the findings by Detmann et al. (2014a), who did not find any relationship between dietary NDF and voluntary dry matter intake in 765 diets offered to cattle in the tropics. The influence of NDF on voluntary intake can be considered multi-dimensional (Tedeschi et al., 2023), in which several dynamics characteristics play functional roles besides the dietary NDF content itself. Even though the NDF digestibility is a static measure of digestion, it results from the integration of dynamic characteristics (e.g., degradation and passage rates; Vieira et al., 1997; Detmann et al., 2014a), which makes it more informative than the sole dietary NDF content regarding forage intake regulation.

On average, increasing total NDF digestibility caused a linear improvement ($P<0.01$) in NMIC (Figure 5). According to the fitted model, an increase of 1.1 g NMIC/d should be expected for each percentage point (or 0.01 g/g) increase in NDF digestibility. This pattern is supported by the ruminal improvement in energy availability from fibre, which in turn allows a greater amount of energy for microbial synthesis.

However, a more elaborate investigation of the relationship described above indicated that the NIMC response to total NDF digestibility depended on dietary NDF content ($P<0.01$, Figure 6). In this sense, the lower the dietary NDF, the greater the NMIC improvement caused by increasing total NDF digestibility. Normally, a decrease in dietary NDF is observed when greater amounts of supplements are supplied to the animals. These supplements tend to present a low-fibre content and a high content of non-fibrous carbohydrates (NFC), whose higher energy availability tends to imply a greater microbial growth (Russell et al., 1992; Firkins, 2021). Consequently, the fitted model

showed steeper slopes as dietary NDF contents decreased, a pattern that has practical implications for cattle supplementation management.

With the increase in dietary NFC, mainly starch, a negative trend on NDF digestibility can occur (Ferrareto et al., 2013; Souza et al., 2018). Normally, such effect is mediated by a lowered rumen pH, which makes the medium less favourable to fibrolytic bacteria growth (Russell and Dombrowski, 1980). Moreover, the presence of highly fermentable carbohydrates in the rumen increases the competition for essential substrates between fibrolytic and non-fibrolytic microbial species. Fibrolytic species present a slower growth rate and tends to be less competitive when compared to non-fibrolytic species, including amylolytic species (Carvalho et al., 2011). Hence, such a competition disfavours fibre degradation, which is known in nutrition as “carbohydrate effect” (El-Shazly et al., 1961). However, these negative impacts can be mitigated if adequate feeding management is adopted, which includes greater availability of basic substrates for microbial growth (e.g., nitrogenous compounds, minerals, branched-chain fatty acids) (Carvalho et al., 2011) and strategies to control large variations in rumen pH. Thus, when adequate supplementation strategies are adopted, the gain in terms of microbial production would be proportional to the supplement amount. Probably, it is associated with a more elaborated nutritional formulation of the supplements when they are provided at greater daily amounts, such as inclusion of additives, buffers, etc. As a consequence, the negative impacts of NFC on fibre digestibility could be minimized and fibre energy adds to NFC energy to maximize rumen microbial N production.

The relationship between total NDF digestibility and dietary energy was based on dietary DOM content. In this sense, on average, we found a linear and positive relationship between these variables ($P < 0.01$; Figure 7). Indeed, this positive relationship has a strong nutritional background, mainly for animals fed forage-based diets as the

digested NDF is the main component of digestible energy in forages (Van Soest, 1994). On average, an increment of 88 g DOM/kg DM is expected for each percentage point (i.e., 0.01 g/g) of improvement in total NDF digestibility.

Nevertheless, similarly to what we verified regarding microbial N production, the effect of total NDF digestibility must also be evaluated alongside dietary NDF content ($P < 0.01$). This evaluation corroborated the positive relationship between total NDF digestibility and dietary DOM content ($P < 0.01$). However, the greater the dietary NDF, the steeper the positive effect of NDF digestibility on dietary DOM content (Figure 8). There is a logical and simple explanation for the positive effect of dietary NDF on this relationship. The greater the proportion of NDF in diet, the more energy can be extracted from fibre and more prominent is the contribution of digested NDF for the total DOM in the gastrointestinal tract. On the other hand, diets with lower quality and higher NDF content are normally observed in grazing cattle during the dry season in the tropics. Under these circumstances, a significant part of energy contained in forage fibre is not available to be used for microbial synthesis due to nutritional constraints, mainly in terms of dietary deficiency of N compounds (Sampaio et al., 2009). This unused energy fraction is known as latent energy (Detmann et al., 2009; 2014c). Hence, when lower quality forages and higher NDF content are fed to the animals, even a strategic supplementation with minimal amounts of supplemental N acts towards improving energy extraction from fibre, which also supports the steeper response of dietary DOM as dietary NDF increases.

The amount of NDI was used as an indicator of metabolisable protein supply. Yet, no direct association of this variable with total NDF digestibility was observed ($P > 0.46$). However, there was a linear and positive relationship ($P < 0.01$) between NMIC and NDI (Figure 9). Considering that we found a linear and positive relationship between NMIC and NDF digestibility (Figures 5 and 6), we consider that the relationship between NMIC

and NDI represents an indirect evidence of a positive effect of NDF digestibility on NDI. According to the slope of the fitted model, an increase of 0.66 g/d in the amount of N digested and absorbed in the intestines should be expected for each 1 g/d of improvement in NMIC. This estimate is nutritionally sound. According to the assumptions by Russell et al. (1992), on average, 60% of microbial CP should be considered true protein and this would be totally available in the small intestine. Hence, taking these assumptions into consideration, for each 1 g of NMIC delivered to the small intestine, a total of 0.6 g of microbial N would be digested and absorbed, which is very close to what we estimated herein (0.66, Figure 9).

The total NDF digestibility was linear and positively associated with NB ($P < 0.01$). On average, an increment of 1.3 g/d in NB is expected for each percentage point (i.e., 0.01 g/g) of improvement in total NDF digestibility (Figure 10). Yet, similarly to what we observed for other response variables, the NB response to NDF digestibility presented an interaction with dietary NDF content ($P < 0.01$, Figure 11). According to the fitted model, the improvements in NB caused by increasing NDF digestibility became more prominent as the dietary NDF decreased. Once more, as previously discussed, it highlights that when high supplementation levels are offered, there would be greater availability of energy for microbial synthesis and animal anabolism.

Additionally, we bring into evidence one relevant aspect associated with NB values used in our analysis (Table 2, Figures 10 and 11). Many NB values were found to be excessively high. It indicates that, if those estimates are converted into muscle protein accretion, they would produce daily weight gains above any biologically sounded standard of cattle body weight gain. We must emphasise that all NB estimates in our dataset were obtained in change-over digestion and metabolism assays. This type of experiments tends to overestimate the N accretion in the animal's body as a possible

reflection of management and processing of urinary and faecal samples (Spanghero and Kowalski, 2021). Despite of this bias, it is assumed that the pattern showed by the fitted models (i.e., response direction and intensity) is able to accurately describe the response pattern and could ensure the reliability of the obtained inferences. Then, in order to settle the bias coming from the change-over assays, the weight gain estimates simulated in our work were based on the partial derivative of the fitted model (Figure 11) as a function of total NDF digestibility (Equation 2).

In this sense, for our initial simulations, we assumed an average dietary NDF content of 600 g NDF/kg DM (i.e., forage plus supplement). Under this specific diet, a one percentage unit (i.e., 0.01 g/g) of improvement in total NDF digestibility would cause increases of 50-60 g/d in ADG. The exact values within this range would vary according to the sexual condition and BW of the animals (Table 3). When animal characteristics are kept constant, the improvements in ADG would be inversely proportional to total dietary NDF content (Figure 12), which is supported by the arguments previously presented along this section.

4. Conclusions

Increasing neutral detergent fibre digestibility in cattle fed tropical forage-based diets improves the voluntary forage intake and the supply of energy and metabolisable protein of microbial origin. This simultaneous effect causes an increase in the animal's nitrogen accretion and weight gain. This effect will be more prominent as the dietary neutral detergent fibre content decreases.

CRedit authorship contribution statement

Edenio Detmann: Writing – original draft, Conceptualization, Formal analysis, Funding acquisition, Project administration. **Luiz Carlos O de Sousa:** Data curation, Writing – review & editing. **Nicole S. A. Lima:** Writing – review & editing. **Marcia O. Franco:** Writing – review & editing.

Declaration of Competing Interest

The authors report no declarations of competing interest.

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Table 1

Summary of the main characteristics of the experiments in dataset

Exp.	References	Animals ^a			Forage ^b			ENV ^c	SUP ^d
		Sex	BW (kg)	GG	Species	CP (g/kg DM)	NDF (g/kg DM)		
1	Detmann et al. (2005a, b)	M	304	HZ	<i>U. decumbens</i>	110	564	G	PE
2	Lazzarini et al. (2009)	F	209	HZ	<i>U. decumbens</i>	51	797	FL	P
3	Figueiras et al. (2010)	M	236	HZ	<i>U. decumbens</i>	76	617	F	P
4	Sampaio et al. (2010)	F	180	HZ	<i>U. decumbens</i>	49	770	FL	P
5	Souza et al. (2010)	F	232	HZ	<i>U. decumbens</i>	52	829	FL	E, P, PE
6	Costa et al. (2011a, b)	M	335	HZ	<i>U. decumbens</i>	100	639	G	P
7	Costa et al. (2011c)	M	211	HZ	<i>U. decumbens</i>	99	646	G	PE
8	Lazzarini et al. (2013)	M	397	HZ	<i>U. decumbens</i>	82	601	G	E, P, PE
9	Figueiras et al. (2015)	M	273	N	<i>U. decumbens</i>	113	571	G	PE
10	Figueiras et al. (2016)	M	296	N	<i>U. decumbens</i>	123	577	G	E, P, PE
11	Rufino et al. (2016)	M	227	N	<i>Cynodon</i> sp.	78	730	FL	P
12	Lazzarini et al. (2016)	M	211	N	<i>U. decumbens</i>	135	550	G	E, P, PE

13	Batista et al. (2016)	F	248	N	<i>U. decumbens</i>	50	801	FL	P
14	Franco et al. (2017)	M	198	HZ	<i>U. decumbens</i>	74	809	FL	E, PE
15	Batista et al. (2017)	M	280	N	<i>Cynodon</i> sp.	99	715	FL	P
16	Reis et al. (2020)	F	299	N	<i>Cynodon</i> sp.	80	758	FL	P, PE
17	Oliveira et al. (2020)	F	283	N	<i>Cynodon</i> sp.	44	757	FL	P
18	Rufino et al. (2020)	M	262	HZ	<i>U. decumbens</i>	47	818	FL	P
19	Franco et al. (2021)	M	381	HZ	<i>U. decumbens</i>	82/96	792/762	FL	P, PE
20	Palma et al. (2023)	F	332	N	<i>Cynodon</i> sp.	78	792	FL	P, PE
21	Vidal et al. (2022)	F	520	B	<i>Cynodon</i> sp.	100	670	FL	NS
22	Rufino (2015)	M	241	HZ	<i>U. decumbens</i>	81	772	FL	P
23	Costa (2021)	F	343	B	<i>Cynodon</i> sp.	57	746	FL	PE
24	Silva (2020)	F	386	N	<i>Cynodon</i> sp.	53	781	FL	PE

^a Sex: M, male; F, female. The BW represents the average BW at the beginning of each experiment. GG, genetic group (HZ, F1 Holstein × Zebu; N, Nellore; B, Brahman).

^b CP and NDF are the average crude protein and neutral detergent fibre contents throughout the experiment on a dry matter basis. These contents were obtained from samples of offered forage in feedlot experiments or from hand-plucked samples in grazing experiments. In the experiment 19, two forages were evaluated.

^c ENV, environment of the experiment (G, under grazing; FL, feedlot experiments where animals were fed hays).

^d SUP, type of supplement evaluated in the experiment (E, energy supplement; P, protein supplement; PE, protein-energy supplement; NS, nitrogen-salt supplement). All the experiments had a control treatment (only forage, without supplementation).

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Table 2

Descriptive statistics of the response variables used in the meta-analysis

Item	Statistics ^a							
	Mean	Minimum	Q1	Median	Q3	Maximum	s	N
Body weight (kg)	293.2	178.0	229.6	289.4	340.3	520.7	77.43	115
Intake (g/kg BW)								
Forage	17.6	9.3	14.7	17.6	20.6	25.7	3.65	105
Supplement	1.5	0.0	0.2	0.7	2.1	10.5	2.21	107
NDF	12.3	7.3	10.8	12.2	14.1	16.3	1.91	115
Diet (g/kg DM)								
Crude protein	113	45	89	113	128	210	35.9	115
NDF	670	388	595	690	759	829	105.1	115
Digested OM	508	265	462	522	573	656	97.2	115
Digestibility (g/g)								
Organic matter (total)	0.545	0.274	0.489	0.563	0.615	0.725	0.1070	115

NDF (total)	0.572	0.333	0.525	0.578	0.637	0.783	0.1030	115
pdNDF (total)	0.867	0.613	0.840	0.883	0.916	0.979	0.0759	76
NDF (ruminal)	0.553	0.341	0.501	0.552	0.627	0.741	0.0953	78
Nitrogen balance (g/d)	18.2	-29.1	4.1	14.2	27.9	102.0	25.95	105
Microbial N production (g/d)	58.3	13.1	44.3	57.6	71.0	108.8	20.92	110
N digested in the intestines (g/d)	54.2	9.7	31.0	53.9	73.4	148.3	26.37	78

^a Q1 e Q3, first and third quartiles; N, number of treatment means.

Table 3

Simulation of the increment in average body weight gain in Zebu animals under grazing caused by a unitary increase in total neutral detergent fibre digestibility (i.e., 1 percentage point or 0.01 g/g) [the estimates were based on a diet with 600 g neutral detergent fibre /kg dry matter]

Body weight (kg)	Sexual class		
	Male	Castrated male	Female
200	0.056	0.056	0.057
225	0.056	0.057	0.057
250	0.057	0.058	0.058
275	0.057	0.058	0.059
300	0.058	0.059	0.059
325	0.058	0.059	0.060
350	0.059	0.060	0.061
375	0.059	0.061	0.061
400	0.060	0.061	0.062
425	0.060	0.062	0.063
450	0.061	0.062	0.063

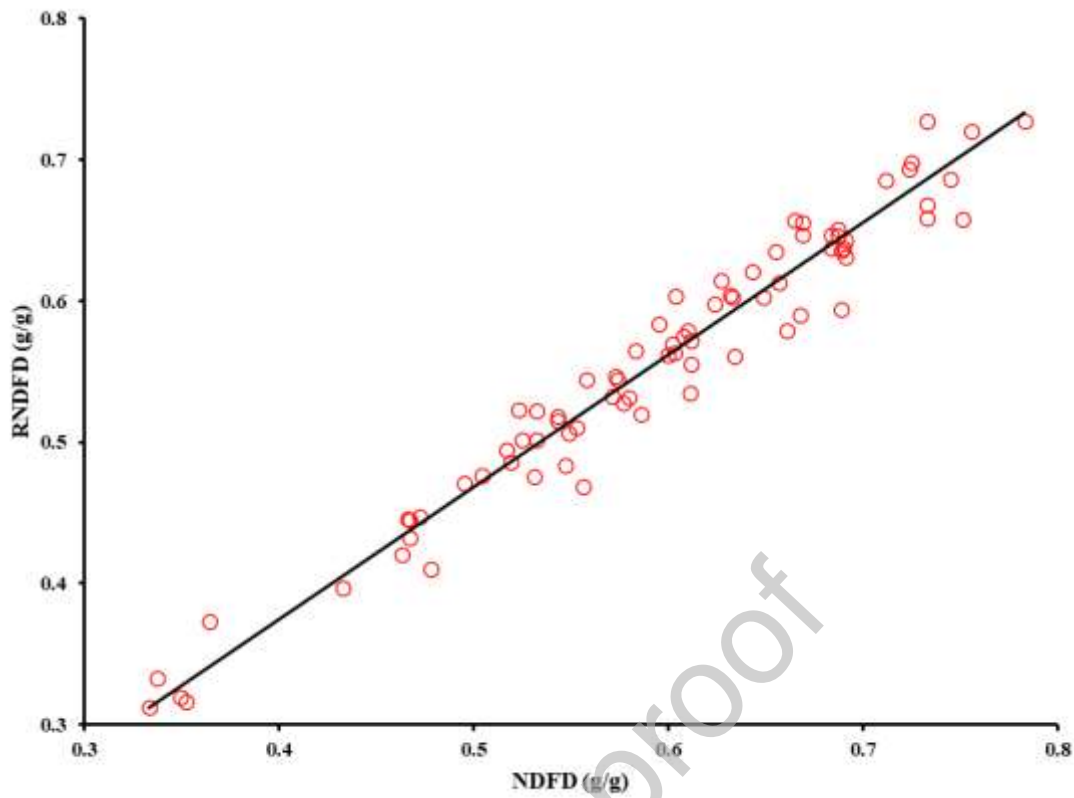


Figure 1

Relationship between total (NDFD) and ruminal (RNDFD) neutral detergent fibre digestibilities in cattle fed tropical forage-based diets with or without supplementation ($\hat{Y} = 0.936 \pm 0.0167 \times X$; $s_{XY} = 0.0503$; $R^2 = 0.955$; $N = 78$). The data points were adjusted for random study effects.

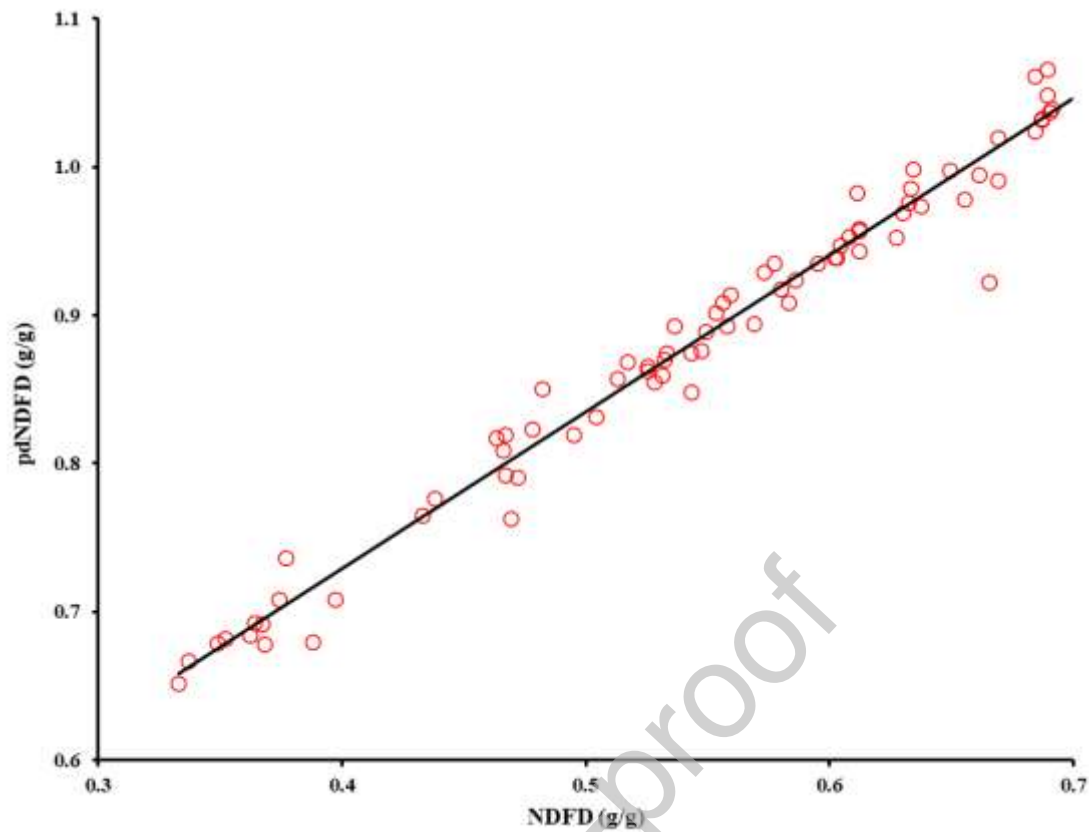


Figure 2

Relationship between total neutral detergent fibre digestibility (NDFD) and total digestibility of potentially digestible neutral detergent fibre (pdNDFD) in cattle fed tropical forage-based diets with or without supplementation ($\hat{Y} = 0.307 \pm 0.0518 + 1.056 \pm 0.1123 \times X$; $s_{XY} = 0.0447$; $R^2 = 0.974$; $N = 76$). The data points were adjusted for random study effects.

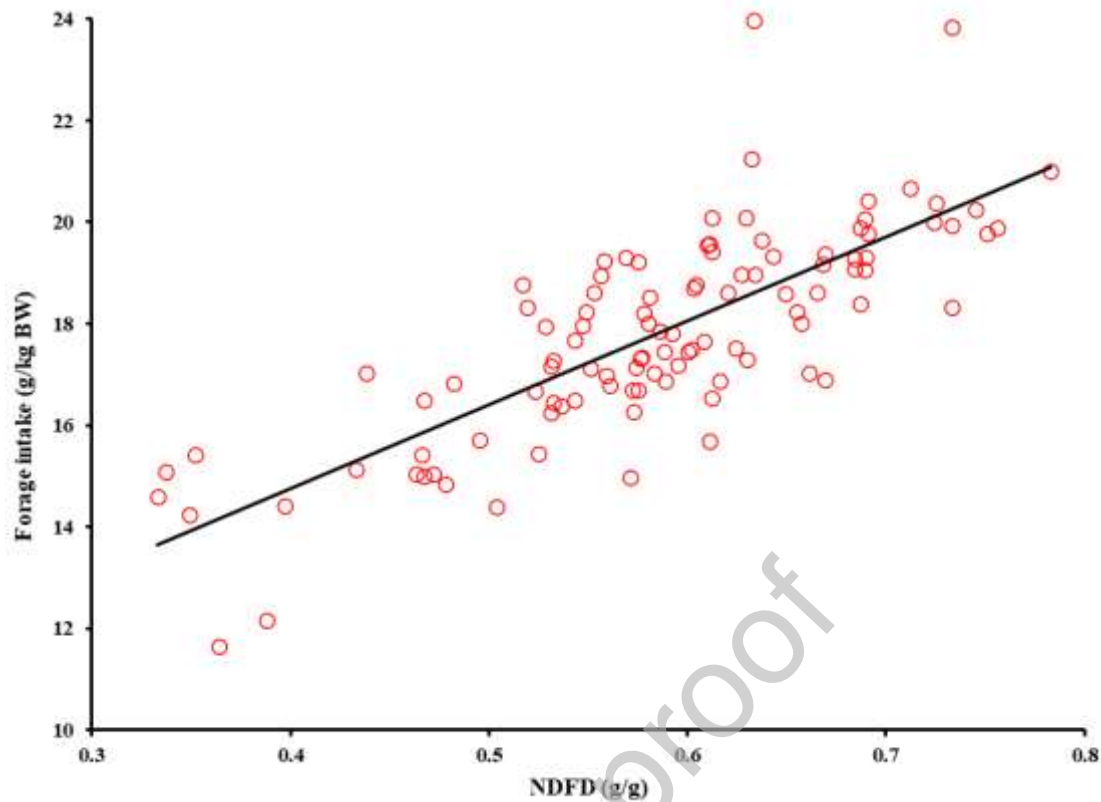


Figure 3

Relationship between total neutral detergent fibre digestibility (NDFD) and the voluntary forage dry matter intake in cattle fed tropical forage-based diets with or without supplementation ($\hat{Y} = 8.11 \pm 1.547 + 16.59 \pm 3.528 \times X$; $s_{XY} = 3.12$; $R^2 = 0.610$; $N = 105$).

The data points were adjusted for random study effects.

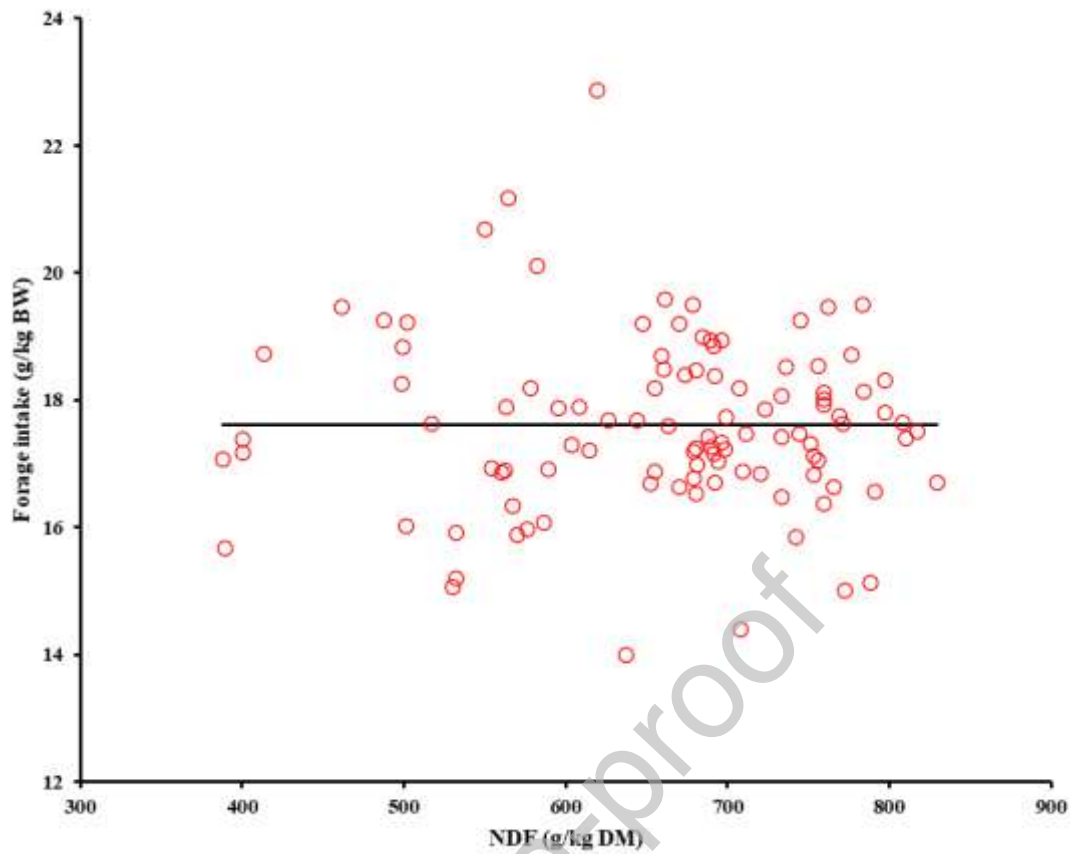


Figure 4

Relationship between dietary neutral detergent fibre (NDF) content and the voluntary forage dry matter intake in cattle fed tropical forage-based diets with or without supplementation ($\hat{Y} = 17.62 \pm 0.725$; $s_{XY} = 3.37$; $N = 105$). The data points were adjusted for random study effects.

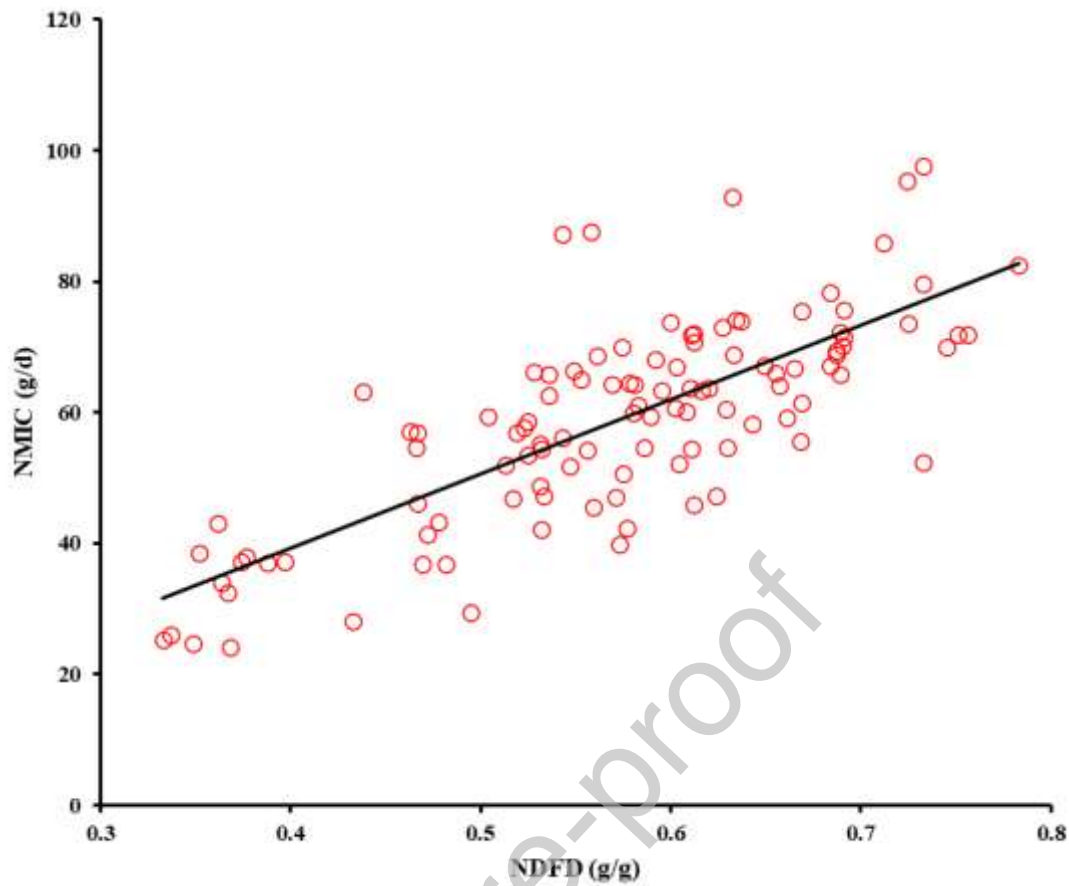


Figure 5

Average relationship between total neutral detergent fibre digestibility (NDFD) and the rumen microbial nitrogen production (NMIC) in cattle fed tropical forage-based diets with or without supplementation ($\hat{Y} = -6.3 \pm 13.54 + 113.80 \pm 25.024 \times X$; $s_{XY} = 24.32$; $R^2 = 0.589$; $N = 110$). The data points were adjusted for random study. Refer to Figure 6 for more details about this relationship.

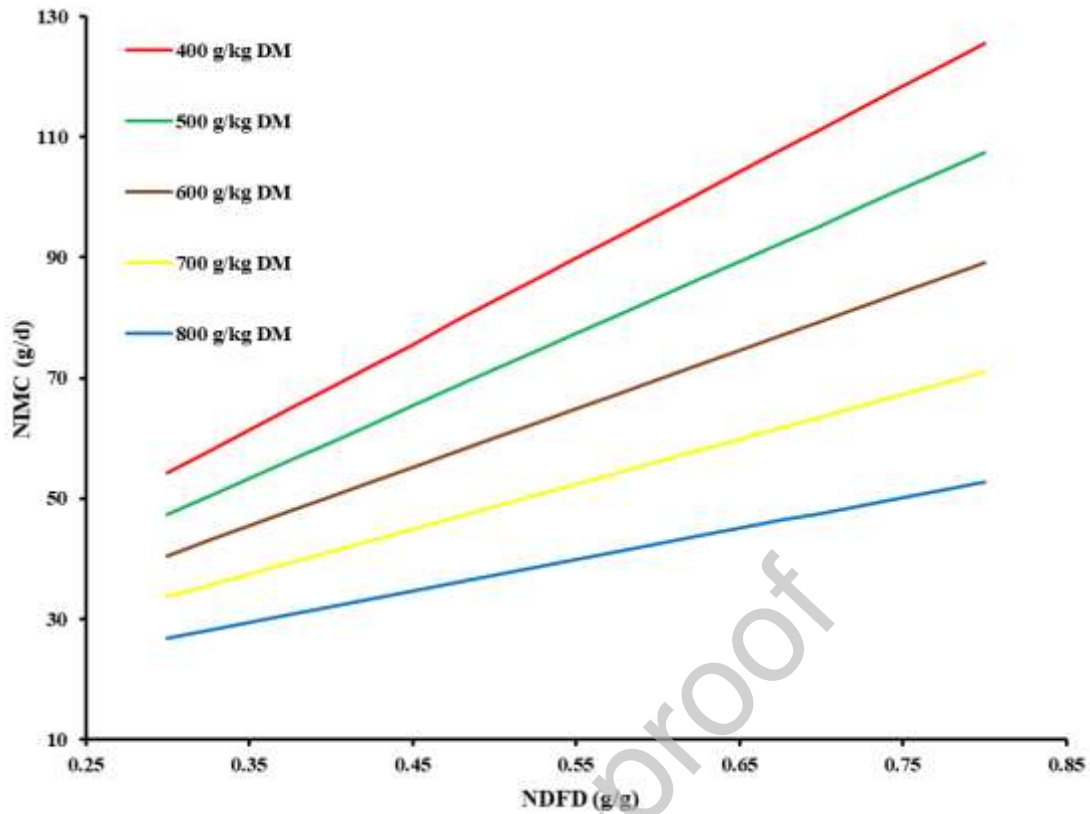


Figure 6

Relationship between total neutral detergent fibre digestibility (NDFD), dietary neutral detergent fibre (NDF) content, and rumen microbial nitrogen production (NMIC) in cattle fed tropical forage-based diets with or without supplementation ($\hat{Y} = -11.33 \pm 13.19 + 233.86 \pm 31.563 \times \text{NDFD} - 0.2275 \pm 0,0379 \times \text{NDFD} \times \text{NDF}$; $s_{XY} = 20.48$; $R^2 = 0.847$; $N = 110$). Refer to Figure 5 for more details about this relationship.

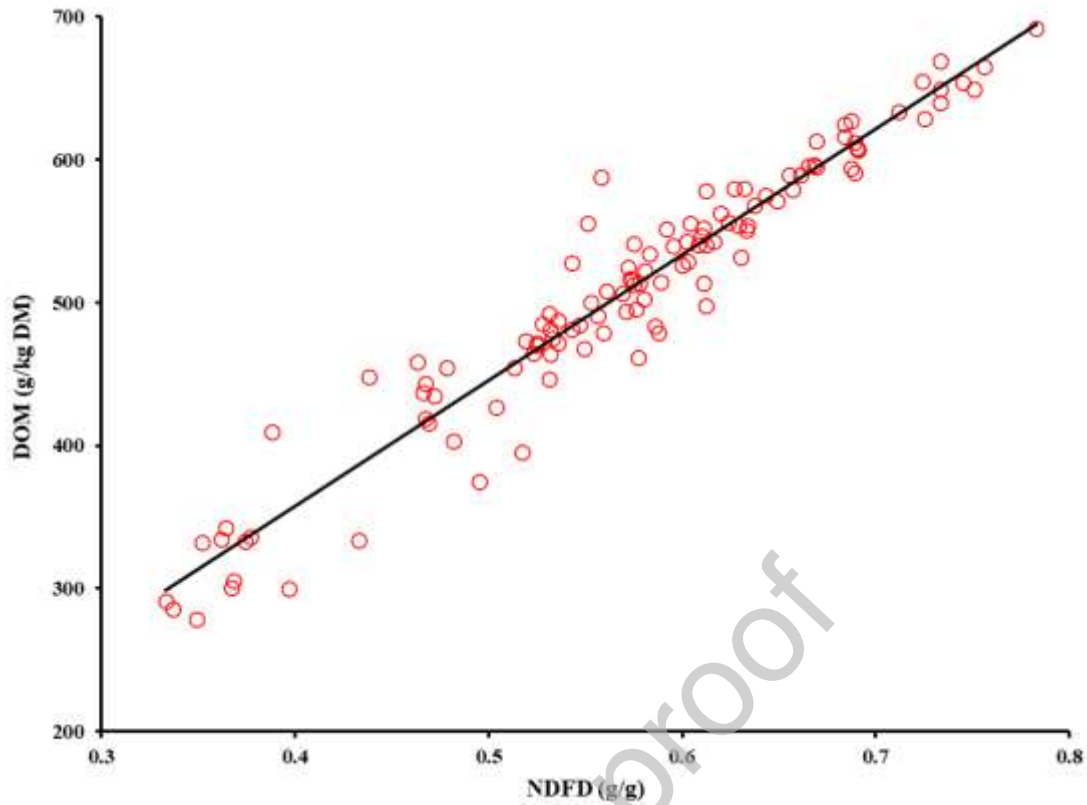


Figure 7

Average relationship between total neutral detergent fibre digestibility (NDFD) and dietary content of digested organic matter (DOM) in cattle fed tropical forage-based diets with or without supplementation ($\hat{Y} = 4.2 \pm 32.52 + 882.3 \pm 59.94 \times X$; $s_{XY} = 58.7$; $R^2 = 0.934$; $N = 115$). The data points were adjusted for random study. Refer to Figure 8 for more details about this relationship.

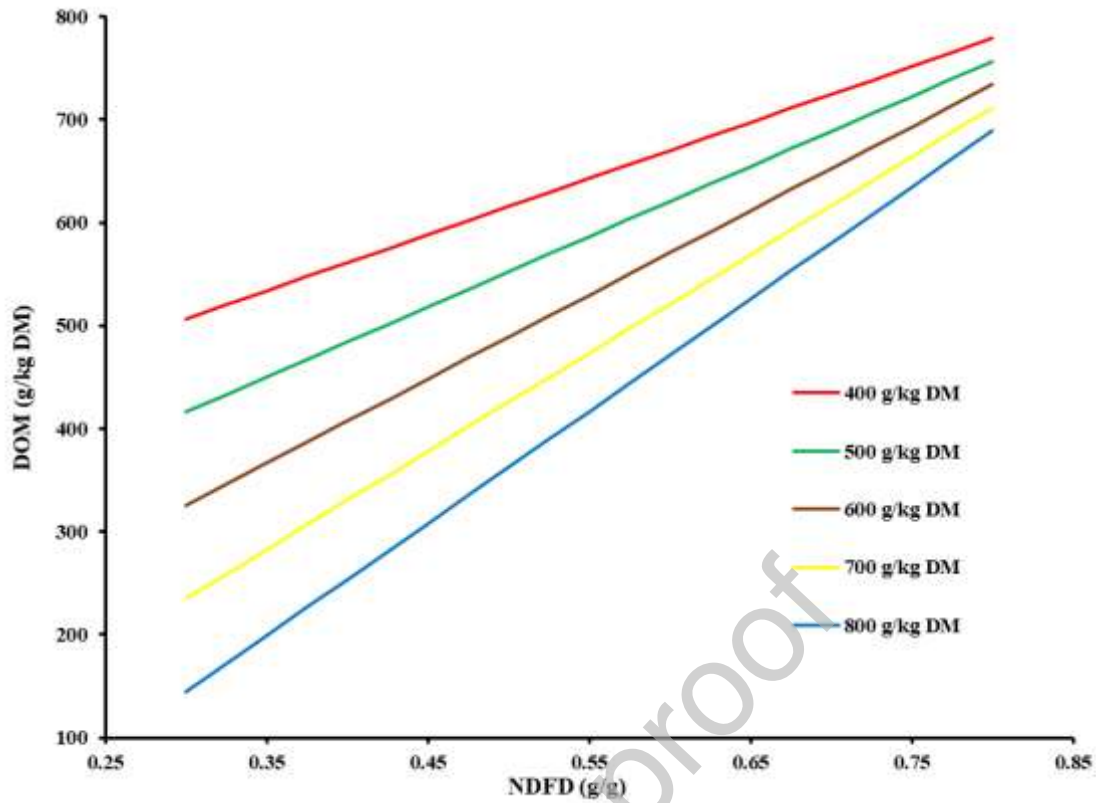


Figure 8

Relationship between total neutral detergent fibre digestibility (NDFD), dietary neutral detergent fibre (NDF) content, and dietary content of digested organic matter (DOM) in cattle fed tropical forage-based diets with or without supplementation ($\hat{Y} = 869.2 \pm 27.38 - 1.3141 \pm 0.06378 \times \text{NDF} + 1.3615 \pm 0.07885 \times \text{NDFD} \times \text{NDF}$; $s_{XY} = 27.4$; $R^2 = 0.993$; $N = 115$). Refer to Figure 7 for more details about this relationship.

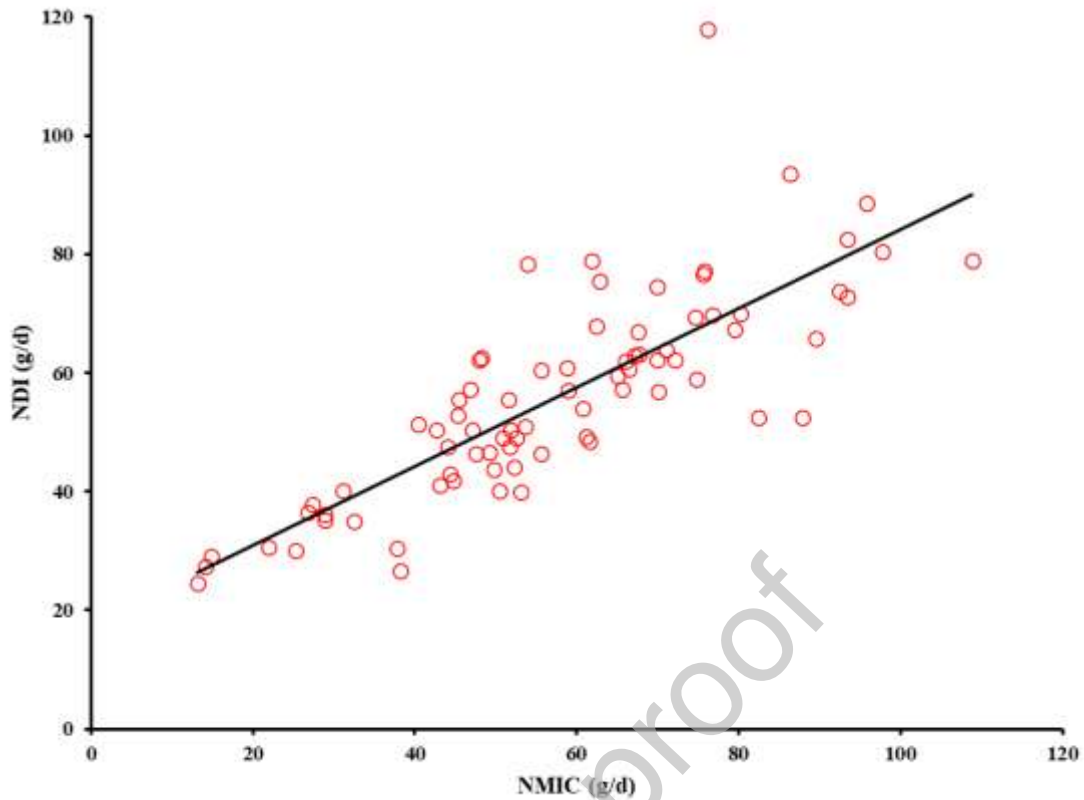


Figure 9

Relationship between rumen microbial nitrogen production (NMIC) and nitrogen compounds digested in intestines (NDI) in cattle fed tropical forage-based diets with or without supplementation ($\hat{Y} = 17.89 \pm 9.391 + 0.661 \pm 0.1682 \times X$; $s_{XY} = 24.4$; $R^2 = 0.651$; $N = 78$). The data points were adjusted for random study.

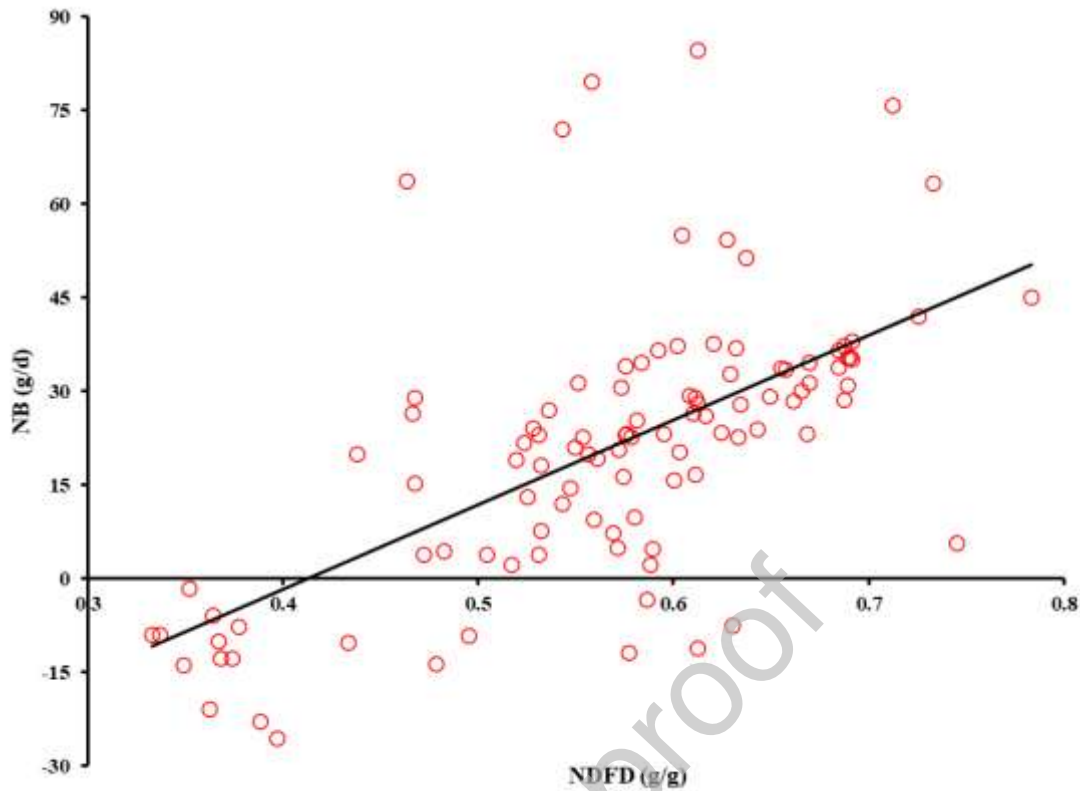


Figure 10

Average relationship between total neutral detergent fibre digestibility (NDFD) and nitrogen balance (NB) in the body in cattle fed tropical forage-based diets with or without supplementation ($\hat{Y} = -55.4 \pm 17.83 + 134.73 \pm 33.872 \times X$; $s_{XY} = 41.4$; $R^2 = 0.381$; $N = 105$). The data points were adjusted for random study. Refer to Figure 11 for more details about this relationship.

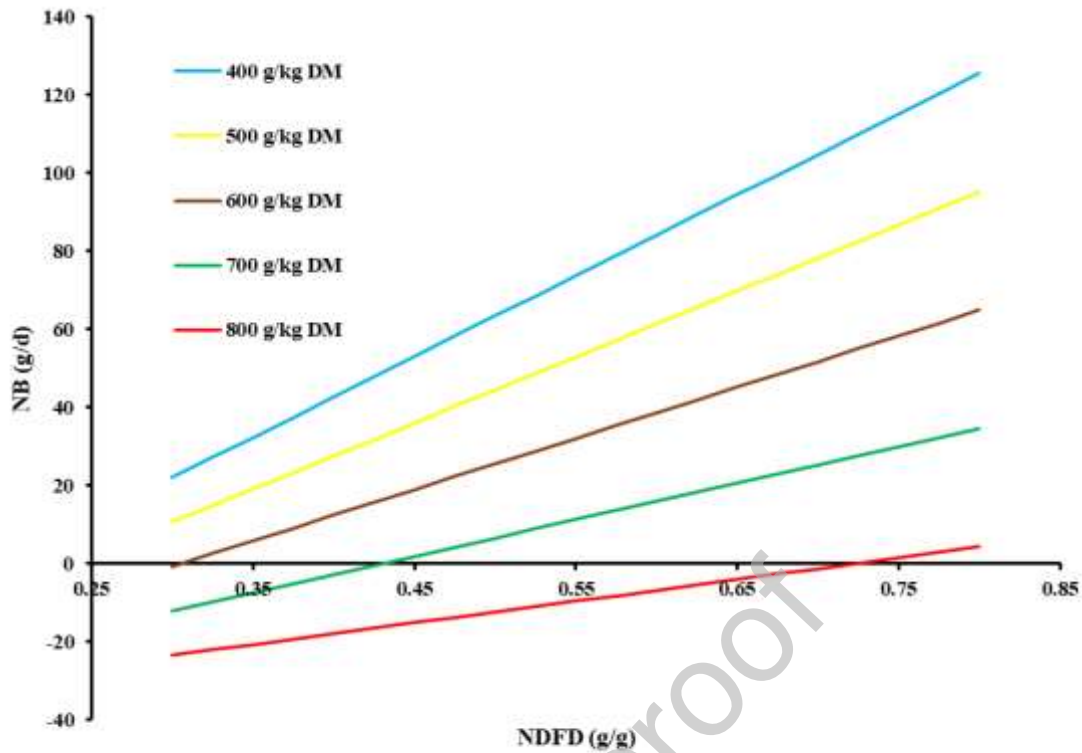


Figure 11

Relationship between total neutral detergent fibre digestibility (NDFD), dietary neutral detergent fibre (NDF) content, and nitrogen balance (NB) in the body in cattle fed tropical forage-based with or without supplementation ($\hat{Y} = -40.1 \pm 17.96 + 358.75 \pm 47.746 \times \text{NDFD} - 0.3791 \pm 0.06007 \times \text{NDFD} \times \text{NDF}$; $s_{XY} = 33.9$; $R^2 = 0.751$; $N = 105$). Refer to Figure 10 for more details about this relationship.

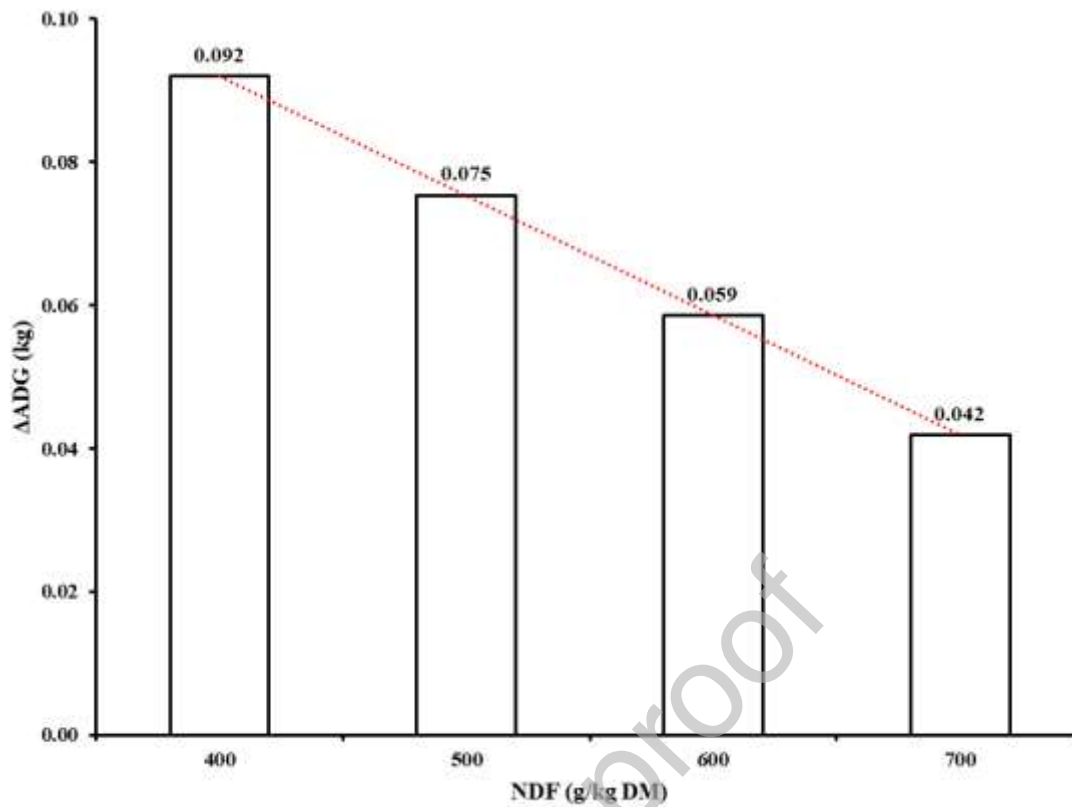


Figure 12

Simulation of the increment in average body weight gain (Δ ADG) in Zebu animals under grazing caused by a unitary increase in total neutral detergent fibre digestibility (i.e., 1 percentage point or 0.01 g/g) according to the dietary neutral detergent fibre content [the estimates were based on a male animal weighing 350 kg BW].

CRedit authorship contribution statement

Edenio Detmann: Writing – original draft, Conceptualization, Formal analysis, Funding acquisition, Project administration. **Luiz Carlos O de Sousa:** Data curation, Writing – review & editing. **Nicole S. A. Lima:** Writing – review & editing. **Marcia O. Franco:** Writing – review & editing.

Declaration of Competing Interest

The authors report no declarations of competing interest.