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Methanogenic potential of forages consumed throughout the year by cattle in a Sahelian pastoral area

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Abstract. Methane (CH₄) emission from ruminants in African pastoral systems may be affected by intake and type of plants, which vary highly between rainy and dry seasons. In each of two sites located in the semiarid Sahelian area of Senegal, three Gobra zebu were monitored throughout 1 year. A representative sample of their diet was obtained once every month. Diet was mainly composed of grasses, herbaceous legumes, tree and shrub foliage and pods, and dried forage residues. CH₄ production and volatile fatty acid (VFA) concentration, which reflects VFA production, were determined *in vitro*. Crude protein, neutral detergent fibre (NDF) and acid detergent fibre were measured by near-infrared spectrophotometry. CH₄ production varied between 24.6 and 35.2 mL/g forage dry matter (DM), being minimal in August (rainy season) and maximal in February (dry season). Seasonal difference disappeared when CH₄ was expressed in mL/g NDF. The acetate : propionate ratio varied in the same way as CH₄ (3.2 and 4.6 in August and February, respectively); VFA concentration was minimum in March and maximum in September (69.2 and 77.4 mmol/L, respectively). CH₄ production was closely related to dietary NDF content ($r = 0.82$) and to acetate : propionate ratio ($r = 0.96$). For six successive periods (February to July), plant categories constituting the diet were incubated separately. Reconstituting the CH₄ production and VFA concentration in the diet on the basis of the proportion of plant components gave values similar to those of the global diet (33.4 and 34.2 mL CH₄/g DM and 75.9 and 70.9 mmol VFA/L, respectively). This result suggests the absence of interaction among plant components on rumen fermentation.

Additional keywords: greenhouse gases, rumen, seasonal variations.

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Introduction

The contribution of livestock to total greenhouse gas (GHG) emissions is evaluated as 14.5% of emissions of anthropogenic origin, of which 39% is represented by enteric methane (CH₄) emissions (Gerber *et al.* 2013). Although regions having a low animal productivity contribute to a low extent to GHG emissions (e.g. 10% for subsaharan Africa), enteric CH₄ emissions per kilogram of milk or meat are the highest when productivity is very low (Gerber *et al.* 2011). However, there are very few direct measurements of CH₄ emissions in tropical countries, and, to our knowledge, there is none for pastoral systems, so that it is necessary to better evaluate emissions and understand factors responsible for emission variation, before proposing ways of mitigation. In pastoral areas, major factors of variation of CH₄ emissions are the level of intake of forages as well as their nature and nutritive value, which vary greatly throughout the year, for grass as for browse species (Ouédraogo-Koné *et al.* 2008). This is especially marked in Sahelian climatic conditions that have high seasonal and inter-annual rainfall variability (Lebel *et al.* 2003). Despite the benefits of partial transhumance for cattle

nutrition (Gaidet and Lecomte 2013), annual changes in intake and forage quality remain high (Chirat *et al.* 2014). On-field *in vivo* measurements of enteric CH₄ emissions are very difficult to implement for methodological reasons. To overcome this difficulty, *in vitro* tests are proposed as a first evaluation method. A preliminary study on Sahelian forages harvested in a pastoral area of Senegal showed the impact of forage chemical composition on CH₄ production *in vitro* (Baccouche *et al.* 2014). The main objective of the present study was to evaluate the potential of CH₄ emissions from forage diets consumed by cattle across different seasons, and to relate CH₄ production with forage chemical composition. A secondary objective was to assess potential interactions between forage components, i.e. changes in CH₄ emission when the different dietary forage components are fermented alone or mixed together, as they are in diets.

Materials and methods

Experimental sites and design

The study took place in two experimental sites in northern Senegal, in the Ferlo silvopastoral area. This is a semiarid

region, with a Sahelian climate (Bwh in the Köppen classification), with annual average temperature and rainfall of 28–30°C and 200–400 mm, respectively (Touré *et al.* 2012). Rainy season generally occurs between July and September; dry season is longer, occurring between October and June. Due to this climatic context, Ferlo area is devoted to transhumant systems for free-ranging cattle; herds move from north in rainy season to south in dry season. The first experimental site (15°21'N, 15°28'W) was the research station of Dahra-Djoloff (ISRA Animal Research Centre, BP 01, Dahra, Senegal). Three Gobra young bulls (aged 2.5 years and weighing on average 230 kg) among a sedentary herd of 120 cattle were monitored between early February and late September 2014. The second experimental site was a larger area around the village of Niassanté (16°10'N, 15°33'W). Three Gobra cows (aged 7.5 years and weighing on average 260 kg) among a herd of 31 transhumant adult cattle belonging to a Fulani breeder were monitored during the same period. Transhumant system in this area has been described by Adriansen and Nielsen (2005). Sites are called S (sedentary) and N (nomadic), respectively. In both sites, nine 3-day periods of measurement were defined, with an interval of 1 month between the measurement periods. Rainfall during these periods was in compliance with the above-mentioned general trend.

Animals were free-ranging and were fed almost exclusively on rangelands composed of grasses, of which the major species were *Aristida mutabilis*, *Chloris prieurii*, *Dactyloctenium aegyptium*, *Eragrostis tremula* and *Schoenefeldia gracilis*, of herbaceous legumes, of which the major species were *Alysicarpus ovalifolius*, *Cassia obtusifolia* and *Zornia glochidiata*, and of shrubs, especially *Balanites aegyptiaca*, *Boscia senegalensis* and *Calotropis procera*. Other herbaceous plants, such as *Achyranthes aspera*, *Borrelia* sp. and *Sporobolus coromandelianus*, were also found.

Measurements and analyses

Forage samples were obtained by the simulated-bite technique that mimics forage intake by animals, described by Guérin *et al.* (1988) and validated by Wallis de Vries (1995). Hand-plucking was performed for 1 day for each cattle between sunrise and sunset, so as to obtain a representative sample of consumed forage for each animal. Sampling was performed on each site and for all periods by the same person for the three cattle on three successive days. Daily samples were collected in a 50-L bag, and then air-dried. From this representative sample, forage diet was sorted into the following categories: grasses, herbaceous legumes, perennial herbs other than grasses and legumes, foliage and pods of ligneous shrubs and trees, and a category called 'straw'. This last category contained diverse undefined forage made of residual grass stems. After sorting, samples of each category were oven-dried at 60°C for 48 h to determine the percentage of each plant category on a dry matter (DM) basis.

In vitro fermentation of forage samples was performed using a batch system, as described in Rira *et al.* (2015). For each period and each animal, a subsample of the global diet was assayed ($n = 54$), and for six periods from February to July for the same animal in Niassanté site, the corresponding subsamples by category (grasses, herbaceous legumes, shrubs

and trees, 'straw', $n = 24$) were also assayed. Each forage sample was assayed in two runs. Successive runs were separated by 3 days. Donor animals were three wethers of Texel breed, weighing on average 70 kg, and receiving daily 1000 g of chopped natural grassland hay from tropical origin. For each run, a 500-g sample of rumen content was obtained from each animal, then strained through a 250-µm mesh polyester cloth. Filtrates of the three wethers were pooled for constituting the fermentation inoculum. Incubations lasted 24 h, with 400 mg of forage, 15 mL inoculum and 25 mL buffer placed in 100-mL vials. Gas production was measured using a pressure transducer. Conditions of fermentation, and gas and liquid sampling procedures are described in Rira *et al.* (2015). CH₄ was determined in a gas sample by gas chromatography (Micro GC 3000A, Agilent Technologies, Les Ulis, France). Volatile fatty acids (VFA) were determined by gas chromatography using crotonic acid as an internal standard (Perkin-Elmer Clarus 580 GC, Perkin Elmer, Courtaboeuf, France), as described by Morgavi *et al.* (2013).

All forage samples were analysed for neutral detergent fibre (NDF), acid detergent fibre (ADF) and crude protein (CP) by near-infrared reflectance spectroscopy (NIRS) using a Foss NIRsystem 5000 monochromator (Foss, Hillerød, Denmark), according to equations determined from the comparison of spectra of more than 1300 tropical forages with chemical analyses (Tran *et al.* 2010).

The first set of data was formed with all results of fermentation and chemical composition of representative forage diets for the six animals and nine periods. ANOVAs were performed using the mixed procedure of SAS (v9.3; SAS Institute Inc., Cary, NC, USA). The first analysis was performed with the model $Y = \mu + \text{month}_i + \text{site}_j + \text{animal}(\text{site})_{jk} + \text{month-site}_{ij} + e$, where μ is the overall mean, month is treated as a repeated factor, animal is nested within site, month-site is the interaction between month and site and e is the error. The second analysis was performed with the model $Y = \mu + \text{season}_i + \text{site}_j + \text{animal}(\text{site})_{jk} + \text{season-site}_{ij} + e$, where the season factor has two levels, namely, dry or rainy. Linear correlations were then established among all selected variables. The second set of data was formed by six representative diets for successive months on one hand, and the six corresponding reconstituted diets, R, on the other, obtained as follows: $R = \sum C_i \times P_i$, where C_i is the value of each variable for forage category i (i = grasses, herbaceous legumes, trees and shrubs, 'straw') and P_i the proportion of each category on a DM basis in the original forage diet. An ANOVA was performed using the model $Y = \mu + \text{method}_i + \text{month}_j + e$, where μ is the overall mean, method is the mode of calculation (initial vs reconstituted sample), month is the month of harvesting and e is the error. For all analyses, significance was declared at $P < 0.05$.

Results

Variation in fermentation according to the season

There was large variation in the chemical composition of forage diets according to the month of harvesting, cell walls being the highest and CP being the lowest in dry season (Table 1). CH₄ production expressed in mL/g DM was the highest in February, April and May (32–35 mL/g DM), when NDF content was the

Table 1. Month-to-month variation of chemical composition and *in vitro* fermentation characteristics of forage diets consumed by cattle in Sahelian pastures
ADF, acid detergent fibre; CP, crude protein; DM, dry matter; NDF, neutral detergent fibre; VFA, volatile fatty acids; M, month; Si, site; M × Si, month × site interaction

Parameter	Month												P-value	M × Si
	Feb.	Mar.	Apr.	May	June	July	Early Aug.	Late Aug.	Sep.	s.e.m.	M	Si		
CP (g/kg DM)	5.56	6.45	4.74	4.72	5.34	11.71	9.66	25.26	18.86	0.853	<0.001	0.015	<0.001	<0.001
NDF (g/kg DM)	71.8	66.0	70.1	70.2	67.2	59.2	59.9	46.7	56.4	2.22	<0.001	0.010	<0.001	0.008
ADF (g/kg DM)	43.2	40.6	43.0	43.5	43.1	38.9	38.8	26.7	30.6	1.46	<0.001	0.053	<0.001	<0.001
Methane (mL/g DM)	35.2	29.7	32.5	32.3	28.6	26.7	24.8	24.6	24.9	1.46	<0.001	0.001	<0.001	<0.001
Methane (mL/g NDF)	48.9	44.8	46.3	45.9	42.5	44.3	41.5	53.1	44.9	1.91	<0.001	0.037	<0.001	<0.001
VFA (mmol/L)	70.0	69.2	71.2	74.2	76.0	74.6	75.1	74.5	77.4	2.70	0.034	0.086	<0.001	0.580
Acetate (% VFA)	72.9	69.7	72.8	72.8	71.4	68.1	67.4	68.0	68.7	1.00	<0.001	<0.001	<0.001	0.033
Propionate (% VFA)	16.0	18.8	16.8	17.0	18.3	20.4	21.4	20.8	20.1	0.79	<0.001	0.002	<0.001	0.004
Acetate : propionate	4.62	3.79	4.37	4.37	3.93	3.51	3.16	3.31	3.27	0.206	<0.001	0.002	<0.001	0.004

highest, and was the lowest between August and September (24–25 mL/g DM), when NDF content was the lowest ($P < 0.001$). CH₄ production expressed in mL/g NDF also varied according to the month ($P < 0.001$), but changes from one harvesting date to the subsequent one could be important; for example, the lowest and the highest production were in early August and late August, respectively. Differences in the VFA concentration were significant but less marked ($P = 0.034$), being lower between February and April (69–71 mmol/L) than between May and September (74–76 mmol/L). VFA pattern also varied, depending on the month of harvest ($P < 0.001$). Acetate was lower between July and September (67–69%) than between February and June (70–73%), propionate was higher between July and September (20–21%) than between February and June (16–19%); as a consequence, the acetate : propionate ratio was higher between February and June (3.79–4.62) than between July and September (3.16–3.61). Butyrate did not change with the month of harvesting ($P = 0.08$, data not shown). Comparison between rainy and dry seasons (Table 2) confirmed most of these results, i.e. a huge difference in CP content (5.4 vs 17.5 g/kg DM for dry and rainy seasons, respectively), significantly higher cell wall content in dry season, significantly lower CH₄ production per g DM (31.5 vs 24.3 mL/g DM for dry and rainy seasons, respectively), significantly lower acetate proportion, acetate : propionate ratio, and significantly higher VFA concentration and propionate proportion in rainy season than in dry season; however, CH₄ production per gram NDF did not vary with season.

Differences in chemical composition were observed between the two sites, forage diets being higher in NDF and lower in CP at Site N than at Site S (63.5 vs 59.6 g/kg DM, respectively), whereas CP and ADF concentrations were not significantly different between the sites. CH₄ production per gram DM was higher for Site N than for Site S (29.8 vs 26.1 g/kg DM, respectively), but CH₄ production per gram NDF remained unchanged. VFA concentration did not change with site; acetate proportion and acetate : propionate ratio were higher, and propionate proportion was lower at Site N than at Site S (70.5, 18.5 and 3.94 for Site N, 68.9, 20.4 and 3.44 for Site S, respectively). Differences in CH₄ production per gram DM between the sites were more marked in

Table 2. Seasonal variation of chemical composition and *in vitro* fermentation characteristics of forage diets consumed by cattle in Sahelian pastures

ADF, acid detergent fibre; CP, crude protein; DM, dry matter; NDF, neutral detergent fibre; VFA, volatile fatty acids. Se, season; Si, site; Se × Si, season × site interaction

Parameter	Season		s.e.m.	P-value		
	Dry	Rainy		Se	Si	Se × Si
CP (g/kg DM)	5.43	17.53	1.192	<0.001	0.352	0.461
NDF (g/kg DM)	68.8	54.3	1.46	<0.001	0.012	0.953
ADF (g/kg DM)	43.1	30.6	0.93	<0.001	0.687	0.230
Methane (mL/g DM)	31.5	24.3	0.91	<0.001	0.001	0.020
Methane (mL/g NDF)	45.6	45.4	1.43	0.876	0.069	0.025
VFA (mmol/L)	72.3	75.8	1.55	0.008	0.146	0.380
Acetate (%VFA)	71.7	67.7	0.58	<0.001	0.008	0.466
Propionate (% VFA)	21.4	17.5	0.45	<0.001	<0.001	0.239
Acetate : propionate	4.19	3.19	0.121	<0.001	<0.001	0.071

dry season than in rainy season (significant interaction between season and site).

When considering the nine periods and the six animals ($n = 54$), CH₄ production per gram DM was significantly ($P < 0.001$) correlated with CP, NDF and ADF concentrations ($r = -0.60, 0.82$ and 0.74 , respectively), with VFA concentration, with acetate, propionate and butyrate proportions, and with acetate : propionate ratio ($r = -0.55, 0.85, -0.96, 0.47$ and 0.96 , respectively). CH₄ production per gram NDF was not correlated with CP and, obviously, with NDF and ADF contents, but was correlated with CH₄ per g DM, propionate proportion and acetate:propionate ratio ($r = 0.52, -0.45$ and -0.53 , respectively, $P < 0.001$), with acetate proportion ($r = 0.36, P < 0.01$), and with VFA concentration and butyrate proportion ($r = -0.33$ and 0.29 , respectively, $P < 0.05$). VFA concentration was significantly correlated with CP, NDF and ADF concentrations ($r = 0.29, P < 0.05, -0.40$ and $-0.35, P < 0.01$, respectively), with acetate proportion ($r = -0.29, P < 0.05$), with propionate and butyrate proportions and with acetate : propionate ratio ($r = 0.51, -0.69$ and $-0.50, P < 0.001$, respectively).

Synergy for fermentation between diet components

The range in the proportion of the different plant categories in forage diets was 8.1–33.8% for grasses, 1.2–63.1% for legumes, 1.0–10.3% for ligneous and 15.0–79.8% for 'straw', according to the month of harvesting. Dry season was characterised by the increase in intake of ligneous plants and straw. Chemical composition did not vary between the initial diet and reconstituted diet (Table 3), which indicates that sampling for analyses was conducted correctly. CH₄ production, VFA concentration and acetate : propionate ratio did not vary between the initial diet and reconstituted diet, whereas proportions of acetate and propionate were or tended to be higher for the reconstituted diet, at the expense of the proportion of butyrate (Table 3).

Table 3. Comparison of methane production and volatile fatty acid (VFA) concentration *in vitro* between a grazed Sahelian diet fermented as a whole, and the reconstitution from diet components fermented separately

The four diet components were grasses, herbaceous legumes, trees and shrubs, and 'straw' containing undefined forage made of residual grass stems. ADF, acid detergent fibre; CP, crude protein; DM, dry matter; NDF, neutral detergent fibre

Item	Diet fermentation	Reconstitution from diet-component fermentation	s.e.m.	P-value
CP (% DM)	5.57	5.30	0.387	0.44
NDF (% DM)	69.7	70.9	1.53	0.38
ADF (% DM)	44.0	45.3	1.34	0.27
Methane (mL/g DM)	34.23	33.41	1.248	0.46
VFA (mmol/L)	70.86	75.95	3.591	0.14
Acetate (% VFA)	73.41	74.36	0.455	0.05
Propionate (% VFA)	16.42	17.59	0.607	0.06
Butyrate (% VFA)	6.26	4.92	0.273	0.002
Acetate : propionate	4.52	4.30	0.186	0.21

Discussion

Changes in methanogenic potential of forage diet with season

Enteric CH₄ emissions in tropical countries are not well estimated, especially for low-producing animals, due to insufficient information on feed intake and diet composition. In these countries, enteric CH₄ calculation for national GHG inventories are often performed using the approximate Tier 1 method of IPCC (2006) that does not account for production level of animals. Improvements are in progress; for example, Kouazounde *et al.* (2015) proposed for enteric CH₄ a Tier 2 method adapted for Benin. However, no method can be applied for pastoral systems having a very low animal productivity.

Pastoral systems are characterised by large changes between dry and rainy season, both in feed intake, which can be very low in dry season (Schlecht *et al.* 1999; Chirat *et al.* 2014), and in chemical composition, with forages being very low in protein in dry season (Rivière 1991; Schlecht *et al.* 1999); these two factors concur to changes in CH₄ emissions. Our results showed a highly significant effect of season on CH₄ production per gram DM, which is higher in dry season than in rainy season. To our knowledge, such result had not been shown previously for tropical pastoral areas. Differences in CH₄ production per gram DM between the two sites could be due to the difference in herd management (nomadic vs sedentary) leading to higher NDF content in the nomadic site, but an effect of local climatic and soil conditions is not excluded. Our results also showed a strong relationship between CH₄ production per gram DM and NDF concentration. This result agrees with results of Gameda and Hassen (2014) who studied 16 grass species in the arid region of Kalahari with comparable climatic conditions, but not with those observed by Baccouche *et al.* (2014) who performed *in vitro* incubations of 83 forages, of which 35 were grasses and legumes, harvested in the Ferlo region as in the present study, or those by Macheboeuf *et al.* (2014) who studied 156 temperate plants, of which only one was grass and 13 were legumes. Our results are especially surprising because CH₄ production from forages depend both on their NDF concentration and on their digestibility, which are the two main drivers of hydrogen production from carbohydrate fermentation (Archimède *et al.* 2011). In the present study, NDF concentration seems to have a much greater effect on CH₄ production than does NDF digestibility; this results in the absence of seasonal differences in CH₄ production per gram NDF. Possibly, the discrepancy between the present study and that of Gameda and Hassen (2014), on one hand, and those of Baccouche *et al.* (2014) and Macheboeuf *et al.* (2014), on the other hand, could be due to the presence of a majority of grasses ('straw' being mainly composed of grasses) and to the higher NDF concentration in the former two studies. Despite the higher CH₄ production per gram DM in the dry season, the very low intake that was simultaneously observed will certainly result in a lower emissions per animal, although CH₄ emission rate for a same diet is lower at low intakes (Chaokaur *et al.* 2015, for Brahman zebus in the tropics).

CH₄ emissions per gram DM were closely and positively related to acetate proportion in VFA and acetate : propionate ratio, and negatively related to VFA concentration and propionate proportion in the VFA. These results partially agree with those

of Gameda and Hassen (2014) who found a loose but significant positive relationship between CH₄ and acetate proportion in the VFA, but no relationship between CH₄ production and VFA concentration, propionate proportion in VFA and acetate:propionate ratio. These results are surprising because methanogenesis is thought to be positively related to VFA. This decoupling between the VFA concentration (and thus production) and CH₄ production was already observed by Bodas *et al.* (2008) who incubated 450 temperate plants, of which a small proportion had an antimethanogenic effect, by Meale *et al.* (2012) for Australian and Ghanaian grasses and leguminous shrubs, and by Baccouche *et al.* (2014) with herbaceous species, but not with ligneous species. Conversely, Macheboeuf *et al.* (2014) found a good relationship between VFA and CH₄ production for 156 temperate species, and a very strong relationship between VFA and total gas production. Collectively, these results suggest that among forages, stoichiometric relationships between VFA and CH₄ cannot be used, and that hydrogen produced by carbohydrate fermentation is not totally directed towards CH₄ production, at least *in vitro*.

The present study is a first step in the knowledge of enteric CH₄ emissions in Sahelian pastoral areas. In the present study, donor sheep from a temperate breed were fed tropical forage. It is assumed that under these conditions, influence of the donor animal is low, because CH₄ emissions depend more on forage (especially temperate vs tropical) than on breed (temperate vs tropical; Archimède *et al.* 2013). However, a relationship between *in vitro* and *in vivo* determination of CH₄ emissions per gram DM cannot be established. Indeed (1) batch fermentations are simplified models of the rumen that do not faithfully reproduce *in vivo* conditions, and (2) all forages were tested with the same inoculum, whereas rumen microbiota certainly varies with the nature of the diet and with undernutrition. The present study showed seasonal variations in CH₄ emission, and *in vivo* on-pasture determination of these emissions is the mandatory next step.

Interaction among diet components

It has been suggested for a long time that interactions between feedstuffs occur in the rumen, especially due to the need of simultaneous supply of carbohydrates and protein. These interactions, studied first between forages and concentrates, have been assessed more recently among different forages (review by Niderkorn and Baumont 2009). These authors identified digestive interactions when a low-nitrogen forage is associated with a high-nitrogen forage, and when forages rich in secondary metabolites such as tannins are associated with grasses. These two types of association are observed in Sahelian natural grasslands. The former contributes to an increase in VFA concentration, and, thus, in hydrogen, and then CH₄ production on a DM basis. The latter one may contribute to a lower VFA concentration if carbohydrate fermentation is reduced, and to an additional decrease in methanogenesis due to a specific action of tannins on methanogens (Martin *et al.* 2010). In the present study, these hypotheses were not confirmed. However, the very high CP content of forage diet in the rainy season showed a selective grazing for an increase in protein intake, as has been demonstrated in a similar ecosystem by Ayantunde *et al.* (1999). In our study,

the 24-h incubation of forages, which is recommended for a global evaluation of the fermentation of low-quality forages, could have offset a synergy between low- and high-protein forage effects, which could occur only in the first hours after intake (Niderkorn *et al.* 2011). In three tropical tannin-rich forages, the absence of interaction among diet components on CH₄ production has been shown by Rira *et al.* (2015). In Senegalese browse species, an interaction among diet components on digestibility has been found for some of them (Fall Touré *et al.* 1998) but the interaction among diet components on CH₄ production is not known. In addition, the percentage of ligneous plants, which are mainly made of foliage and pods of shrubs and trees and have a low methanogenic potential (Soliva *et al.* 2008; Gameda and Hassen 2015), was always lower than 10% in our study.

Conclusions

The present study has provided an overview of seasonal changes in potential CH₄ emissions in forage diets grazed in arid tropics. It has also shown the importance of NDF as a determinant of methanogenic potential. However, several questions are raised. Can CH₄ emissions be predicted only by chemical composition and digestibility of forages? Which kind of forages can limit CH₄ emissions without impairing nutrient supply to animals? The *in vitro* approach can partially address these issues, in spite of limits in the interpretation of results. Nevertheless, a decisive step would be an *in vivo* experiment in which enteric CH₄ emissions, intake and digestibility would be determined on grazing animals throughout the year.

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