



The role of small ruminants on global climate change

Alda Lúcia Gomes Monteiro^{1*}, Amanda Moser Coelho da Fonseca Faro², Mylena Taborda Piquera Peres³, Rafael Batista³, Cesar Henrique Espirito Candal Poli⁴, Juan Jose Villalba⁵

¹Departamento de Zootecnia, Universidade Federal do Paraná, Rua dos Funcionários, 1540, 80035-050, Curitiba, Paraná, Brazil. ²Instituto Federal Catarinense, Camboriú, Santa Catarina, Brazil. ³Programa de Pós-Graduação em Zootecnia, Universidade Federal do Paraná, Curitiba, Paraná, Brazil. ⁴Departamento de Zootecnia, Universidade Federal do Rio Grande do Sul, Porto Alegre, Rio Grande do Sul, Brazil. ⁵Utah State University, Logan, Utah 84322-5230 USA. *Author for correspondence. E-mail: aldaufpr@gmail.com

ABSTRACT. Global warming, as a consequence of excessive CO₂ production mainly due to anthropogenic actions, is one of the main concerns of society due to the effects it can cause in the survival of humans, plants and animals. Several climatic consequences have already been reported, such as warming the oceans and changing biodiversity in various regions of the planet. One of the greenhouse gases responsible for global warming, which causes a lot of concern, is methane gas from digestion of food by ruminants. Besides that, emissions of greenhouse gases are represented also by waste management, rice cultivation, burning of residues from agriculture and soil management for agricultural production. Among ruminants, sheep and goats play an important economic role mainly in Oceania, Asia and Africa. More than 50% of small ruminants of the world are located in arid region, indicating their adaptability and future suitability to increasing temperatures. The purpose of this review is to report current knowledge about the methane emission produced by small ruminants, addressing the different interfaces of this theme, and considering possible mitigation strategies.

Keywords: climate change; goats; methane; sheep.

O papel dos pequenos ruminantes na mudança climática global

RESUMO. O aquecimento global, como consequência da produção excessiva de CO₂, principalmente devido a ações antrópicas, é uma das principais preocupações da sociedade devido aos efeitos que pode causar na sobrevivência de seres humanos, plantas e animais. Diversas consequências climáticas têm sido relatadas, como o aquecimento dos oceanos e a alteração da biodiversidade em várias regiões do planeta. Um dos gases de efeito estufa responsáveis pelo aquecimento global, que causa muita preocupação, é o gás metano proveniente da digestão de alimentos por ruminantes. Além disso, as emissões de gases de efeito estufa são representadas também pela gestão de resíduos, pelo cultivo de arroz, pela queima de resíduos da agricultura e pelo manejo do solo para produção agrícola. Entre os ruminantes, os ovinos e os caprinos desempenham um importante papel econômico, especialmente na Oceania, Ásia e África. Mais de 50% dos pequenos ruminantes do mundo estão localizados em regiões áridas, indicando sua adaptabilidade e possível adequação futura ao aumento das temperaturas. O objetivo desta revisão é relatar o conhecimento atual sobre a emissão de metano produzida por pequenos ruminantes, abordando as diferentes interfaces deste tema e considerando possíveis estratégias de mitigação.

Palavras-chave: aquecimento global; caprinos; metano; ovinos.

Introduction

The sustainability of agricultural production systems depends, among other factors, on maintaining the good quality of the environment. Climate change, greenhouse effects or global warming are terms related to the same problem, quite current, that may be influenced by anthropogenic interventions regarding the carbon and nitrogen cycle in agroecosystems. The consequences of these changes can affect the natural reproductive cycle of plants and animals, the migration of certain species of birds, even the extinction

of several species, significantly affecting the planet's biodiversity (Ministry of Agriculture and Forestry [MAF], 2012). Thus, according to Skuce, Morgan, Van Dijk, and Mitchell (2013), these circumstances of anthropogenic origin are considered the greatest threat faced by the world population, since they will affect the production of food and natural resources.

Emissions of greenhouse gases (GHG) are directly related to this theme and are represented mainly by the ruminal fermentation of production animals, waste management, rice cultivation, burning of residues from agriculture and soil

management for agricultural production. Approximately 80% of the anthropogenic CH₄ emissions are derived from ruminant production, especially in extensive production systems (Gill, Smith, & Wilkinson, 2010). Recognized as the third most polluting GHG, the annual growth rate of methane emissions was reported as 7% (Intergovernmental Panel on Climate Change [IPCC], 2006), with agricultural activities accounting for 70% of this value. However, according to the IPCC (2014), although the agriculture and land use sectors are responsible for 25% of the anthropogenic net greenhouse gas emissions, there are indications of declining to less than half of that share between 2010 and 2050, becoming the sector a net CO₂ sink before the end of the century, due to reforestation and changes in land management and agriculture.

The small ruminant production sector is of great relevance in the world, as sheep and goats represent approximately 56% of the world ruminant population (Food and Agriculture Organization of the United Nations [FAO], 2016). Small ruminant production plays a crucial socioeconomic role on the different continents. Besides the production of approximately 1.5 million tons of meat and 25.6 million tons of milk (FAO, 2016), this sector contributes to the preservation of landscapes and ecosystems, cooperating with biodiversity conservation and supplying products to niche markets (Marino et al., 2016).

More than 50% of the small ruminant's world population is located in arid regions, indicating the adaptability of these animals to such environmental conditions and their future suitability to regions predicted to sustain increasing temperatures. The plasticity of small ruminants is highlighted by the ability of sheep to graze in wasteland – particularly in Asian and African countries – to pasturelands in Australia.

The purpose of this review is to report current knowledge about methane emissions produced by small ruminants, addressing the different interfaces of this theme, and considering possible mitigation strategies. The contribution of small ruminants to global methane emissions are also discussed.

Methanogenesis

Unlike monogastric animals, ruminants maintain a symbiosis with microorganisms present in the first part of the gastrointestinal tract. The rumen is sheltered with a microbial population highly capable of fermenting dietary carbohydrates, recognized as the main energetic source of ruminants (Van Soest,

1994). Among the microbial groups, species of bacteria, protozoa, fungi and, with a population ranging from 0.5 to 3.0%, are the organisms of the domain *Archae*, also known as methanogenic bacteria (Hackmann & Spain, 2010). The ingested foods are anaerobically fermented and converted into short chain fatty acids (SCFA), mainly acetate, propionate and butyrate, branched chain fatty acids, microbial protein, vitamins from the K and B complex (Berchielli, Pires, & Oliveira, 2011) and gases from the fermentation process, such as carbon dioxide (CO₂), nitrous oxide (N₂O), hydrogen (H₂) and methane (CH₄) (Sejian et al., 2017). From the synthesis of acetate and butyrate via the Embden-Meyerhof pathway, popularly known as glycolysis, H₂ is produced in the process. However, the anaerobic fermentation capacity of the lignocellulosic components is directly related to the elimination of H₂ from the ruminal environment (Kozloski, 2011). The most common form of H₂ elimination from the rumen is known as methanogenesis, in which there is a combination of four molecules of hydrogen with a molecule of carbon dioxide through the action of the microorganisms of the *Archae* domain. Thus, methanogenic bacteria maintain the biochemical ruminal balance from the restructuring of the NAD⁺, FAD⁺ and NADP⁺ cofactors (Martin, Morgavi, & Doreau, 2010). In contrast to acetate and butyrate, the production of propionate does not result in the release of H₂, being the path of this SCFA considered competitive to the use of H₂ in the rumen (Martin et al., 2010).

Through flatulence and, mainly, eructation, CH₄ is eliminated from the ruminal environment and such activities are natural consequences to prevent gas accumulation (Muñoz, Yan, Wills, Murray, & Gordon, 2012). However, production and elimination of CH₄ causes energy losses in the range of 2 to 12% of the gross energy ingested by ruminants (Moss, Jouany, & Newbold, 2000). In sheep, the estimate reported by the IPCC (2006) of energy loss in methanogenesis is, on average, 6.5%.

Ruminal methane emitted by ruminants

Small ruminants are found on all continents, predominantly in countries known as emerging. According to FAO (2016), the world herd has approximately 1.2 billion sheep and 1 billion goats, growing at around 1.5% per year in the last five years (Figure 1). In relation to Brazil, the national herd reached 18.43 million sheep and 9.78 million goats in 2016, with the greatest concentration in the

Northeast (63%) and South (23.9%) regions (ANUALPEC, 2017).

In Brazil, ruminal fermentation of beef cattle was the main cause (75%) of methane emissions in 2012, according to the Annual Estimates of Greenhouse Gases (Ministério da Ciência, Tecnologia e Inovação [MCTI], 2014). The dairy herd ranks second, accounting for 12% of methane emissions. The size of beef and dairy cattle populations in relation to that of small ruminants in Brazil (Figure 1) explain this difference in emissions (Table 1). Cattle reared on pasture account for 41% of direct methane emissions, and this has been considered the largest contribution within the category of ruminants (MCTI, 2014). Relative to impacts per unit of production, the meat sector represents lower potential of CH₄ emissions per kg of final product than the milk sector. In addition, small ruminants destined to meat have a lower CH₄ emitting potential than cattle, when evaluated in kg CO_{2-eq} per kg of final product (Table 1).

Table 1. World and Brazilian emission of ruminal methane for sheep, goats and cattle.

| Variables | Sheep | Goats | Cattle | Source |
|--|---------|---------|-----------|-------------------------|
| World Emission (Gg CH ₄) | 6,564 | 5,014 | 71,910 | FAO (2016) |
| World Emission (Gg CO _{2-eq}) | 137,840 | 105,295 | 1,510,106 | FAO (2016) |
| Brazilian Emission (Gg CH ₄) | 353.4* | 353.4* | 11,876 | MCTI (2014)** |
| Brazilian Emission (Gg CO _{2-eq}) | 92.2 | 48.9 | 12,536 | FAO (2016) |
| Brazilian Emission (Gg CO _{2-eq}) | 1,936 | 1,027 | 263,245 | FAO (2016) |
| Emission by Product (kg CO _{2-eq} kg meat ⁻¹) | 23.4 | 23.3 | 67.4 | Gerber et al. (2013)*** |
| | 24.4 | 23.5 | 53.4 | |

*Data from sheep, goats, buffaloes, pigs and equines together. ** Estimates for the year 2012; ***Values estimated by GLEAM 2.0 software developed by FAO.

Sheep and goats contribute with about 6.5% of the world emissions, corresponding to 429 thousand Gg CO_{2-eq}, of which 59% is attributed to sheep and

41% to goats; with 299 thousand Gg CO_{2-eq} derived from meat and 130 thousand Gg CO_{2-eq} derived from milk, greater numbers than those indicated by the FAO (2016) (Table 1), demonstrating the variation in the reported data in inventories.

The contribution to the global production of meat from small ruminants is characterized by a dichotomy between regions; the world production of lamb meat is largely concentrated in Western Europe and Oceania, while goat meat production occurs in regions of lower socioeconomic development (Asia). The gas emissions derived from small ruminant meat is lower in Oceania and Western Europe (the main producers), due to intensification and greater efficiency of the production systems than in developing regions (Opio et al., 2013).

Emissions from dairy small ruminants is generally greater than from meat production, especially in regions such as Asia and Africa, due to extensive production systems and management, directed mainly for subsistence (Patra, 2014). Sheep and goats are recognized as the only species of domesticated ruminants able to live on mountain and areas with soils poor in nutrients. These animals also express the ability to excavate the soil in search of shoots and buried parts of perennial species for ingestion in dry seasons or semi-arid regions (Sejian et al., 2017), thus they are found in more inhospitable regions, and in less efficient systems, leading to longer production cycles. On the other hand, the carbon footprint of milk from small ruminants is greater than that of bovine milk, 6.5 kg CO_{2-eq} kg milk⁻¹ versus 2.8 kg CO_{2-eq} kg milk⁻¹ (Opio et al., 2013), due to the high productivity of dairy cattle compared to sheep and goats.

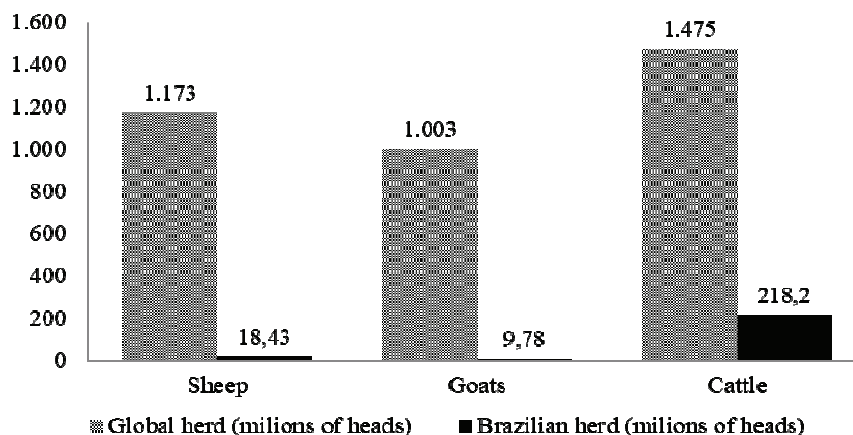


Figure 1. Global and Brazilian herds of sheep, goats and cattle, in millions (FAO, 2016).

Emission of enteric methane by sheep

The commercial production of sheep meat worldwide is known by the low "carbon footprint", which makes the activity convenient to sustainable farming systems. It is estimated that the main sheep-producing countries, concentrated in Oceania and Western Europe, are contributing with the least amount of enteric CH₄ emissions, compared to goat-producing countries in developing areas. As already discussed, this is due to the greater intensification of production in developed countries, and the model of subsistence in emerging regions (Salem, 2010). According to Marino et al. (2016), greater prolificacy, leading to greater number of lambs born per lambing cycle, and short cycles for the production of meat contribute to the efficiency of the system. In fact, sheep meat production can effectively contribute to food production in an efficient and sustainable way, favoring the carbon balance of production systems.

In order to generate more robust greenhouse gas emission information from sheep production, Muetzel and Clark (2015) conducted four experiments that measured the emissions of adult and young animals fed pastures of different qualities. The result of this study (510 measurements in 115 sheep) showed that dry matter intake (DMI) in kg day⁻¹ explained 80% of CH₄ production variation per animal (g d⁻¹), and if CH₄ emissions were to be estimated using a single equation, that would be:

$$pCH_4 = 0.792 \times DMI + 3.1$$

where:

pCH₄: methane production (g d⁻¹)

DMI: dry matter intake (kg day⁻¹)

However, when the results were analyzed as two separate sets of data (<1 year, and > 1 year), it was identified that when the animals were younger than 1 year of age the prediction was improved, including metabolizable energy (ME) of the diet, in addition to DMI.

Sheep older than 1 year:

$$pCH_4 = (0.826 \times DMI) + 3.15$$

Sheep younger than 1 year:

$$pCH_4 = (0.749 \times DMI + (0.051 \times ME)) + 2.45$$

where pCH₄ = methane production (g d⁻¹); DMI = dry matter intake (kg d⁻¹), ME = metabolizable energy (MJ kg DM⁻¹).

Therefore, estimates of digestibility and dietary intake can be used to identify corresponding seasonal changes in the production of CH₄ from ruminants managed on pasture. Thus, the emission of methane should be measured and integrated to the measurements of DM intake, energy values, fiber quality and quantity in the diet in order to know more about potential mitigations in pasture production systems (Berndt & Tomkins, 2013).

Table 2 shows annual values of methane (kg CH₄ year⁻¹) from sheep of different body weights obtained from studies in different regions of the world. It can be observed that the emissions are between 5 and 15 kg CH₄ animal⁻¹ year⁻¹ (average of 8 kg CH₄ year⁻¹) for animals of different weights and categories. Considering the Brazilian sheep herd of 17 million animals (Anuário da Pecuária Brasileira [ANUALPEC], 2017), this would result in about 130 Gg CH₄ year⁻¹, slightly greater than values estimated by FAO (2016).

Table 2. Annual methane ruminal emission of sheep, according to body weight (BW) in different regions of world.

| Emission (kg CH ₄ year ⁻¹) | BW (kg) | Local | Source |
|--|------------|----------------|---|
| 8 | 55 | Global | IPCC (2006) |
| 6.9 | 37 | New Zealand | Lasey, Ulyatt, Martin, Walker, and Shelton (1997) |
| 8 | - | Several | Pelchen and Peters (1998) |
| 9.8 | 65 | United Kingdom | Murray, Moss, Lockyer, and Jarvis (1999) |
| 5.7 | 35 | New Zealand | Ulyatt, Lasey, Shelton, and Walker (2002) |
| 7.3 | 47 | New Zealand | Hammond et al. (2014) |
| 7.5 | 42 | New Zealand | Pinares-Patiño et al. (2011) |
| 6.1 | 36 | New Zealand | Sun, Hoskin, Muetzel, Molano, and Clark (2011) |
| 9.2 | 51 | New Zealand | Hammond et al. (2014) |
| 8.3 | 35 | Brazil | Savian et al. (2014) |
| 14.6 | 59 | Brazil | Savian et al. (2014) |
| 8.6 | 60 | Australia | Goopy et al. (2014) |
| 6.6 | 52 | Mongolia | Zhai et al. (2015) |
| 8.6 | 24 | Brazil | Savian et al. (2018) |
| 7.2 | 56 | France | Archimède et al. (2018) |

Ruminal methane emission by goats

The lack of data on emissions by goats limits reliable estimates of ruminal methane emissions. The IPCC (2006) reports the emission of 5 kg CH₄ animal⁻¹ year⁻¹ for goats with 40 kg of body weight, assuming daily emission of 13 g CH₄ animal⁻¹ day⁻¹, which is in agreement with the reported data in the literature (Table 2). Some authors have developed mathematical models to predict methane emission by goats. Patra and Lalhriatpuii (2016) elaborated a model based on the nutritional composition of the diet and intake variables, using a review with 42 published works. The linear model developed based on metabolizable energy intake (ME) and digestible energy (DE) accurately predicted methane

production. However, the model of Patra and Lalhriatpuii (2016) does not distinguish the prediction by production type; while Fernández, Espinós, López, García-Diego, and Cervera (2013) developed models exclusively for dairy goats. The authors' model was based on body weight, milk production and diet. According to this model, it was observed that there was an overestimation of values described by IPCC (2007), showing the need for further research to refine the emission estimates. Effects of feed restriction on ruminal methane emission by goats were observed by Lima et al. (2016), mentioning that the emission decreases linearly with the reduction of the dry matter intake, although the loss of energy in the form of methane proportional to the organic matter intake did not present differences due to the food restriction.

The effect of dietary supplementation on methane emission was reported by Debruyne et al. (2018) in kids. The supplementation with coconut oil until 11 weeks of life suppressed the methanogenic activity, inhibiting the colonization of the rumen by *Archaea* bacteria, reducing the *in vitro* emission of methane. Jeong et al. (2012) also observed this effect of the inclusion of vegetable oils (coconut, soybean and palm) on ruminal methane emission, reducing on average 25% of the emission in relation to animals that did not receive oils. Thus, the use of food alternatives to manipulate the ruminal microbiota to reduce ruminal methane emissions has been widely evaluated and has frequently shown positive results regarding its action.

The effect of the inclusion of condensed tannins on the diet of goats on methane emission was evaluated by Bhatta et al. (2013); this inclusion significantly reduced methane emissions at 12 and 25% of the daily emission rate, due to the inclusion of 2.8 and 5.7 g kg⁻¹ DM from the diet, respectively. Condensed tannins inhibit methanogenesis by a direct effect on ruminal methanogens and an indirect effect on hydrogen production due to lower feed degradation (Martin et al., 2010; Tavendale et al., 2005). The direct effect can be attributed to cell death by the formation of complexes with sterols in protozoal cell membranes. This modifies ruminal fermentation by suppressing ruminal protozoa and selectively inhibiting methanogenic bacteria. Condensed tannins have an inhibitory capacity for methanogenic activity, and may be present in plants of extensive goat production regions.

Table 3 presents annual CH₄ emission data for dairy and non-dairy goats of different weights and animal categories in various regions of the world.

The values indicate an average of 6 kg CH₄ year⁻¹ for non-dairy animals, which are the majority of the Brazilian herd located in the Northeast, and 14 kg CH₄ year⁻¹ for dairy goats. Considering the average for non-dairy animals, it would result in 54 Gg CH₄ year⁻¹, close to the estimate by FAO (2016).

Table 3. Annual methane ruminal emission of goats, according to body weight (BW) in different regions of world.

| Emission (kg CH ₄ year ⁻¹) | BW (kg) | Local | Source |
|---|------------|-------------|---|
| Non Dairy Goats | | | |
| 5 | 40 | Global | IPCC (2006) |
| 6.8 | 34 | USA | Animut et al. (2008) |
| 3 | 25 | Africa | Herrero, Thornton, Kruska, and Reid (2008) |
| 9 | 40 | New Zealand | MAF (2012) |
| 6.2 | 24 | China | Yang, Mao, Long, and Zhu (2012) |
| 5 | 45 | South Korea | Jeong et al. (2012) |
| 5.8 | 34 | Japan | Bhatta et al. (2013) |
| 5.6 | 34 | India | Miri, Tyagi, Ebrahimi, and Mohini (2013) |
| 4.6 | 45 | Denmark | Nielsen, Kiani, Tejada, Chwalibog, and Alstrup (2014) |
| 5 | 38 | Spain | Martínez-Fernández et al. (2014) |
| 9 | 47 | Spain | Ibáñez, López, Criscioni, and Fernández (2015) |
| 6.6 | 30 | Brazil | Criscioni and Fernández (2016) |
| 9.7 | 46 | Spain | Lima et al. (2016) |
| 6 | 20 | Brazil | Criscioni, and Fernández (2016) |
| 3.4 | 19 | South Korea | Barbosa et al. (2018) |
| 0.5 | 7 | Bangladesh | Na, Li, and Lee (2017) |
| 0.85 | 13 | Bangladesh | Hoque, Islam, Selim, Ahmed, and Rahman (2017) |
| Dairy Goats | | | |
| 14.3 | | France | Vermorel et al. (2008) |
| 13.7 | | Spain | Ibáñez et al. (2016) |

Factors interfering in the emission of methane

Voluntary intake of food by the animal is the main factor that affects the efficiency by which the ingested nutrients are used. The greater the voluntary intake, the higher the productivity of animals, and the lower the nutrient requirements for each unit of animal production (Mertens, 2007). In ruminants, intake is the result of a dynamic combination between the animal, the type of food, more specifically the plant in the case of grazing animals, and ruminal fermentation.

Therefore, it is essential to measure dry matter (and nutrient) intake by ruminants (Berndt & Tomkins, 2013) to estimate the production of CH₄ and the influence of dietary intake and nutritional composition on this parameter. Studies have shown that when forage intake increases, CH₄ emission also increases, indicating a positive relationship between DM intake and methane emission (Amaral et al., 2016; Charmley et al., 2016; Hammond et al., 2013; Kurihara, Magner, Hunter, & McCrabb, 1999; Moorby, Fleming, Theobald, & Fraser, 2015; Savian et al., 2014; Zhao, O'Connell, & Yan, 2016). It is also

important to understand the role of the components of the diet offered to the animals, especially with regard to the type of carbohydrate, since carbohydrates are important for the production of CH_4 . For instance, carbohydrates influence ruminal pH which in turn can alter the ruminal microbiota (Johnson & Johnson, 1995). It is well known that increasing the level of starch in the diet reduces the proportion of dietary energy converted to CH_4 (Blaxter & Clapperton, 1965) mainly due to a change in fermented substrate from fiber to starch and the concomitant decline in ruminal pH. The concentration and chemical characteristics of plant fiber also influence fermentation and thus the production of CH_4 (Van Soest, 1994).

Herbivores exhibit a complex pattern of interactions with their pastoral environment, making the plant-animal relationship a cause-and-effect function between pasture structure and ingestion patterns. Carvalho (2013) stated that herbivores select plants and their morphological components to optimize nutrient intake. Thus, the ultimate goal would be to achieve the highest possible intake of metabolizable energy (Boval & Dixon, 2012).

In conjunction with research evaluating nutritional influence on rumen CH_4 emissions, preliminary studies in the area of genetic improvement in sheep are being carried out. These studies were conducted to observe heritability and repeatability in methane emissions from animals considered to be low and high emitters. The results were 0.30 ± 0.26 for heritability and 0.16 ± 0.10 for repeatability, differing also in relation to concentrate ($17.8 \text{ g kg DMI}^{-1}$, pelleted) and forage based diets (Pinares-Patiño et al., 2011), suggesting that this may be a way to achieve greater mitigation potentials in small ruminant production.

Mitigation strategies on small ruminant production

Global environmental pressures indicate that the reduction of CH_4 emissions from livestock is one of the main factors to guide ruminant production research (Machmüller, 2006). The three main methods of mitigating methane emissions are: 1) nutritional strategies, the most widespread ones; 2) selection of animals by breed or genetics, and intensification of production systems; 3) modification of the ruminal environment (Marino et al., 2016).

In intensive systems, some strategies can be adopted in order to modify the ruminal fermentation pattern, aiming a higher production of

propionate, such as supplementation with food enzymes, addition of acrylate, malate and fumarate, inclusion of organic acids, fat and oils, perform defaunation (McAllister & Newbold, 2008), use of probiotics (Lynch & Martin, 2002), condensed tannins (Waghorn, Jones, Shelton, & McNabb, 1990), and ionophores (Beauchemin, Kreuzer, O'Mara, & McAllister, 2008).

It is known that the type of food ingested by small ruminants directly determines the proportion of SCFAs produced; thus, diets rich in non-fibrous carbohydrates (starch and sugars) result in a higher proportion of propionate during ruminal fermentation. Therefore, CH_4 production tends to be lower in diets with increased levels of concentrate (Moss et al., 2000). In addition, Castillo-González, Burrola-Barraza, Domínguez-Viveros, and Chávez-Martínez (2014) reported that the reduction of ruminal pH, with the presence of concentrate in the diet, has a deleterious effect on protozoa and cellulolytic bacteria, leading to lower production of H_2 .

The addition of enzymes optimizes the fermentation of dietary fibers and is responsible for the reduction of up to 9% in CH_4 production, since the inclusion of lipids leads to a decrease in the population of methanogenic microorganisms (Beauchemin et al., 2008). Commercial ionophores, such as monensin, lasalocid, salinomycin, and tetronasin, passes the single porous membrane of Gram-positive bacteria and interfere with cell energy production. Thus, there is inhibition of H_2 production by these microorganisms (Tedeschi, Callaway, Muir, & Anderson, 2011).

According to Herrero et al. (2016), improving reproductive indices, food availability and average daily gain (ADG) reduce the production cycle and therefore are effective in reducing GHG emissions. Moreover, the same authors estimate that better management practices will reduce GHG emissions by $0.2 \text{ Gt CO}_2\text{-eq}$ by 2050. Accordingly, authors affirm that well-applied pasture management techniques lead to intensified production and to the reduction in CH_4 emissions per kilogram of final product (Andrade et al., 2014; DeRamus, Clement, Giampola, & Dickison, 2003; Savian et al., 2014). Berndt and Tomkins (2013) emphasize that farm management with the objective of mitigation will be observed in the emissions of kg GHG per kg of final product (milk and/or meat), and most probably not in the individual emissions of the animals. Thus, in pastoral systems, the mitigation potential can be achieved mainly by improvements in pasture

management. This strategy is related to the intensification of production such as food supplementation, implantation of the intermittent pasture management system and alternative systems such as crop-livestock integration and silvopastoral systems (Berchielli, Messina, & Canesin, 2012).

However, the real challenge is to find strategies for animals kept in pastures, and these strategies be persistent in their effects. Regardless of the production system, two challenges to achieve mitigation are recurrent. The first is related to the reduction of the CH₄ production per unit of ingested food, or per unit of final product, and for this, it will require the execution of an integrated number of strategies. The second challenge refers to the application of the former strategy, since it will only occur if the profitability exceeds implementation costs (Berndt & Tomkins, 2013). Therefore, the best mitigation strategy should increase profitability of production and/or other livestock products, as well as promote a persistent reduction of methane emissions (Grainger, Williams, Clarke, Wright, & Eckard, 2010).

Regarding genetic improvement, as a tool to mitigate the adverse effects of climate change on animal production, the selection of breeds and individuals seeking high production efficiency, and also animals tolerant to these adverse effects on the wool, meat and milk production are very important strategies (Sejian et al., 2017). They are important since in the current scenario it is commonly reported effects of increase in environmental temperature and reduction in rainfall.

Another point to consider is the balance between CO₂ emissions eq. from animals and their absorption by pasture plants. The potential of soil carbon sequestration in pasture systems may be significantly greater than methane emissions from enteric fermentation or manure management (Berchielli et al., 2012; IPCC, 2014). According to Henderson et al. (2015), adjustments in grazing pressure, allowing the maximization of forage production, can lead to the sequestration of 148.4 Tg of CO₂ per year in pastures worldwide, also indicating that animal emissions can be fully offset by higher gains in carbon sequestration. Thus, when CH₄ emissions were analyzed in experiments on pasture systems, factors such as grazing intensity and their spatial distribution, carbon sequestration of pasture, and the impact of animal production alter and increase the variability of these emissions (Savian et al., 2014).

Despite being a major emitter, livestock farming shows great potential for carbon sequestration through well-managed pastures. The Brazilian national emission is slightly higher than 1 Mg CO₂-eq ha⁻¹, while sequestration can reach 0.78 Mg CO₂-eq ha⁻¹ (Zen, Barioni, Bonato, Almeida, & Ritti, 2008). According to Gerber et al. (2013) carbon sequestration of pastures can significantly offset GHG emissions, with global estimates of approximately 0.6 Gt CO₂-eq year⁻¹. Thus, investment in pasture could increase animal production efficiency and reduce the amount of GHG emitted per kilogram of meat produced, which could reach neutral or even negative carbon balances.

Conclusion

The search for strategies that increase carbon footprint mitigation and animal adaptations to the adverse effects of climate change on small ruminant production systems is very important, since a large part of the world's herd is in regions where animals are exposed to extensive systems and thus subjected to substantial fluctuations in environmental conditions. In all regions of the world, increases in environmental temperature have been reported and predicted, indicating a trend towards a continuous increase for the next 50 years. In this way, the adaptation of animals and production systems to environmental variations and the possible lower input of resources may be fundamental for the sustainability of food production in agroecosystems.

References

- Amaral, G. A., David, D. B., Gere, J. I., Savian, J. V., Kohmann, M. M., Nadin, L. B., ... Carvalho, P. C. F. (2016). Methane emissions from sheep grazing pearl millet (*Penisetum americanum* (L.) Leeke) swards fertilized with increasing nitrogen levels. *Small Ruminant Research*, 141, 118-123.
- Andrade, E. A., Ribeiro-Filho, H. M. N., Liz, D. M., Almeida, J. G. R., Miguel, M. F., Raupp, G. T., ... Almeida, E. X. (2014). Herbage intake, methane emissions and animal performance of steers grazing dwarf elephant grass with or without access to *Arachis pintoi* pastures. *Tropical Grasslands-Forrajes Tropicales*, 2(1), 4-5.
- Animut, G., Puchala, R., Goetsch, A. L., Patra, A. K., Sahl, T., Varel, V. H., & Wells, J. (2008). Methane emission by goats consuming diets with different levels of condensed tannins from lespedeza. *Animal Feed Science and Technology*, 144(3-4), 212-227. doi: 10.1016/j.anifeedsci.2007.10.014

- Anuário da Pecuária Brasileira [ANUALPEC]. (2017). *Anuário da Pecuária Brasileira* (Vol. 1, 20a ed.). São Paulo, SP: Instituto FNP.
- Archimède, H., Rira, M., Eugène, M., Fleury, J., Lastel, M. L., Périacarpin, F., ... Doreau, M. (2018). Intake, total-tract digestibility and methane emissions of Texel and Blackbelly sheep fed C4 and C3 grasses tested simultaneously in a temperate and a tropical area. *Journal of Cleaner Production*, 185, 455-463.
- Barbosa, A. L., Voltolini, T. V., Menezes, D. R., Moraes, S. A., Nascimento, J. C. S., & Rodrigues, R. T. S. (2018). Intake, digestibility, growth performance, and enteric methane emission of Brazilian semiarid non-descript breed goats fed diets with different forage to concentrate ratios. *Tropical Animal Health and Production*, 50(2), 283-289.
- Beauchemin, K. A., Kreuzer, M., O'Mara, F., & McAllister, T. A. (2008). Nutritional management for enteric methane abatement: a review. *Animal Production Science*, 48(2), 21-27.
- Berchielli, T. T., Messana, J. D., & Canesin, R. C. (2012). Produção de metano entérico em pastagens tropicais. *Revista Brasileira de Saúde e Produção Animal*, 13(4), 954-968.
- Berchielli, T. T., Pires, A. V., & Oliveira, S. G. (2011). *Nutrição de Ruminantes*. Jaboticabal, SP: Funep.
- Berndt, A., & Tomkins, N. W. (2013). Measurement and mitigation of methane emissions from beef cattle in tropical grazing systems: a perspective from Australia and Brazil. *Animal*, 7(2), 363-372.
- Bhatta, R., Enishi, O., Yabumoto, Y., Nonaka, I., Takusari, N., Higuchi, K., ... Kurihara, M. (2013). Methane reduction and energy partitioning in goats fed two concentrations of tannin from Mimosa spp. *The Journal of Agricultural Science*, 151(1), 119-128.
- Blaxter, K. L., & Clapperton, J. L. (1965). Prediction of the amount of methane produced by ruminants. *British Journal of Nutrition*, 19(1), 511-522.
- Boval, M., & Dixon, R. M. (2012). The importance of grasslands for animal production and other functions: a review on management and methodological progress in the tropics. *Animal*, 6(5), 748-762.
- Carvalho, P. C. F. (2013). Harry stobbs memorial lecture: can grazing behavior support innovations in grassland management? *Tropical Grasslands-Forrajes Tropicales*, 1(2), 137-155.
- Castillo-González, A. R., Burrola-Barraza, M. E., Domínguez-Viveros, J., & Chávez-Martínez, A. (2014). Microorganismos y fermentación ruminal. *Archivos de medicina veterinaria*, 46(3), 349-361.
- Charmley, E. D., Williams, S. R. O., Moate, P. J., Hegarty, R. S., Herd, R. M., Oddy, V. H., ... Hannah, M. C. (2016). A universal equation to predict methane production of forage-fed cattle in Australia. *Animal Production Science*, 56(3), 169-180.
- Criscioni, P., & Fernández, C. (2016). Effect of rice bran as a replacement for oat grain in energy and nitrogen balance, methane emissions, and milk performance of Murciano-Granadina goats. *Journal of Dairy Science*, 99(1), 280-290.
- Debruyne, S., Ruiz-González, A., Artiles-Ortega, E., Ampe, B., Van Den Broeck, W., Keyser, E., ... Fievez, V. (2018). Supplementing goat kids with coconut medium chain fatty acids in early life influences growth and rumen papillae development until 4 months after supplementation but effects on in vitro methane emissions and the rumen microbiota are transient. *Journal of animal science*, 96(5), 1978-1995.
- DeRamus, H. A., Clement, T. C., Giampola, D. D., & Dickison, P. C. (2003). Methane emissions of beef cattle on forages. *Journal of Environmental Quality*, 32(1), 269-277.
- Food and Agriculture Organization of the United Nations [FAO]. (2016). *Statistical Yearbook* (Vol. 1). Rome, Italy: Food and Agriculture Organization of the United Nations.
- Fernández, C., Espinós, F. J., López, M. C., García-Diego, F. J., & Cervera, C. (2013). Representation of a mathematical model to predict methane output in dairy goats. *Computers and electronics in agriculture*, 91(0), 1-9. doi: 10.1016/j.compag.2012.11.013
- Gerber, P. J., Steinfeld, H., Henderson, B., Mottet, A., Opio, C., Dijkman, J., ... Tempio, G. (2013). *Tackling climate change through livestock: a global assessment of emissions and mitigation opportunities*: Food and Agriculture Organization of the United Nations (FAO).
- Gill, M., Smith, P., & Wilkinson, J. M. (2010). Mitigating climate change: the role of domestic livestock. *Animal*, 4(3), 323-333.
- Goopy, J. P., Donaldson, A., Hegarty, R., Vercoe, P. E., Haynes, F., Barnett, M., & Oddy, V. H. (2014). Low-methane yield sheep have smaller rumens and shorter rumen retention time. *British Journal of Nutrition*, 111(4), 578-585.
- Grainger, C., Williams, R., Clarke, T., Wright, A. D. G., & Eckard, R. J. (2010). Supplementation with whole cottonseed causes long-term reduction of methane emissions from lactating dairy cows offered a forage and cereal grain diet. *Journal of Dairy Science*, 93(6), 2612-2619.
- Hackmann, T. J., & Spain, J. N. (2010). Invited review: ruminant ecology and evolution: perspectives useful to ruminant livestock research and production. *Journal of Dairy Science*, 93(4), 1320-1334.
- Hammond, K. J., Burke, J. L., Koolaard, J. P., Muetzel, S., Pinares-Patiño, C. S., & Waghorn, G. C. (2013). Effects of feed intake on enteric methane emissions

- from sheep fed fresh white clover (*Trifolium repens*) and perennial ryegrass (*Lolium perenne*) forages. *Animal Feed Science and Technology*, 179(1-4), 121-132.
- Hammond, K. J., Pacheco, D., Burke, J. L., Koolaard, J. P., Muetzel, S., & Waghorn, G. C. (2014). The effects of fresh forages and feed intake level on digesta kinetics and enteric methane emissions from sheep. *Animal Feed Science and Technology*, 193, 32-43.
- Henderson, B. B., Gerber, P. J., Hilinski, T. E., Falcucci, A., Ojima, D. S., Salvatore, M., & Conant, R. T. (2015). Greenhouse gas mitigation potential of the world's grazing lands: modeling soil carbon and nitrogen fluxes of mitigation practices. *Agriculture, Ecosystems & Environment*, 207, 91-100.
- Herrero, M., Henderson, B., Havlík, P., Thornton, P. K., Conant, R. T., Smith, P., ... Gill, M. (2016). Greenhouse gas mitigation potentials in the livestock sector. *Nature Climate Change*, 6(5), 452.
- Herrero, M., Thornton, P. K., Kruska, R., & Reid, R. S. (2008). Systems dynamics and the spatial distribution of methane emissions from African domestic ruminants to 2030. *Agriculture, Ecosystems & Environment*, 126(1-2), 122-137.
- Hoque, S. A. M., Islam, M. M., Selim, A. S. M., Ahmed, S., & Rahman, M. M. (2017). Estimation of total methane emission from enteric fermentation of ruminant livestock in Bangladesh. *Asian Journal of Medical and Biological Research*, 3(2), 245-253.
- Ibáñez, C., Criscioni, P., Arriaga, H., Merino, P., Espinós, F. J., & Fernández, C. (2016). Murciano-Granadina goat performance and methane emission after replacing barley grain with fibrous by-products. *PlosOne*, 11(3), e0151215.
- Ibáñez, C., López, M. C., Criscioni, P., & Fernández, C. (2015). Effect of replacing dietary corn with beet pulp on energy partitioning, substrate oxidation and methane production in lactating dairy goats. *Animal Production Science*, 55(1), 56-63.
- Intergovernmental Panel on Climate Change [IPCC]. (2006). *IPCC guidelines for national greenhouse gas inventories*. Kanagawa, JP: Institute for Global Environmental Strategies.
- Intergovernmental Panel on Climate Change [IPCC]. (2007). *The Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Geneva. SW: IPCC.
- Intergovernmental Panel on Climate Change [IPCC]. (2014). *Mitigation of Climate Change. Contribution of Working Group III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. New York, NY: Cambridge University Press.
- Jeong, W. Y., Yi, O. H., Choi, H. J., Nam, K. T., Kim, B. G., & Lee, S. R. (2012). Effects of dietary vegetable oils on intake, digestibility and methane emission from black goats. *Journal of Animal and Veterinary Advances*, 11(24), 4689-4692.
- Johnson, K. A., & Johnson, D. E. (1995). Methane emissions from cattle. *Journal of Animal Science*, 73(8), 2483-2492.
- Kozloski, G. V. (2011). *Bioquímica dos ruminantes* (Vol. 2, 3a ed.). Santa Maria, RS: Universidade Federal de Santa Maria.
- Kurihara, M., Magner, T., Hunter, R. A., & McCrabb, G. J. (1999). Methane production and energy partition of cattle in the tropics. *British Journal of Nutrition*, 81(3), 227-234.
- Lassey, K. R., Ulyatt, M. J., Martin, R. J., Walker, C. F., & Shelton, I. D. (1997). Methane emissions measured directly from grazing livestock in New Zealand. *Atmospheric Environment*, 31(18), 2905-2914.
- Lima, A. R. C., Fernandes, M. H. M. R., Teixeira, I. A. M. A., Frighetto, R. T. S., Bompadre, T. F. V., Biagioli, B., ... Resende, K. T. (2016). Effects of feed restriction and forage: concentrate ratio on digestibility, methane emission, and energy utilization by goats. *Revista Brasileira de Zootecnia*, 45(12), 781-787.
- Lynch, H. A., & Martin, S. A. (2002). Effects of *Saccharomyces cerevisiae* culture and *Saccharomyces cerevisiae* live cells on in vitro mixed ruminal microorganism fermentation. *Journal of Dairy Science*, 85(10), 2603-2608.
- Machmüller, A. (2006). Medium-chain fatty acids and their potential to reduce methanogenesis in domestic ruminants. *Agriculture, Ecosystems & Environment*, 112(2-3), 107-114.
- Ministry of Agriculture and Forestry [MAF]. (2012). *Methane emissions and nitrogen excretion rates for New Zealand goats*. Wellington, NZ: MAF.
- Marino, R., Atzori, A. S., D'Andrea, M., Iovane, G., Trabalza-Marinucci, M., & Rinaldi, L. (2016). Climate change: Production performance, health issues, greenhouse gas emissions and mitigation strategies in sheep and goat farming. *Small Ruminant Research*, 135, 50-59.
- Martin, C., Morgavi, D. P., & Doreau, M. (2010). Methane mitigation in ruminants: from microbe to the farm scale. *Animal*, 4(03), 351-365.
- Martínez-Fernández, G., Abecia, L., Ramos-Morales, E., Martín-García, A. I., Molina-Alcaide, E., & Yáñez-Ruiz, D. R. (2014). Effects of propyl propane thiosulfinate on nutrient utilization, ruminal fermentation, microbial population and methane emissions in goats. *Animal Feed Science and Technology*, 191, 16-25.
- McAllister, T. A., & Newbold, C. J. (2008). Redirecting rumen fermentation to reduce methanogenesis. *Australian Journal of Experimental Agriculture*, 48(2), 7-13.

- Ministério da Ciência, Tecnologia e Inovação [MCTI]. (2014). Estimativas anuais de emissões de gases de efeito estufa no Brasil. Brasília, DF: MCTI.
- Mertens, D. R. (2007). Digestibility and intake. In R. F. Barnes, C. J. Nelson, K. J. Moore, & M. Collins (Eds.), *Forages. The science of grassland agriculture* (6th ed., p. 487-507). Ames, IA: Blackwell Publishing Ltda.
- Miri, V. H., Tyagi, A. K., Ebrahimi, S. H., & Mohini, M. (2013). Effect of cumin (*Cuminum cyminum*) seed extract on milk fatty acid profile and methane emission in lactating goat. *Small Ruminant Research*, 113(1), 66-72.
- Moorby, J. M., Fleming, H. R., Theobald, V. J., & Fraser, M. D. (2015). Can live weight be used as a proxy for enteric methane emissions from pasture-fed sheep?. *Scientific Reports*, 5, 1-9.
- Moss, A. R., Jouany, J.-P., & Newbold, J. (2000). *Methane production by ruminants: its contribution to global warming. Annales de Zootechnie*, 49(3), 231-253.
- Muetzel, S., & Clark, H. (2015). Methane emissions from sheep fed fresh pasture. *New Zealand Journal of Agricultural Research*, 58(4), 472-489.
- Muñoz, C., Yan, T., Wills, D. A., Murray, S., & Gordon, A. W. (2012). Comparison of the sulfur hexafluoride tracer and respiration chamber techniques for estimating methane emissions and correction for rectum methane output from dairy cows. *Journal of Dairy Science*, 95(6), 3139-3148.
- Murray, P. J., Moss, A., Lockyer, D. R., & Jarvis, S. C. (1999). A comparison of systems for measuring methane emissions from sheep. *The Journal of Agricultural Science*, 133(4), 439-444.
- Na, Y., Li, D. H., & Lee, S. R. (2017). Effects of dietary forage-to-concentrate ratio on nutrient digestibility and enteric methane production in growing goats (*Capra hircus hircus*) and Sika deer (*Cervus nippon hortulorum*). *Asian-Australasian Journal of Animal Sciences*, 30(7), 967-972.
- Nielsen, M. O., Kiani, A. I., Tejada, E., Chwalibog, A., & Alstrup, L. (2014). Energy metabolism and methane production in llamas, sheep and goats fed high-and low-quality grass-based diets. *Archives of Animal Nutrition*, 68(3), 171-185.
- Opio, C., Gerber, P., Mottet, A., Falcucci, A., Tempio, G., MacLeod, M., ... Steinfeld, H. (2013). *Greenhouse gas emissions from ruminant supply chains—A global life cycle assessment*. Rome, IT: FAO.
- Patra, A. K. (2014). Trends and projected estimates of GHG emissions from Indian livestock in comparisons with GHG emissions from world and developing countries. *Asian-Australasian journal of Animal Sciences*, 27(4), 592-599.
- Patra, A. K., & Lalhriatpuii, M. (2016). Development of statistical models for prediction of enteric methane emission from goats using nutrient composition and intake variables. *Agriculture, Ecosystems & Environment*, 215, 89-99.
- Pelchen, A., & Peters, K. J. (1998). Methane emissions from sheep. *Small Ruminant Research*, 27(2), 137-150.
- Pinares-Patiño, C. S., Lassey, K. R., Martin, R. J., Molano, G., Fernandez, M., MacLean, S., ... Clark, H. (2011). Assessment of the sulphur hexafluoride (SF₆) tracer technique using respiration chambers for estimation of methane emissions from sheep. *Animal Feed Science and Technology*, 166, 201-209.
- Salem, H. B. (2010). Nutritional management to improve sheep and goat performances in semiarid regions. *Revista Brasileira de Zootecnia*, 39, 337-347.
- Savian, J. V., Neto, A. B., de David, D. B., Bremm, C., Schons, R. M. T., Genro, T. C. M., ... Bayer, C. (2014). Grazing intensity and stocking methods on animal production and methane emission by grazing sheep: Implications for integrated crop-livestock system. *Agriculture, Ecosystems & Environment*, 190, 112-119.
- Savian, J. V., Schons, R. M. T., Marchi, D. E., Freitas, T. S., Silva Neto, G. F., Mezzalana, J. C., ... Carvalho, P. C. F. (2018). Rotatinoous stocking: A grazing management innovation that has high potential to mitigate methane emissions by sheep. *Journal of Cleaner Production*, 186, 602-608.
- Sejian, V., Bhatta, R., Gaughan, J., Malik, P. K., Naqvi, S. M. K., & Lal, R. (2017). *Sheep Production Adapting to Climate Change*. Singapore, SG: Springer.
- Skuce, P. J., Morgan, E. R., Van Dijk, J., & Mitchell, M. (2013). Animal health aspects of adaptation to climate change: beating the heat and parasites in a warming Europe. *Animal*, 7(s2), 333-345.
- Sun, X. Z., Hoskin, S. O., Muetzel, S., Molano, G., & Clark, H. (2011). Effects of forage chicory (*Cichorium intybus*) and perennial ryegrass (*Lolium perenne*) on methane emissions in vitro and from sheep. *Animal Feed Science and Technology*, 166, 391-397.
- Tavendale, M. H., Meagher, L. P., Pacheco, D., Walker, N., Attwood, G. T., & Sivakumaran, S. (2005). Methane production from in vitro rumen incubations with *Lotus pedunculatus* and *Medicago sativa*, and effects of extractable condensed tannin fractions on methanogenesis. *Animal Feed Science and Technology*, 123-124, 403-419. doi: 10.1016/j.anifeeds.2005.04.037
- Tedeschi, L. O., Callaway, T. R., Muir, J. P., & Anderson, R. C. (2011). Potential environmental benefits of feed additives and other strategies for ruminant production. *Revista Brasileira de Zootecnia*, 40, 291-309.
- Ulyatt, M. J., Lassey, K. R., Shelton, I. D., & Walker, C. F. (2002). Methane emission from dairy cows and wether sheep fed subtropical grass dominant pastures in

- midsummer in New Zealand. *New Zealand Journal of Agricultural Research*, 45(4), 227-234.
- Van Soest, P. J. (1994). *Nutritional ecology of the ruminant* (Vol. 1). Ithaca, NY: Cornell University Press.
- Vermorel, M., Jouany, J. P., Eugène, M., Sauvant, D., Noblet, J., & Dourmad, J.-Y. (2008). Evaluation quantitative des émissions de méthane entérique par les animaux d'élevage en 2007 en France. *INRA - Productions Animales*, 21(5), 403-418.
- Waghorn, G., Jones, W., Shelton, I., & McNabb, W. (1990). *Condensed tannins and the nutritive value of herbage*. Proceedings of the New Zealand Grassland Association, 51, 171-176.
- Yang, C. J., Mao, S. Y., Long, L. M., & Zhu, W. Y. (2012). Effect of disodium fumarate on microbial abundance, ruminal fermentation and methane emission in goats under different forage: concentrate ratios. *Animal*, 6(11), 1788-1794.
- Zen, S., Barioni, L. G., Bonato, D. B. B., Almeida, M. H. S. P., & Ritti, T. F. (2008). *Pecuária de corte brasileira: impactos ambientais e emissões de gases efeito estufa (GEE)*. Piracicaba, SP: Esalq/Cepea.
- Zhai, X., Lu, T., Tang, S., Liu, X., Ma, X., Han, G., ... Wang, C. (2015). Methane emission from sheep respiration and sheepfolds during the grazing season in a desert grassland. *The Open Atmospheric Science Journal*, 9(1), 23-28.
- Zhao, Y. G., O'Connell, N. E., & Yan, T. (2016). Prediction of enteric methane emissions from sheep offered fresh perennial ryegrass (*Lolium perenne*) using data measured in indirect open-circuit respiration chambers. *Journal of Animal Science*, 94(6), 2425-2435.

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