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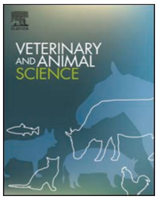

Effect of tannins from tropical plants on methane production from ruminants: A systematic review

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ABSTRACT

Methane (CH_4) is a greenhouse gas generated during the feed fermentation processes in the rumen. However, numerous studies have been conducted to determine the capacity of plant secondary metabolites to enhance ruminal fermentation and decrease CH_4 production, especially those plants rich in tannins. This review conducted a descriptive analysis and meta-analysis of the use of tannin-rich plants in tropical regions to mitigate CH_4 production from livestock. The aim of this study was to analyse the effect of tannins supplementation in tropical plants on CH_4 production in ruminants using a meta-analytic approach and the effect on microbial population. Sources of heterogeneity were explored using a meta-regression analysis. Final database was integrated by a total of 14 trials. The 'meta' package in R statistical software was used to conduct the meta-analyses. The covariates defined *a priori* in the current meta-regression were inclusion level, species (sheep, beef cattle, dairy cattle, and cross-bred heifers) and plant. Results showed that supplementation with tropical plants with tannin contents have the greatest effects on CH_4 mitigation . A negative relationship was observed between the level of inclusion and CH_4 emission (−0.09), which means that the effect of CH_4 mitigation is increasing as the level of tannin inclusion is higher. Therefore, less CH_4 production will be obtained when supplementing tropical plants in the diet with a high dose of tannins.

1. Introduction

A major problem facing our world today is climate change caused by the emission of greenhouse gases (GHG) of anthropogenic activity (Cardona-Iglesias, Mahecha-Ledesma, and Angulo-Arizala, 2016). Overall, livestock contributes to 14–15% of the anthropogenic GHG emissions, and ruminants are responsible for two-thirds of this production (FAO, 2013; Gerber et al., 2013). These GHG could be methane (CH_4), carbon dioxide (CO_2), and nitrous oxide (NO_2) which are major contributors to global warming (Ugbogu et al., 2019). In particular, ruminants produce around 115 million tons of CH_4 per year, a gas generated from rumen fermentation, carried out by a microbial complex of bacteria, archaea, protozoa and fungi, called "ruminal microbiota" (Sandoval-Pelcastre, Ramírez-Mella, Rodríguez-Ávila, & Candelaria-Martínez, 2020).

Because CH_4 has a global warming effect 23 times greater than CO_2 (Ugbogu et al., 2019), the increase in global temperature is having effects on many species of animals and plants. These effects will increase in the coming years, causing crops and fodder to be affected by extreme weather (Olesen and Bindi, 2002). In the search for solutions to reduce

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GHG emissions, the use of tropical plants with anti-methanogenic potential has been suggested (Canul-Solis et al., 2020; Jayanegara et al., 2020; Ku-Vera et al., 2020a,b; Rivera et al., 2015). However, due to the great diversity of tropical plant species with an anti-methanogenic effect, more research is needed in order to assess which ones have major impact on CH_4 emissions and the amount whereby the need to be included in the diet (Sandoval-Pelcastre, Ramírez-Mella, Rodríguez-Ávila, & Candelaria-Martínez, 2020). Ruminant production systems in the tropics and subtropical areas are characterized by grazing native and introduced grasses varying in quantity and quality throughout the year (Becholie, Tamir, Terrill, Singh, and Kassa, 2005). Tropical trees (TT) as *Leucaena leucocephala, Acacia pennatula, Enterolobium cyclocarpum, Gliricidia sepium* may contribute to an improvement in ruminants' feeding due to their high nutritive value (Topps, 1992). Furthermore, TT contain a range of plant secondary metabolites (PSM) (Montoya-Flores et al., 2020; Piñeiro-Vázques et al., 2018), which could alter rumen fermentation and consequently reduce CH_4 emissions (El-Zaiat et al., 2020; Piñeiro-Vázques et al., 2018).

Tannins are containing into the PSM, and reduce methane due to their inhibitory effect on methanogens, protozoa and other hydrogen-producing microbes (Patra and Saxena, 2010; Tavendale et al., 2005). Temperate climate plants, rich in tannins such as *Lotus pedunculatus*, have been shown to reduce methane production up to 30% (Woodward, Waghorn, and Laboyrie, 2004) and can replace other forages in the diet. Therefore, the objective of this review and meta-analysis is to show the main tropical tannin plants that can be used as natural additives for mitigation of CH_4 emissions in ruminants.

2. Controlling rumen-level methane production

Reducing the output of CH_4 generated by ruminal fermentation is a great challenge for nutritionists. In fact, the digestive system of ruminants has evolved over the years to use cellulose and polysaccharides by means of a pre-gastric fermentation system that produces CH_4, however, this system represents a disadvantage for the environment in terms of contamination (Gill, Smith, and Wilkinson, 2010). On the other hand, the level of CH_4 yield emitted by ruminant animals related to the amount of feed intake (Monteny, Bannink, and Chadwick, 2006). This means that, although CH_4 yield levels increase directly with feed intake (Benchaar, Pomar, and Chiquette, 2001). It is important to consider, that not all feed ingredients will ferment in the same way in the rumen, as different amounts of CH_4/unit of fermented carbohydrate are produced. Within concentrate feeding, soluble sugars will produce more CH_4 than starch per MJ of GE intake, so replacing sugars with starch in concentrated feeds will decrease CH_4 by 15%, as well as the emission of other gases into the environment (Mills et al., 2001). Most studies on dairy cows have reported that increasing the proportion of concentrate in the diet increases milk production since feed digestibility is improved; however, these studies were conducted with cows that produce more than 20 kg of milk per day in temperate climates (Olijhoek et al., 2018; Yan et al., 2010). However, Robles-Jimenez et al. (2021) reported that crossbred F1 dual-purpose cows (½ *Bos taurus* – ½ *Bos indicus*) grazing in tropical systems and supplemented with 150 – 450 g of concentrate per kg of daily milk production did not improve milk yield but increased CH_4 and N_2O production per cow as the concentrate increased in the diet, which agrees with Lawrence, O'Donovan, Boland, Lewis, and Kennedy (2015) and Dale, McGettrick, Gordon, and Ferris (2015).

Another aspect to consider is to know that, in diets rich in concentrates, the ruminal pH decreases (this is due to the yield of a large amount of volatile fatty acids, VFA), which facilitates the production of more propionate, acting as a sink for H_2 and, consequently, producing less CH_4/unit organic matter fermented (OMF) in the rumen (Monteny et al., 2006). A second approach aims to reduce the production of CH_4 by using ingredients or additives specifically intended for that purpose. The function of these ingredients is to directly or indirectly inhibit the process of methanogenesis. Some PSM and plant extracts are included in this category as main secondary compounds that directly inhibit methanogens (García-González, González, and López, 2010).

3. Effect of secondary plant metabolites on CH_4 emission

Due to their availability, TT and fodder is often the main ingredient in the diet of animals in tropical and subtropical regions of the world (Ayasan, Cetinkaya, Aykanat, and Celik, 2020; Canul-Solis et al., 2020; Schultze-Kraft et al., 2018). Feed ingredients (tree foliage, grasses, and legumes) from these regions differs from those from temperate regions, due to their structure, chemical composition and digestibility (Assoumaya, Sauvant, and Archimède, 2007). Phytochemicals, circumscribed but appropriately chosen (primarily PSM) are attractive because they are naturally produced by plants and can be include it in feed rations. However, forages from tropical regions may contain secondary metabolites that can alter rumen methanogenesis, decreasing the CH_4 yield (Bodas et al., 2012; Canul-Solis et al., 2020; Jouany and Morgavi, 2007; Vélez-Terranova, Campos-Gaona, and Sánchez-Guerrero, 2014). Ruminants fed tropical forage and pasture have been reported to produce more enteric CH_4 than ruminants fed temperate forage and pastures under different climatic conditions (Ku-Vera et al., 2020b), because in each climatic region the chemical composition and content of PSM will vary. It should be noted that while the IPCC (2006) provides default values for emission calculations (i.e., Ym 6.5%), which are used in most publications, it also specifies that emission factors need to be precise and validated in each country (Van Lingen et al., 2019). In this sense the values of Ym change (Ym 0.54% of energy intake) under tropical conditions as well as the type of animaĺs genetics used in this region (Montoya-Flores et al., 2020).

4. Tannin chemistry

Tannins are natural chemical substances that belong to the group of PSM and are produced by plants in their intermediate metabolism. Plant secondary metabolites play a role of protection from herbivores, pests and pathogens. Secondary metabolites prevent toxicity and act as precursors to physical defence systems (Bennett and and Wallsgrove, 1994).

Tannins are polyphenolic compounds of high molecular weight and are able to precipitate protein (Patra and Saxena, 2009). Tannins found in plants are presented as condensed tannins (CT) and hydrolysable tannins (HT) and both vary between fodders (Naumann, Tedeschi, Zeller, and Huntley, 2017).

Due to their lower risk of toxicity for the animal, anti-methanogenic activity has been studied mainly for CT-rich plants or extracts than HT (Beauchemin, Kreuzer, O'Mara, and McAllister, 2008), However, there are few studies related to the addition of tropical plants containing tannins and their antimethanogenic effect. These polyphenolic compounds chemically have variable molecular weights and the ability to bind to natural polymers such as proteins and carbohydrates, and are found in the wood, bark, fruits, flowers, nuts, leaves, and roots of most plant species (Min et al., 2020; Mueller-Harvey, 2006; Ortiz-Domínguez, Posada, & Noguera, 2014). Compared to tropical plants, temperate climate plants such as *Lotus pedunculatus*, which are rich in tannins, have also been shown to reduce CH_4 excretion by up to 30% (Woodward et al., 2004) and can replace the use of other forages in the diet.

In this way, knowing the plants, tree foliage, legumes and other natural resources with high potential in the mitigation of CH_4 would be beneficial for environment protection. However, what is currently known is that these substances are antimicrobial compounds that have the ability to inhibit abundance of some ruminal microorganisms. This is because they have bactericidal or bacteriostatic activities, which prevent growth or activity of methanogens in the rumen, which is due to the binding of microbial cell proteins and enzymes (Liu, Vaddella, and Zhou, 2011; Tavendale et al., 2005). The challenge in ruminant nutrition is to implement the use of these natural resources with high tannin content in arid and subtropical areas, since in production systems where it is possible to use these supplements, today is a viable alternative to reduce environmental pollution. Furthermore, most of the research published today on the use of tannins shows positive results (Albores-Moreno et al., 2018; Alves, Dall-Orsoletta, and Ribeiro-Filho, 2017).

5. Effect of tannins on rumen microbial population

The diet has been reported as a predominant factor affecting the microbial community composition in the rumen on the host and the rumen environment (Henderson et al., 2015). Therefore, when PSM are included in the feed, they alter the availability of nutrients and metabolites and/or inhibit ruminal microbial metabolism of bacteria, protozoa, fungi and archea populations (Bodas et al., 2012; Henderson et al., 2015; Vasta et al., 2019).

5.1. Effect of tannins on rumen bacteria and methanogens

The high molecular weight and polyphenolic nature of tannins result in the formation of complexes with microbial enzymes or cell walls. Thus, the exerted activity may cause the inhibition of cellulolytic or proteolytic bacteria or methanogens (Mannelli et al., 2019; McSweeney, Palmer, Bunch, and Krause, 2001). The mode of action of tannins is strictly dependant on their chemical structure as well as the bacteria species (Vasta et al., 2019). Condensed tannins (CT) were recognized to have a stronger binding with nutrients than hydrolysed tannins (HT), mainly due to the fact they have a higher grade of polymerization, which makes their degradation in the rumen environment more difficult (Jayanegara, Goel, Makkar, and Becker, 2015). On the contrary, HT have been reported to have a greater protein precipitation capacity that has been related to higher biological activity and a higher methane mitigation capacity in comparison to CT. Additionally, the HT activity may be enhanced by the direct toxic methanogenic activity exerted by HT fractions, produced as a consequence of HT degradation by rumen microorganism enzymes, i.e. tannase (Bhat, Singh, and Sharma, 1998; Jayanegara et al., 2015).

The CT have been proposed to directly inhibit some ruminal gram-positive specialized fibrolytic bacteria (*Fibrobacter succinogenes, Ruminococcus albus, Ruminococcus flavefaciens, Butyrivrio proteoclasticus*) in an in vivo study with fistulated ewes (Costa et al., 2018). In another study, *Fibrobacter succinogenes* and total methanogens population inhibition (up to 36%), have been reported in vitro, either supplementing CT or HT (Jayanegara et al., 2015).

Salami et al. (2018), included 4% of either CT (*Mimosa pudica, Uncaria gambir*) or HT (*Castanea* sp.*, Caesalpinia spinosa*) in lambs' diet, and did not observe a difference in absolute abundance of bacteria and fungi, while methanogens (−12%) abundance decreased similarly with both types of tannins. In a recent in vitro study, the same concentration of chestnut tannins (HT) was fermented, and methane produced was reduced by 12.5% compared to control, while acetate production increased (Cappucci et al., 2021). Goel and Makkar (2012) suggested that HT directly inhibit methanogens activity, and, therefore, they might affect less fibre digestibility, which can be compromised by the inclusion of CT in the diet. Tavendale et al. (2005) evaluated in broth culture the growth and methane production of t*Methanobrevibacter ruminantium* testing either polymeric or oligomeric CT fractions from *Lotus pedunculatus*. The polymeric CT fractions were the only effective in inhibiting the growth, thus demonstrating the importance of PSM chemical structure and synergistic effect of all components to directly inhibiting methanogens along with other rumen microorganism activities (Mannelli et al., 2019). The reduction of fibre digestibility, when CT sources were included in the diet, was thereby supported by the reduction of total VFA production mainly explained by the reduction of acetate production, as evaluated in sheep fed with an inclusion of 16 g/Kg dry matter (DM) intake of quebracho extract (Buccioni et al., 2015). However, total VFA production was not impaired with a level of tannins inclusion less of than 2 g/Kg DM (Table 1). This low dosage might be not always sufficient to achieve a methane mitigating effect. Hence, a dosage above 20 g/Kg of tannins has been proposed by Jayanegara, Leiber, and Kreuzer (2012). In accordance with Salami et al. (2018) both HT and CT extracts could impact the ruminal microbiome when supplemented at moderate levels (<50 g/Kg DM, Mueller-Harvey, 2006), but their detrimental effect on fibrolytic bacteria should be considered when animals are fed with high-fibre diets. The contrasting results concerning rumen fermentation traits, microbial population, and methane production can be at least partially explained by the heterogeneity of tannin chemical structures from plants, the various dosages intake and the feeding regimen (Patra and Saxena, 2011; Vasta et al., 2019). Moreover, microbial adaptation to tannins might occur through mechanisms of some bacteria such as the formation of protective exopolysaccharide layer around the cells, degradation of tannins, and modification of cell membrane (Patra and Saxena, 2011).

5.2. Effect of tannins on rumen protozoa

The antiprotozoal activity of some PSM might be relevant since methanogens colonizing ciliate protozoa were suggested to be responsible for 9 – 25% of methanogenesis in rumen fluid (Henderson et al., 2015; Newbold, Lassalas, and Jouany, 1995). The antiprotozoal activity of tannins is contrasting, and Patra and Saxena (2009) suggested that the effect is plant dependant, having the tannin structure-activity relationship a major role in the mechanism of action (Mueller-Harvey, 2006). HT have been proposed to permeate through protozoa membranes, thus compromising methanogens associations (Patra and Saxena, 2011). In the study by Malik et al. (2017), male sheep diets were supplemented with tanniniferous tropical tree leaves (*Ficus benghalensis, Artocarpus heterophyllus* and *Azadirachta indica*) containing 7.1–10.8 g/Kg DM of CT. The digestibility was not compromised, whereas methane production was reduced (up to 26%). The authors suggested that methane reduction can be explained by the decrease of protozoa number (−23%). Moreover, CT appeared to affect *Entodinimorphs* protozoa more than *Holotrichs* protozoa (Malik et al., 2017). A similar reduction of protozoa number (−21%) was reported by Salami et al. (2018), including 4% of both CT (mimosa, gambier) or HT (chestnut, tara) in lamb's diet. However, other studies conducted *in vivo* and reported in Table 2 showed that methane reduction was not always related to a decrease of protozoa number.

6. Effect of tannins on CH4 emission

6.1. In vitro studies

The inclusion of tannins directly from plants or as plant extracts, in ruminant diets, has been showed to decrease CH_4 above 20 g/kg (Jayanegara et al., 2011). In this sense, Goel and Makkar (2012) reported that CH_4 synthesis from ruminal fermentation has been reduced by to 50% in response to tannin or plant extracts containing these polyphenolic compounds (Patra and Saxena, 2010). Authors who conducted experiments on plants with high tannin content (Molina-Botero et al., 2019; Morgavi, Martin, Jouany, and Ranilla, 2012; Patra and Saxena, 2011; Tavendale et al., 2005) agreed that tannin plants reduce CH_4 production due to their antimicrobial properties, for example, Jayanegara et al. (2015) found that all tannins decreased CH_4 concentration in a linear or quadratic manner, and they also reported that the magnitude of the decrease was greater for plants containing hydrolysable tannins than for those plants rich in condensed tannins. The mode of action and the effects that tannins have on the animal will continue to be the subject of research. Reduction of nematode egg excretion and worm burden have been also reported in small ruminants fed with tanniferous plants (Birhan, Gesses, Kenubih, Dejene, and Yayeh, 2020; Marley, Cook, Keatinge, Barrett, and Lampikin, 2003; Mengistu et al., 2017; Minho, Filippsen, Amarte, & Abdalla, 2010;

Table 1
Effect of dietary tannins on methane production and other major effects *in vitro* and *in vivo* studies.

Plant	Dosage	Trial type	Unit	Methane reduction potential (% of control)	Other major effects reported	References
Acacia tannins	50 g/kg DM	*In vitro*	mL/ 24h	15%	−11% of total VFA	Staerfl, Kreuzer, and Soliva, 2010
Chestnut and sumarch (HT) and mimosa and quebracho (CT)	1 g/L	*In vitro*	mL/ L	3% CT 7% HT	−14% CT and −5.8% HT of total VFA	Jayanegara et al., 2015
Chestnut leaves	~24 mg/g DM of HT tannin	*in vitro*	mL/ 24h	28%	−13% total VFA	Terranova, Kreuzer, Braun, and Schwarm, 2018
CT from leaves of Gliricidia sepium, Leucaena leucocephala, and Manihot esculenta.	0, 0.25, 0.5, 0.75, and 1.0 g CT/Kg, respectively	*In vitro* and *in vivo* (rumen-cannulated sheep)	mL/ 24h	Up to 22% (in vitro)	Up to −25% (in vitro) of total VFA No effect on Methanogens population (in vivo)	Rira et al., 2015
Vaccinium vitis idaea	140 g of extract containing 2 g of tannins/kg DM	*In vivo* (Polish Holstein-Friesian dairy)	mM	8%	−46% rumen NH_3 −35% Protozoa −21% Methanogens No effect on total VFA	Cieslak, Zmora, Pers-Kamczyc, and Szumacher-Strabel, 2012
Acacia mearnsii tannin extract	7 g/Kg DMI	*In vivo* (dairy cows)	g/ day	32%	No effect on milk production	Alves et al., 2017
Chestnut or Chestnut+Quebracho tannin extract	1.5 g/Kg	*In vivo* (crossbred steers)	g/ day	No effect	No effect on Protozoa population No effect on total VFA production	Aboagye et al., 2018

CT, Condensed tannins; HT, Hydrolysable tannins; VFA, Volatile Fatty Acids.

Table 2
Effect of dietary tropical taniferous plants on methane production in vivo studies.

Plant	CT (g kg^{-1} of DM)[1]	Doses (g kg^{-1} of DM)	Species	CH_4 Production	% CH_4 reduction[2]	Effect on microbial population	References
Leucaena leucocephala	2.70, 8.20 and 12.30	120, 240 and 360	Crossbred heifers	162.9, 154.8 and 140.00 g/d^{-1}	6.49, 11.14 and 19.64	No changes in Protozoa, Bacteria and Methanogens counts	Montoya-Flores et al. (2020)
Samanea saman + *Pennisetum purpureum*	1.20, 2.40 and 3.60	900, 935 and 965	Crossbred heifers	89.63, 72.03 and 59.30 L/d^{-1}	25.83, 40.40 and 50.93	No changes in Protozoa count	(Valencia-Salazar et al., 2017)
Leucaena leucocephala	21.00 in all doses	200, 400, 600 and 800	Crossbred heifers	101.20, 87.40, 74.90 and 53.50 L/d^{-1}	26.30, 36.35, 45.45 and 61.03	No changes in Protozoa count	Piñeiro-Vázques et al. (2018)
Lolium perenne	-	185	Dairy cattle	260.00 g/d^{-1}	10.34	-	Woodward et al. (2002)
Hedysarum coronarium	2.72	130	Dairy cattle	253.90 g/d^{-1}	15.37	-	Woodward et al. (2002)
Lolium perenne	-	161	Dairy cattle	360.63 g/d^{-1}	10.00	-	Woodward et al. (2004)
Lotus corniculatus	-	121	Dairy cattle	343.24 g/d^{-1}	14.19	-	Woodward et al. (2004)
Sericea lespedeza	153.00	881	Goat	6.30 g/d^{-1}	12.00	Protozoa count increased in the long period	Puchala et al. (2012)
Leucaena leucocephala	40.00	820	Sheep	7.80 g/d^{-1}	25.71		Dias-Moreira et al. (2013)
Styzolobium aterrimum	40.00	690	Sheep	10.40 g/d^{-1}	0.95	-	Dias-Moreira et al. (2013)

[1] CT, Condensed tannins (g kg^{-1} of DM).
[2] % CH_4 reduction compared with the control diet, CT, Condensed tannins ((g kg−1 of DM)),.

Naumann et al., 2017; Oliveira et al., 2011). The inclusion of tropical tanniferous plants *in vitro* studies has been reported (Table 3). For example, Albores-Moreno et al. (2018) reported that supplementation with *Leucaena leucocephala* at a concentration of 950 g/kg DM in an in vitro study on diets for cattle based on *Pennisetum purpureum* grass, is a feeding alternative that can promote greater efficiency and synthesis of microbial biomass, increase the proportions of propionic and butyric acid, and decrease the output of enteric CH_4 up to 15.6 to 31.6%. Rodríguez, Britos, Rodríguez-Romero, and Fondevila (2011) studied the effect of inclusion of plant tanniferous extracts equivalent to 240 mg of *Acacia cornigera* or *Albizia lebbekoides* added to 800 mg *Pennisetum purpureum, A. cornigera,* and *A. lebbekoides and reported that* CH_4 concentration (ml/ml gas) was lower (14 and 7%, respectively) than *Pennisetum Purureaum* as a control after 24 h of incubation. Tan et al. (2011) evaluated the effects of CT from *Leucaena leucocephala* at 15 mg of CT/500 mg DM reducing CH_4 excretion by ~47%, while Carulla, Kreuzer, Machmüller, and Hess (2005) reported that supplementation of 25 g/kg of CT (12.5 mg CT/500 mg DM) from *Acacia mearnsii* in sheep fed ryegrass with a reduction of CH_4 emissions by ~12%. In an in vitro study, Petlum, Paengkoum, Liang, Vasupen, & Paengkoum, 2019 evaluated the inclusion of CTs of a higher molecular weight as *Azadirachta indica*, showing stronger effect than those of a lower molecular weight as *Leucaena leucocephala* on CH_4 excretion. The inclusion of *Siamese neem* suppressed CH_4 output at inclusion levels of 2, 4 or 6 mg/100 g DM,

Table 3
Effect of dietary tropical taniferous plants on methane production *in vitro* studies.

Plant	CT (g kg^{-1} of DM	Doses (g kg^{-1} of DM)	CH_4 Production	% CH_4 reduction [1]	References
Pennisetum purpureum + Neomillspaughia emargiata; P. purpureum + Tabernaemontana amygdalifolia; P. purpureum + Piscidia piscipula; P. purpureum + Leucaena leucocephala; P. + Havardia albicans	*P. p + N. e* = 52.90; *P. p + T. a* = 0.52, *P. p + P. pis*=8.19, *P. p + L. l* = 5.90, *P. p + H. a* = 5.40	950	25.80 – 33.00 L/kg^{-1} of digested DM	12.47 – 31.57	Albores-Moreno et al. (2018)
Pennisetum purpureum + Acacia cornigera; P. purpureum + Albizia lebbekoides; P. purpureum + Leucaena leucocephala	*P. p + A.c* = 19.7; *P.p + A.l* = 88.6; *P.p + L.l* = 66.0	104	0.22 mL	4.35	Rodríguez et al. (2011)
Leucaena leucocephala + Panicum maximum	-	53	5.50 mL/g DM	63.09	Tan et al. (2011)
Acacia mearnsii, Schinopsis balansae, Castanea sativa, Quercus aegilops	*A. m* = 820.00; *S. b* = 904.00; *C. s* = 57.00; *Q. a* = 80.00	200	4.48 – 4.77 mL	36.4 – 40.27	Hassanat and Benchaar (2012)
Delonix regia seed meal	-	6.6, 20 and 30	114.4, 105.4 and 94.1 mL	9.07, 16.22 and 25.20	Supapong et al. (2017)
Digitaria eriantha+ Leucaena leucocephala	4.10	60	5.8 mL/g DM of substrate	42.00	Petlum, Paengkoum, Liang, Vasupen, & Paengkoum, 2019
Digitaria eriantha+ Azadirachta indica A. Juss.	7.90	20, 40 and 60	3.3, 1.7 and 0.01 mL/g DM of substrate	67.00, 83.00 and 99.90	Petlum, Paengkoum, Liang, Vasupen, & Paengkoum, 2019
Desmanthus leptophyllus, Desmanthus virgatus, Desmanthus bicornutus	-	1000	29.8 – 33.6 mL/g OM fermente	11.79 – 21.77	Vandermeulen et al. (2018)
Leucaena leucocephala, Acacia saligna, Atriplex halimus	L.*l* = 67.00; *A.s* = 72.00; *A.h* = 5.3.00	500	9.5 – 9.7 mL / g DM	22.40 – 24.00	El-Zaiat et al. (2020)
Calliandra calothyrsus, Acacia nilotica, Gliricidia sepium, Leucaena leucocephala, Manihot esculenta, Musa spp	*C.c* = 58.20; *A.n* = 73.00; *G.s* = 94.90; L.*l* = 77.80; *M.e* = 88.60; *M.spp* = 84.30	100	1.41 mL/d	64.04	Rira, Morgavi, Popova, Maxin, and Doreau, 2021
Acacia nilotica leave, Acacia nilotica leaves	*A.n.l* = 80.00; *A.n.p* = 157.00	25, 50, 75, 100	1.41 mL/d	64.04	Rira et al., 2019
Castanea sativa, Schinopsis lorentzii	53.80	15 and 30	54.70 mL/ g DM	44.40	Menci et al., 2021
Arachis pintoi, Cratylia argéntea, Calliandra calothyrsus	29.00	200	0.78 g/d	50.31	Hess et al., 2003
Brachiaria humidicola, Vigna unguiculata, Calliandra calothyrsus, Flemingia macrophylla	-	15	13.00 mL/d	80.92	Tiemann et al., 2008

[1] % CH_4 reduction compared with the control diet.

while supplementation of *Leucaena* leaves showed reductions on CH_4 production at 6 mg/100 mg DM of supplementation. Huang et al. (2010), 2011) suggested that chemical structure and molecular weight of the CTs influenced their efficacy to manipulate rumen fermentation, with specific effect on CH_4 mitigation output. Hassan and Benchaar (2012) added Valonea (*Quercus aegilops*; Nutriad-Adisseo®) extracts as sources of HT, showing that CH_4 excretion reduced up to 11% at 50 g/kg DM. On the other hand, Vandermeulen et al. (2018) evaluated the effect of *Desmanthus* spp. which emitted less CH_4 (mL/g OM incubated) than the reference grass hay at 72 h (*C. gayana*) up to 23%. In vitro studies vary in their response to CH_4 production and that seems to depend on the concentration of CT, which is affected by various management and environmental factors such as nutrient soil composition, light intensity, and temperature (Albores-Moreno et al., 2019; Frutos, Hervas, Giraldez, and Mantecon, 2004; Yang et al., 2018). Thus, we can notice that the differences in the concentrations of CT amongst studies vary with plant species, and geographical locations of plants. It is difficult to extrapolate in vitro to in vivo results, due to the variation between results and doses. Therefore, it is highly recommended to evaluate the effect of the supplementation of tanniferous plants on CH_4 mitigation *in vivo* studies.

7. Meta-analysis: methodology

To quantify the overall effect of the inclusion of tannins on CH_4 emissions in ruminants (*In vivo* studies), a meta-analysis process was carried out. A compressed and structured search of articles was carried out using the search engines Google Scholar, PubMed. Different sets of the following keywords were provided to field experts to integrate the study database: "ruminants", "tropical plants", "secondary metabolites", "tannins", "methane emission", "treatment" (control vs tropical plant), “*in vitro*”, and “*in vivo*”.

Only articles peer reviewed, written in English containing an experimental set up were included in the current literature review. To be considered, the studies must met the following inclusion and exclusion criteria according with Lean, Thompson, and Dunshea (2014): a) studies published in an international peer-reviewed scientific journal, b) specific procedures for random assignment of animals to each treatment (experimental design), c) report minimum means squares and a measure of variability, and c) report the sample size of each group (Fig. 1).

The final database included the publications from 2002 to 2021 and comprised the following information of least squares means, variability measures [standard error of mean (SEM), standard error of differences (SE) or standard deviation (SD)] and number of experimental units for both groups to each output variables, animal species as sheep (*Ovis aries*), goat (*Capra hircus*), cattle (*Bos Taurus and Bos indicus*), beef and dairy cattle and crossbred heifers, plant, dose, CH_4 emission from the control and tannin groups, as well as the number of repetitions. The CH_4 values from *in vitro* studies were homogenized to mL/g DM, g/d, or mL/d. With regard to in vivo studies all were adjusted and expressed in g CH_4/d. Current analysis, random effects models were fitted to estimate the effect size (ES), the 95% confidence interval and the statistical significance of ES for each outcome variable, using the ’meta’ package version 4.6–0 (Schwarzer, Carpenter, & Rücker, 2015) in the R statistic software version 3.3.1 (R Core Team, 2016). The ES was calculated as standardized mean difference (SMD) using the methods described by Hedges (1981) for the fixed effects and by DerSimonian and Laird, (2015) for random effects models. The studies that reported outcome variables in the same unit of measure aid to calculate the raw mean difference (RMD), which permits ES interpretation under original measures units (Appuhamy et al., 2013). The current systematic review analyses studies performed in different places with different methods and under different animal management; hence, the heterogeneity was needed (Higgins, 2008). Heterogeneity of results amongst trials was reported using the I^2 statistic (Higgins & Green, 2011). The I^2 represents the approximate proportion of total variability and indicate estimates that can be attributed to heterogeneity, which was calculates as:

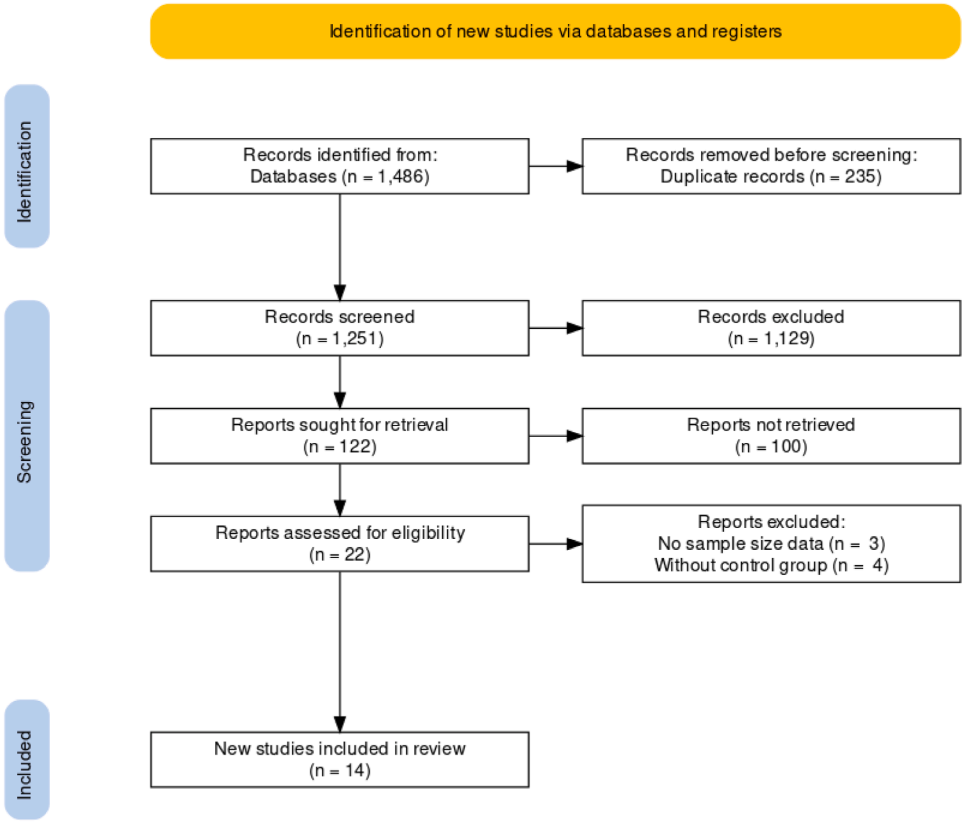
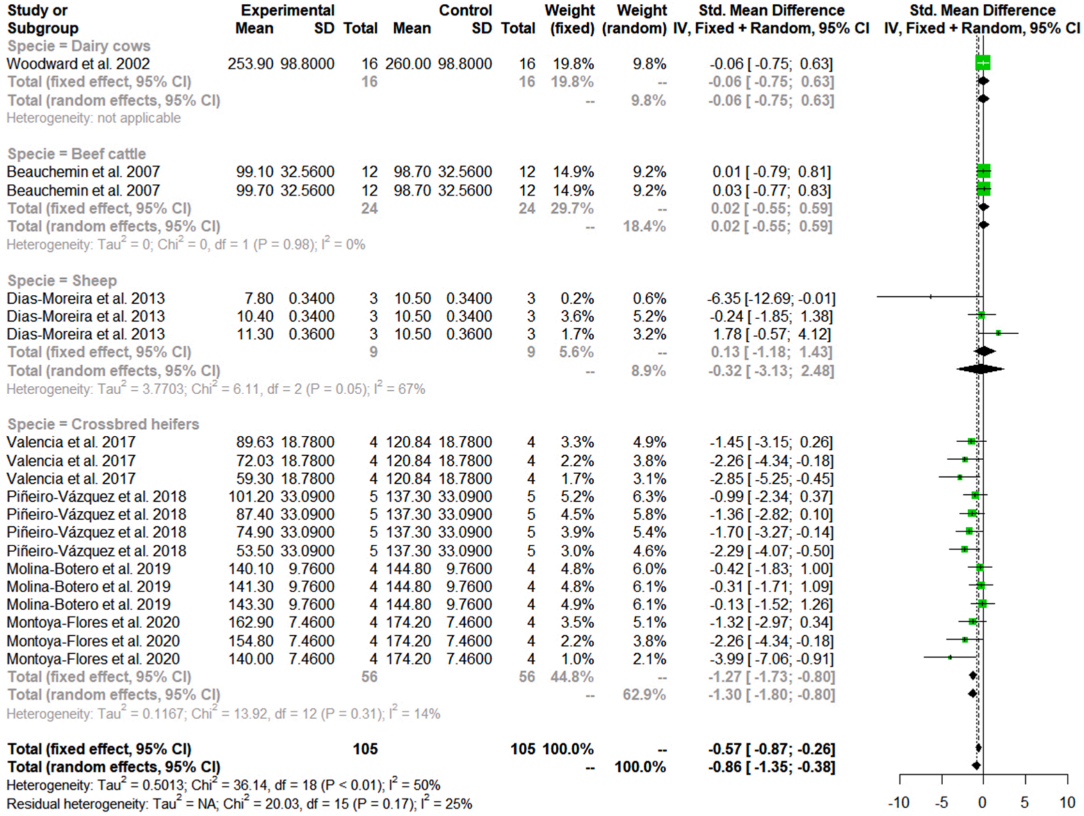


Fig. 1. PRISMA flow diagram of the systematic review from initial search and screening of publications included in the meta-analysis.



Study or Subgroup	Experimental Mean	SD	Total	Control Mean	SD	Total	Weight (fixed)	Weight (random)	Std. Mean Difference IV, Fixed + Random, 95% CI
Specie = Dairy cows									
Woodward et al. 2002	253.90	98.8000	16	260.00	98.8000	16	19.8%	9.8%	-0.06 [-0.75; 0.63]
Total (fixed effect, 95% CI)			16			16	19.8%	--	-0.06 [-0.75; 0.63]
Total (random effects, 95% CI)							--	9.8%	-0.06 [-0.75; 0.63]
Heterogeneity: not applicable									
Specie = Beef cattle									
Beauchemin et al. 2007	99.10	32.5600	12	98.70	32.5600	12	14.9%	9.2%	0.01 [-0.79; 0.81]
Beauchemin et al. 2007	99.70	32.5600	12	98.70	32.5600	12	14.9%	9.2%	0.03 [-0.77; 0.83]
Total (fixed effect, 95% CI)			24			24	29.7%	--	0.02 [-0.55; 0.59]
Total (random effects, 95% CI)							--	18.4%	0.02 [-0.55; 0.59]
Heterogeneity: $Tau^2 = 0$; $Chi^2 = 0$, df = 1 (P = 0.98); $I^2 = 0\%$									
Specie = Sheep									
Dias-Moreira et al. 2013	7.80	0.3400	3	10.50	0.3400	3	0.2%	0.6%	-6.35 [-12.69; -0.01]
Dias-Moreira et al. 2013	10.40	0.3400	3	10.50	0.3400	3	3.6%	5.2%	-0.24 [-1.85; 1.38]
Dias-Moreira et al. 2013	11.30	0.3600	3	10.50	0.3600	3	1.7%	3.2%	1.78 [-0.57; 4.12]
Total (fixed effect, 95% CI)			9			9	5.6%	--	0.13 [-1.18; 1.43]
Total (random effects, 95% CI)							--	8.9%	-0.32 [-3.13; 2.48]
Heterogeneity: $Tau^2 = 3.7703$; $Chi^2 = 6.11$, df = 2 (P = 0.05); $I^2 = 67\%$									
Specie = Crossbred heifers									
Valencia et al. 2017	89.63	18.7800	4	120.84	18.7800	4	3.3%	4.9%	-1.45 [-3.15; 0.26]
Valencia et al. 2017	72.03	18.7800	4	120.84	18.7800	4	2.2%	3.8%	-2.26 [-4.34; -0.18]
Valencia et al. 2017	59.30	18.7800	4	120.84	18.7800	4	1.7%	3.1%	-2.85 [-5.25; -0.45]
Piñeiro-Vázquez et al. 2018	101.20	33.0900	5	137.30	33.0900	5	5.2%	6.3%	-0.99 [-2.34; 0.37]
Piñeiro-Vázquez et al. 2018	87.40	33.0900	5	137.30	33.0900	5	4.5%	5.8%	-1.36 [-2.82; 0.10]
Piñeiro-Vázquez et al. 2018	74.90	33.0900	5	137.30	33.0900	5	3.9%	5.4%	-1.70 [-3.27; -0.14]
Piñeiro-Vázquez et al. 2018	53.50	33.0900	5	137.30	33.0900	5	3.0%	4.6%	-2.29 [-4.07; -0.50]
Molina-Botero et al. 2019	140.10	9.7600	4	144.80	9.7600	4	4.8%	6.0%	-0.42 [-1.83; 1.00]
Molina-Botero et al. 2019	141.30	9.7600	4	144.80	9.7600	4	4.8%	6.1%	-0.31 [-1.71; 1.09]
Molina-Botero et al. 2019	143.30	9.7600	4	144.80	9.7600	4	4.9%	6.1%	-0.13 [-1.52; 1.26]
Montoya-Flores et al. 2020	162.90	7.4600	4	174.20	7.4600	4	3.5%	5.1%	-1.32 [-2.97; 0.34]
Montoya-Flores et al. 2020	154.80	7.4600	4	174.20	7.4600	4	2.2%	3.8%	-2.26 [-4.34; -0.18]
Montoya-Flores et al. 2020	140.00	7.4600	4	174.20	7.4600	4	1.0%	2.1%	-3.99 [-7.06; -0.91]
Total (fixed effect, 95% CI)			56			56	44.8%	--	-1.27 [-1.73; -0.80]
Total (random effects, 95% CI)							--	62.9%	-1.30 [-1.80; -0.80]
Heterogeneity: $Tau^2 = 0.1167$; $Chi^2 = 13.92$, df = 12 (P = 0.31); $I^2 = 14\%$									
Total (fixed effect, 95% CI)			**105**			**105**	**100.0%**	**--**	**-0.57 [-0.87; -0.26]**
Total (random effects, 95% CI)							**--**	**100.0%**	**-0.86 [-1.35; -0.38]**
Heterogeneity: $Tau^2 = 0.5013$; $Chi^2 = 36.14$, df = 18 ($P < 0.01$); $I^2 = 50\%$									
Residual heterogeneity: Tau^2 = NA; $Chi^2 = 20.03$, df = 15 (P = 0.17); $I^2 = 25\%$									

Fig. 2. Forest plot of methane production, expressed as Dry Matter Intake (DMI, g tannins/d) from studies focused on tannins supplementation in ruminants.

$$I^2 = \frac{Q-(k-1)}{Q} \times 100$$

Where Q is the X^2 heterogeneity statistic and K is the number of trials. I^2 values of 25%, 50% and 75% represented small, moderate, and high levels of heterogeneity, respectively. For output variables that showed substantial heterogeneity (I^2>50%), mixed effects regression models (meta-regression analysis) were constructed to explore sources of heterogeneity using the 'metaphor' package (Viechtbauer, 2010). The covariates defined a priori in the current meta-regression were inclusion level, species (*sheep, beef cattle, dairy cattle, and cross-bred heifers*) and plant.

8. Results from meta-analysis

A total of 14 articles were analysed to assess the effect of tannins supplementation on CH_4 emissions of ruminants (Fig. 2). According to the obtained database, two meta-analysis were carried out in the current work. The first meta-analyses assessed the effect of tannins supplementation on CH_4 enteric emission in ruminant using *in vivo* studies (n = 19 trials). *In vivo* technique's database allowed to estimate the raw mean difference (RMD) and standardized mean difference (SMD) because all studies reported the CH_4 emission in the same unit (g/d). The second meta-analysis evaluated the effect of tannins supplementation on CH_4 emissions of overall studies (*in vivo = 19; vitro = 45 trials*). However, because those studies reported CH_4 emission in different units of measurement, only the SMD was estimated (Table 4). In both meta-analyses the values of heterogeneity (I^2) were greater than 25%, therefore the sources of heterogeneity were explored.

8.1. In vivo studies meta-analysis

The *in vivo* studies showed a positive response in mitigating CH_4 emission due to the inclusion of tannins in the diets of ruminants through the feeding of tropical plants (SMD = −0.86; P = 0.005) (Fig. 2). The response to tannin content has a moderate heterogeneity (I^2 = 50.5%) that can be explained by the type of plant offered, level of inclusion and animal species. With regard to the type of animal that was fed *Leucaena leucocephala* and the combination of *Samanea saman* + *Pennisetum purpureum,* showed the greatest mitigation effects of CH_4 according to the meta-regression analysis (Fig. 3, Table 4). The effect of tannins was most evident in heifers with an effect size of −1.3 compared to dairy cows (ES = −0.06), beef cattle (ES = 0.02) and sheep (ES = −0.32) (Fig. 2). Finally, a negative relationship was observed between the level of inclusion of tannins and CH_4 emission (−0.09), by increasing the dose of tannins, the difference between control and treatment increases, although in a negative direction (Fig. 3). This means that, the higher the dose of tannins, the treatment group will emit less CH_4 compared with control, showing differences between the type of plant used, with a rather interesting effect on *Leucaena leucocephala and Samanea saman*, being mostly condensed tannins in ruminant animal production.

Table 4
Standardized mean difference (SMD) and 95% CI of enteric CH_4 emissions of ruminants supplemented with tannins.

Source	Effect size (SMD)	95% CI	
		Lower	Upper
Acacia cornigera	−0.49	−1.92	0.92
Acacia mearnsii	−0.58	−1.24	0.06
Acacia nilotica	−0.76	−5.53	3.9
Albizia lebbekoides	−0.78	−2.26	0.70
Caesalpinia gaumeri	0.15	−0.98	1.28
Calliandra calothyrsus	−0.93	−1.96	0.09
Castanea sativa	−0.67	−1.32	−0.01
Flemingia macrophylla	−2.21	−3.53	−0.89
Gliricidia sepium	−0.13	−2.23	1.96
Havardia albicans	0.21	−0.91	1.35
Hedysarum coronarium	−0.06	−0.75	0.63
Leucaena leucocephala	−1.46	−1.95	−0.97
Manihot esculenta	0.02	−1.93	1.99
Mimosa caesalpiniaefolia	1.77	−0.56	4.12
Musa spp	−0.88	−6.28	4.50
Neomillspaughia emargiata	0.04	−1.08	1.17
Piscidia piscipula	−0.03	−1.16	1.09
Quercus aegilops	−0.50	−1.15	0.14
Samanea saman	−2.02	−3.17	−0.86
Schinopsis balansae	−0.54	−1.20	0.10
Schinopsis lorentzii	−3.31	−6.88	0.26
Schinopsis quebracho	0.021	−0.54	0.58
Styzolobium aterrimum	−0.23	−1.85	1.38
Tabernaemontana amygdalifolia	−0.12	−1.26	1.00
Vigna unguiculata	2.07	0.79	3.32
Gliricidia sepium+Enterolobium cyclocarpum+Brachiaria brizantha sepium	−0.28	−1.09	0.52

SMD is the standardized mean difference estimated of the random model.

8.2. Overall meta-analysis

The global response of tannins supplementation in ruminants (*in vivo* and *in vitro* studies) when all available studies where analysed depicts a SMD of −0.60 to the random effect model. The heterogeneity was considerably lower than overall meta-analysis (I^2 = 27%) in comparison with the meta-analysis of *in vivo* studies (I^2 = 50%). Sub-group analysis revealed differences of tannins supplementation response according with the measure technique of CH_4 emission. The effect size of *in vitro* studies was lower (−0.51; 95% CI −0.76 – −0.26) compared with *in vivo* studies (−0.86; 95% CI −1.35 – −0.38) (Fig. 4). With regard to sources of tannins (Table 4), the highest mitigation response was observed in *Flemingia macrophylla* (−2.21; 95% CI −3.53 – −0.89) followed by *Samanea saman* (−2.02; 95% CI −3.17 – −0.86) and *Leucaena leucocephala* (−1.46; 95% CI −1.95 – −0.97). The studies that supplemented *Schinopsis lorentzii* showed a higher effect size (−3.31; 95% CI −6.88 – −0.26), however the confidence intervals were wide and included zero value.

9. Discussion from meta-analysis

The combination of *Samanea saman* and *Pennisetum purpureum* (Valencia-Salazar et al., 2017) in cattle diets have been shown to contribute to the reduction of CH_4 up to 50.9% (Table 2), showing the greatest mitigation effects of CH_4 according to the results of the meta-regression analysis. On the other hand, in an *in vivo* study with lambs, Dias-Moreira et al. (2013) evaluated the effect of three forages, *Leucaena leucocephala, Styzolobium terrimum* and *Mimosa caesalpiniaefolia* , reporting that with the use of *Leucaena leucocephala* there is a greater reduction in CH_4 emissions (~25%). El-Zaiat et al. (2020) carried out *in vitro* and *in vivo* studies on sheep (Table 3), confirming that in the *in vitro* study, the supplementation of *Leucaena leucocephala, Atriplex halimus* or *Acacia saligna* to the diet (50/50) reduced CH_4 output to almost 23% compared with the control group, and in the *in vivo* study in sheep diets, showed reductions of 11.45% in the CH_4 production. Tiemann et al. (2008) in an *in vitro* study found an 80% reduction of CH_4 by including *Flemingia macrophyla*, followed by *Leucaena leucocephala* with variations in CH_4 reduction (30–60%) in vitro studies (Table 3), which may be due to the different levels of inclusion, which coincided with our results (Table 4).

Ku-Vera et al. (2020a) confirmed that the use of *Leucaena leucocephala* in beef cattle has a mitigating effect on CH_4 when fed at levels of up to 30–35% DM. Furthermore, Ku-Vera et al. (2020a) mentioned that the legume *Samanea saman* which contains saponins, has demonstrated to have a mitigating effect on enteric CH_4 in cattle and sheep housed in respiration chambers, since saponins break the membrane of the rumen protozoa thus decreasing the number of methanogenic protozoa and archaea. This result of the use of tropical plants was confirmed by Ku-Vera et al. (2020b) who, by incorporating ground foliage and pods

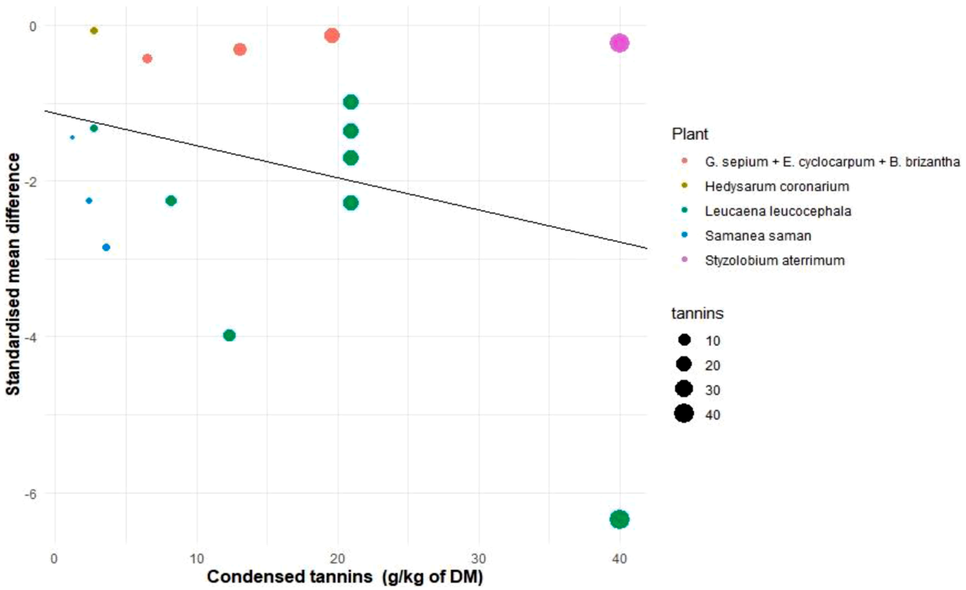


Fig. 3. Relationship between the level of inclusion of tannins (g/kg dry matter intake) from tropical plants and methane production in ruminants.

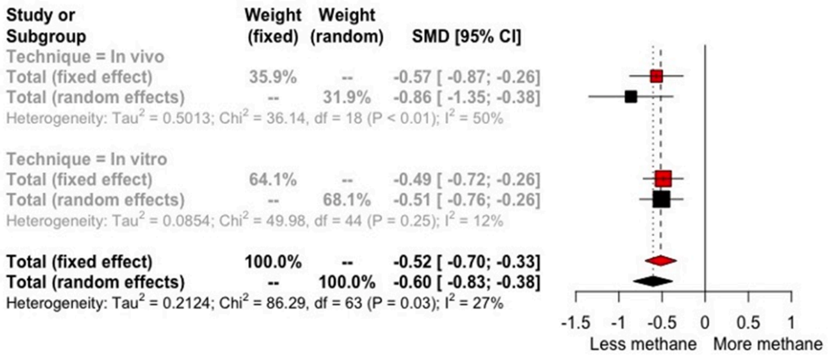


Fig. 4. Forest plot of methane production (SMD) according with measurement technique from studies of ruminants supplemented with tannins. SMD is the standardized mean difference estimated of the random model.

from tropical trees and shrubs into beef cattle rations, obtained a decrease of between 10% and 25% in CH_4 (g CH_4/kg DM intake), and those responses depended on the species of plant and the level of intake of the ration.

Piñeiro-Vázques et al. (2018) evaluated the use of *Leucaena leucocephala* in crossed heifers and reported that, the higher the dose concentration, the lower the CH_4 emission, indeed they obtained a 61% decrease in CH_4 at a dose of 800 g/kg DM of *Leucaena leucocephala*. This result agrees with Montoya-Flores et al. (2020) and Valencia-Salazar et al. (2017) in another study with crossed heifers, reporting that the use of *Samanea saman* + *Pennisetum purpureum* pod meal decreases CH_4 emissions as its inclusion increases, since, from the inclusion of 0, 10, 20 and 30%, the latter decreased 50.9% of CH_4 in L/d.

Rumen CH_4 yield represents an energy loss of up to 0.12 of the total feed intakes (Olijhoek et al., 2018). In this sense, if the inclusion of tannins reduce CH_4 output (Ku-Vera et al., 2020a,b), plants containing these compounds should have a positive impact on energy utilization, as well as a reduction of the environmental impact of livestock production (Vázquez-Carrillo, Montelongo-Pérez, González-Ronquillo, Castillo-Gallegos, & Castelán-Ortega, 2020). However, a selective effect of tannins on fibrolytic bacteria occurred, with *Ruminococcus albus* being most affected, in agreement with the negative effects of saponins on this species (Galindo et al., 2016). These different bacterial responses to tannins might be due to the specific attachment mechanisms to the substrate and the fermentation pattern (Koike and Kobayashi, 2009), as well as by the different modes of action of tannins depending on their source (Tiemann et al., 2008). In the present study, the inclusion of tropical forage rich in tannins seems to reduce CH_4 emission *in vivo* trials, but responses vary amongst plant sources, doses and animal species (Figs. 2, 3).

Since the concentration of tannins varies depending on the plant, (Fig. 3, Table 4) it is observed that *Leucaena leucocephala* shows a better effect in terms of CH_4 reduction compared with *Styzolobium térimum* at the same concentration. Likewise, it was observed that *Leucaena leucocephala* and *Samanea saman* showed a greater effect in the decrease of CH_4, compared to other plants such as *Brachiaria brizantha, Gliricidia sepium, Enterolobium cyclocarpum*, this effect was found in cross breed cattle. Puchala et al. (2012) found a 12% decrease in CH_4 in goats when adding *Sericea lespedeza* (Table 2). Likewise, Dias-Moreira et al. (2013) obtained a reduction of CH_4 in sheep up to 25% when supplementing *Leucaena leucocephala*, being lower when supplementing *Styzolobium térimum* (0.99%), although both plants contained the same concentration of tannins (40 g CT/kg^{-1} of DM), this effect may be due to the fact that 19% more *L. Leucocephala* was administered compared to *Styzolobium térimum*. On the contrary, when supplementing *Mimosa caesalpiniaefolia* there was no effect on the reduction of CH_4, possibly due to the amount administered in the diet (530 g/kg DM), being 34% less TC compared with *L. leucocephala*. Beauchemin, McGinn, Martinez, and

McAllister (2007) when supplementing *Schinopsis balansae* in beef cattle, found a CH_4 reduction of 0.96%, being very similar to that found by Puchala et al. (2012) when supplementing *Mimosa caesalpiniaefolia*. When supplementing *Hedysarum coronarium*, Woodward, Waghorn, Lassey, and Laboyrie (2002) found CH_4 reductions of 14%, with a concentration of condensed tannins of 2.72 g/100 g DM in *Hedysarum coronarium*. However, in general a negative relationship was observed between the level of tannin inclusion and CH_4 emission. The reduction in CH_4 production observed with the use of tannins could be attributed to the fact that they inhibit the activity of microbial enzymes, decrease the populations of protozoa and cellulolytic bacteria and form links with forage proteins, reducing the degradation of ruminal protein (Jakhmola, Taruna, and Raghuvans, 2010; Moscoso et al., 2017). However, an important factor to consider is that the concentration of plant tannins (HT and CT) are known to have both adverse and beneficial effects depending on their concentration and nature, besides other factors such as season, geographical region, animal species and genetics, animal physiological stage and dietary composition (Goel and Makkar, 2012; Piluzza, Sulas, and Bullitta, 2014) and derived from it, the effect on the decrease of CH_4 excretion in ruminants (Fig. 2). Therefore, supplementing tropical and subtropical plants in the diet with a high dose of tannins will result in less CH_4 production.

10. Final remarks

The efficacy of CTs from plant materials to reduce CH_4 emission depends on the plant species and possibly to the environment in which they are grown. Supplementation of tannin-rich plants such as *Leucaena leucocephala, Flemingia macrophylla and Samanea saman in vitro* and *in vivo* studies, have a positive effect on the reduction of CH_4 in ruminants. Other tropical tannin-rich plants such as *Shinopsis lorentzii, Musa spp, Acacia* spp.*,* and *Albizia* spp. can reduce CH_4 , but further *in vivo* studies are suggested to determine rumen microbiome and rumen metabolites.

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Compliance with ethical standards

Due to the nature of the work (systematic review), the authors have nothing to declare.

Ethical statements

The authors state that no animals were used in this study, as it is a review of previous work in the tannin supplementation in ruminants and the effect on CH4

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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