Agroforest Syst (2020) 94:1541–1553
https://doi.org/10.1007/s10457-019-00411-6

Plants extract and bioactive compounds on rumen methanogenesis

Dinesh Kumar Dhanasekaran · Tairon Pannunzio Dias-Silva · Adibe Luiz Abdalla Filho · Gabriel Zanuto Sakita · Adibe Luiz Abdalla · Helder Louvandini · Mona M. M. Y. Elghandour

Received: 30 January 2019

Abstract Feed additives are used in animal diets various beneficial reasons including animal growth, remedy for nutrient deficiency, adsorption of toxins, breakdown of anti-nutritional factors and reduced methane production in the rumen. In past 2 decades, many investigations have focused on studying effects of antibiotics on ruminal fermentation, however, European Union has banned the use antibiotics in animal feeds due to human food safety. Therefore, using plant extracts containing a high level of plant secondary metabolites (PSM) can be an alternative for improving animal performance without compromising food security issues. Most of the plant extracts contains PSM that can be serve as natural resource for animal production systems, nevertheless it is largely unexploited as it is considered as anti-nutritional factors. However, in recent years, various studies emphasized that a group of PSM (e.g. tannins, essential oil and saponins) has ability to manipulate rumen fermentation in a favorable way, thus can be used as natural alternatives for improving ruminant production systems. However, the role of PSM still remains unclear due to limited data and need to be more fully exploited to better understand their properties as bioactive compounds. The present review will discuss the use of plant secondary metabolites in rumen metabolism in terms of biochemical and physiological performance on ruminant production systems, covering topics on proven effectiveness, consumer acceptance, environment, animal safety and welfare.

Keywords Forestry trees · Secondary metabolites · Methane · Ruminants

Introduction

Climate change is one of the major threats on our planet with increasing population and also economical demand (Skuce et al. 2013). The International Panel of Climate Change (IPCC) reported that the rate of climate change is faster than never before in the last 1000 years and there is a possibility of rise in average global temperatures between 1.8 and 4.0 °C within the next 90 years could occur (Yatoo et al. 2012). Hence, the impact of global climate change are predominately threatening factors for the well-being of current and future generations (Marinoa et al. 2015). Livestock

---

D. K. Dhanasekaran · T. P. Dias-Silva ·
A. L. A. Filho · G. Z. Sakita · A. L. Abdalla ·
H. Louvandini
Centre of Nuclear Energy in Agriculture, University of
São Paulo, São Paulo, Brazil

M. M. M. Y. Elghandour (✉)
Facultad de Medicina Veterinaria y Zootecnia,
Universidad Autónoma del Estado de México, Toluca,
Estado de México, Mexico
e-mail: lola.mona2004@yahoo.com

sector significantly contributes towards the greenhouse gas emissions (GHG) worldwide (i.e. carbon-dioxide (CO_2) and methane (CH_4)) from enteric fermentation and nitrous oxide (N_2O) from manure management (Gerber et al. 2011). CH_4 is produced in rumen by fermentation of feeds through methanogenic archaea. Almost 95 million tons of CH_4 are emitted by a domestic animals through enteric fermentation with increasing emission rate of 0.90% worldwide (Patra 2014). CH_4 emissions through enteric fermentation may contributes 17% of global CH_4 and 3.3% GHG emissions mostly on ruminant livestock (Knapp et al. 2014).

There is a growing realization that mitigation action may not be isolated and it should be packed with increase in animal productivity. Currently, many researchers focus on mitigation strategies and potentials that simultaneously improves the animal productivity.

There are many mitigation practices used to reduce enteric CH_4 emissions for improving livestock productivity. The feed additives are included in animal diets to improve feed quality, growth, nutrient deficiency, adsorb toxins, breakdown of anti-nutritive factors and reduce methane production in the rumen (Durmic et al. 2014), antibiotics (McAllister and Newbold 2008), On the other hand, supplement of probiotics into the rumen microorganisms is shown to increase propionate or butyrate and reduce the protozoa number that can eventually reduce methane production (Iqbal et al. 2008). However, the usage of probiotics in large scale production to mitigate CH_4 emissions is very expensive. In contrast, there are few mitigation options banned by several countries. For example, European Union banned antibiotics use in animal feeds due to human food safety (European Union 2003). Therefore, use of tannin containing plants has been studied and is a promising option for mitigating enteric CH_4 emissions (Hristov et al. 2013).

Beauchemin et al. (2007) reported that, tannin has potential for reducing enteric CH_4 emission by up to 20%. However, tannins are reported as anti-nutritional at higher concentrations though at lower concentrations it ca improve animal productivity in terms of alterations of ruminal fermentation and microbial protein synthesis (Bhatta et al. 2012a). Hence, researchers had an opportunity to exploit plant secondary metabolites (PSM) as natural alternatives to improve livestock productivity. The use of plant extracts containing high level of PSM could improve animal performance and resolve human safety issues. Several studies emphasized that a group of plant secondary metabolites (e.g. saponins, flavonoids, and tannins) seems to present the ability to manipulate rumen fermentation in a favorable way thus lessening the CH_4 formation (Hristov et al. 2013).

The present review will discuss the use of PSM in rumen metabolism in terms of biochemical and physiological performance on animal productions systems. Much of what is known about the roles of PSM on animal performance is circumstantial with tenuous data. Thus, it is important to understand the modes of action of plant extracts for fully exploit their properties for the benefit of animal production. Uptake will be dependent on proven effectiveness and consumer acceptance of assurances relating to animal safety, animal welfare, and the environment.

Ruminal ecosystem

Ruminant stomach is composed of rumen, reticulum, omasum, and abomasum, where rumen is the largest among them. Rumen is a fermentation chamber with specific characteristics that allow the ruminants to obtain nutrients from fibrous feed by the action of microbial flora specifically adapted to such environment (McSweeney and Mackie 2012; Agarwal et al. 2015). Rumen is inhabited by a large range of microorganisms living in symbiotic relationship in an anaerobic environment (Qi et al. 2010). Ruminants are able to convert human inedible feed in high-quality products such as meat, milk, and wool (Wadhwa et al. 2016).

The ability of ruminants to utilize complex plant polysaccharides for energy production is due to the population of microorganisms that inhabit the rumen, because like other mammals, ruminants do not produce enzymes to degrade this type of feed. These microorganisms ferment the polysaccharides from plant cell wall and produce energy and microbial protein (high-quality protein) to the host (Qi et al. 2010). However, for a good performance of microorganisms and to maintain rumen function, host animal needs to provide good conditions for the microbes, which comprises a temperature between 38–41 °C and pH between 6.0 and 7.0. In this way, both ruminants and ruminal microorganisms live in a mutualistic relationship with each other. (McSweeney and Mackie 2012).

The microbial populations of rumen are composed of bacteria (most extensively studied), protozoa, fungi and virus. These population can degrade a large diversity of substrates, where some of them are more substrate specific and while others are general (Weimer 2015). The population of bacteria vary between 10^{10} to 10^{12} mL^{-1}, protozoa 10^5 to 10^6 mL^{-1}, fungi 10^4 to 10^5 mL^{-1}, and methanogenic archaea 10^8 to 10^{10} mL^{-1} (Patra 2012). These numbers could be larger because a high quantity of microbes are non-culturable (Kamra 2005). Variations in rumen population depends on host species, diet, livestock management, and geographical localizations. However, some species of microorganisms are found in most of the ruminants all over the world (Henderson et al. 2015). Ruminal microorganisms hydrolyze the ingested feed into monomers and then ferment these substrates into short-chain fatty acids (SCFA), methane (CH_4), carbon dioxide (CO_2), ammonia, lactic acid (McSweeney and Mackie 2012), microbial protein, and vitamins (Qi et al. 2010).

Feed digestion depends on mastication, flow rate of digesta, retention time on rumen, and continuous removal of fermented end-products (Agarwal et al. 2015). Acetate, propionate, and butyrate are the main SCFA produced and used as energy for animals, which represents more than 60% of the metabolized energy. Acetate is the SCFA with the higher production, followed by propionate and then butyrate (McSweeney and Mackie 2012).

The microbial fermentation end-products like SCFA and ammonia are absorbed through the rumen epithelium tissue, or removed from the rumen through eructation, like CH_4 and CO_2, or exit the rumen to be absorbed in the small intestine, like microbial protein (McCann et al. 2014). After absorption acetate reach the peripheral blood and is used by peripheral tissues. Propionate is used is converted to glucose, while butyrate is metabolized into ketone bodies (Bergman 1990). The ammonia absorbed is metabolized to urea in the liver following two pathways either being excreted in urine or recycled through saliva. Microbial protein is digested in the small intestine and absorbed as amino acids (McCann et al. 2014). CH_4 is produced by the reduction of CO_2 with hydrogen by methanogens bacteria to obtain energy for their growth (Patra 2012). For the ruminants, CH_4 represent a loss of energy intake varying between 2 and 12%. The removal of hydrogen from the rumen environment is important to maintained good conditions for rumen fermentation (Morgavi et al. 2010).

Plant secondary metabolites

Plant primary metabolites are substances widely distributed in nature, often concentrated in seeds and vegetative storage organs which are needed for physiological development because of their role in basic cell metabolism (Balandrin et al. 1985). Derived from primary metabolites with diverse physiological activities, PSM isa group of chemical bioactive compounds such as tannins, essential oils, saponins, alkaloids, flavonoids, glucosides, etc., that are not involved in the primary biochemical processes of growth and reproduction (Patra and Saxena 2010; Mueller-Harvey 2006), but play a vital role in the interaction between plants and the environment (Kliebenstein 2013).

The content of PSM varies from species to species and also in the plants of same species (Barton and Koricheva 2010), PSM being key compounds that contribute to odor, taste, and color of the plants which protect them in adverse conditions from pathogens, herbivory and environmental stresses (Verma and Shukla 2015). Temperature, drought, salinity, seasonality, altitude, light, UV radiation, metal ions, wounding and nutrient deficiencies can affect their concentration (Gouvea et al. 2012) and these are also dependent on the growing conditions and metabolic pathways of related PSM (Ramakrishna and Ravishankar 2011). About 200 years ago the study of PSM started and since then more than 2,00,000 defined structures have been identified (Hartmann 2007) and these classified into three major groups: Terpenes, Phenolic compounds and Nitrogen containing compounds (Fang et al. 2011).

Terpenes, also known as terpenoids or isoprenoids, are generally insoluble in water and play important role in the growth of plants (gibberellins, sterol, carotenoids, and abscisic acid) and a vital role in defense, as toxic to insects and mammals (pyrethroids). Also, some plants have volatile terpenes known as essential oils and glycosides terpene called saponins which has applications in pharmacology (Bodas et al. 2012; Verma and Shukla 2015). Phenolic compounds is a group of heterogeneous molecules that include more than 10.000 soluble and insoluble compounds that have a phenyl ring bearing at least one acidic hydroxyl group (Taiz and Zeiger 2006; Achakzai et al. 2009).

Flavonoids and tannins are examples of phenolic compounds groups (Fang et al. 2011). Phenolic compounds can play many physiological roles in plants including defense against biotic or abiotic stresses, also having allelopathic and antioxidant activity (Achakzai et al. 2009; Naghiloo et al. 2012; Verma and Shukla 2015; Sharma et al. 2016). Because they are increased by the exposure to toxic chemicals and stresses in the plants, phenolic compounds can be used as stress indicator (Siddiqui and Arif 2004; Achakzai et al. 2009). Flavonoids have important role in plant defense against insects and microbes, also acting in the development of petals color to attract pollinators (Taiz and Zeiger 2006; De Sousa et al. 2007; Khatiwora et al. 2010). Plant phenolic compounds can also produce a specific taste and smell due to which animals, insects and humans do not eat them and these phenolic compounds known as anti-grazing factors in plants (Strack 1997).

Nitrogen containing compounds such as alkaloids, glucosinolates and cyanogenic glycosides are the third important category of secondary metabolites. Alkaloids are low molecular weight compounds, synthesized from amino acids such as lysine, tyrosine and tryptophan (Facchini 2001; Taiz and Zeiger 2006). A group of alkaloids named terpenoid indole alkaloids include more than 3.000 compound such as antineoplastic agents, anti-malarial drug and strychnine that are known to play a role in plant protection against pests and pathogens (Facchini 2001; Verma and Shukla 2015). While cyanogenic glycosides release hydrogen cyanide (HCN) and their higher amount present in cassava (*Manihot esculenta*) can cause limb paralysis, glucosinolates are responsible for smell and taste in vegetable such as cabbage, broccoli, radish, etc. (Taiz and Zeiger 2006; Verma and Shukla 2015).

Tannins, essential oils, and saponins are examples of PSM that have been shown to selectively modulate the rumen microbial ecosystem (Samal et al. 2016), and due the biological activity on other living organisms that they can present, drug an animal nutrition companies routinely screen these compounds in order to obtain new drugs or feed additives (Bodas et al. 2012). In order to improve the animal performance and mitigation options, many recent studies were also reported that these chemical groups and their bioactive compound can help to enhance the ruminal ecosystem efficiently (Table 1).

Effect of tannins on rumen methanogenesis

Tannins are polyphenolic polymers with high molecular weight presenting solubility in water. These bioactive compounds have capacity to form complexes mainly with proteins and others macromolecules due to the presence of a large number of phenolic hydroxyl groups. Usually, tannins are subdivided into two major groups: hydrolysable tannins (HT) and condensed tannins (CT). Tannins have beneficial or adverse effects depending on their concentration in the extract or plant species as well as other factors such as animal species, phenological stage, physiological state and diet composition (Makkar 2003; Gea et al. 2011; Fig. 1).

The HT is characterized as complex molecules with a polyol as a central core (glucose, glucitol, quinic acids, quercitol and shikimic acid) with a phenolic group that is partially or totally esterified (Haslam 1989). Hydrolysis of HT occurs in acids and alkaline conditions as well as by esterases yielding polyol and the constituent phenolic acids. CT are proanthocyanidins that produce red anthocyanidins when heated in acid (Haslam 1989). It is categorized by polymers of the flavan-3-ol (epi) catechin and (epi) gallocatechin units, which are linked by C_4–C_8 and C_4–C_6 interflavonoid linkages (Ferreira et al. 1999; Hagerman and Butler 1989). Biological activities of CT depend of the molecular weight and chemical structures.

Tannins properties such as bacteriostatic, bactericidal or through the inactivation of the enzymes can adversely affect ruminal fermentation (Faixova and Faix 2005) and may inhibit several different processes including digestive tract functions and thus may have an impact on animal production (Brooker et al. 1999). These specific characteristics (anti-microbial effect on various biochemical reactions in the rumen) allow the tannins to be used for selective inhibition of some of the undesirable reactions in the rumen such as inhibition of methanogen growth (Tavendale et al. 2005) by deactivation of methanogens (*Methanobrevibacter ruminantium*), linked to reduction of produced methane (Tavendale et al. 2005; Pellikaan et al. 2011). Therefore, it can be used as rumen modifiers (Ingale et al. 2013).

Table 1 Chemical groups and their bioactive compounds and roles in ruminant production

Chemical group	Bioactive compounds (plant source)	Roles in ruminant production	References
Tannins	Condensed tannins (*Leucaena leucocephala*)	Reduced of methane production	Dias Moreira et al. (2013)
	Condensed tannins (*Leucaena leucocephala* hybrid-Rendang)	Altered the size of populations and diversity of rumen methanogenic archaea	Saminathana et al. (2016)
	Condensed tannins (*Bauhinia pulchella*)	Anthelmintic activity against *Trichostrongylus colubriformis*, affected egg viability and reduced pasture contamination	Lopes et al. (2016)
	Condensed tannins (*Ficus benghalensis*) (*Artocarpus heterophyllus*) (*Azadirachta indica*)	Reduced methane production and protozoa numbers, without affecting dry matter digestibility	Malik et al. (2017)
	Condensed tannins (*Orbignya phalerata*) (*Combretum leprosum*)	Affected ruminal short-chain fatty acids and microbial population, without compromising animal production potential, carcass characteristics and meat fatty acid profile	Abdalla Filho et al. (2017)
	Tannic acid solution—hydrolysable tannin	Inhibited isolated ruminal bacteria from the sheep rumen	Cipriano-Salazar et al. (2018)
	Tannins (*Macrotyloma axillare*)	Reduced total gas and methane in vitro and increased intake and apparent total tract digestibility of crude protein	Lima et al. (2018)
Essential oils	Carvacrol (*Origanum vulgare*)	Reduced methane production	Hundal et al. (2016)
	Eugenol (*Syzygium aromaticum*)	Increased dry matter digestibility	Righi et al. (2017)
	Eucalyptus (*Eucalyptus camaldulensis*)	Reduced gas production and protein deamination	Chouchen et al. (2018)
	Anise (*Pimpinella anisum)*	Improved the partitioning factor and reduced ammonia concentration	Chahaardoli et al. (2018)
	Essential Oil-Cobalt complex	Improved growth performance, meat quality and fiber quality	Lei et al. (2018)
	Essential Oil-Cobalt complex	Improved fermentation in the rumen, increased metabolism of butyrate	Lei et al. (2019)
	Santalum spicatum	Reduced of methane, ammonia-N and promotion of propionate production	Jahani-Azizabadi et al. (2019)
Saponins	*Yucca schidigera* and *Quillaja saponaria*	No effect in nutrient digestibility, milk production, rumen fermentation pattern, and methane production	Holtshausen et al. (2009)
	Tea seed saponin (*Camellia sinensis* L.)	Reduced dry matter intake. No effect in methane production, fermentation pattern, and protozoa population	Ramírez-Restrepo et al. (2016)
	Tea saponin extract	No effect in methane production and total protozoa. Reduction in dry matter intake. Increasing in acetate production	Guyader et al. (2017)
	Tea saponins (triterpenoid saponin)	Improved immunity of dairy cows	Wang et al. (2017)
	Tea seed saponin (*Camellia sinensis* L.)	Reduced methane and ammonia-N production and protozoa count	Jadhav et al. (2018)
	Alfalfa saponins (*Medicago sativa* L.)	Improved nutrient digestibility, liver protection, and regulated lipid metabolism	Liu et al. (2018)

Table 1 continued

Chemical group	Bioactive compounds (plant source)	Roles in ruminant production	References
	Tea saponin	Increased organic matter, nitrogen, neutral detergent fiber, and acid detergent fiber apparent digestibility. Reduced methane emission scaled to metabolic body weight. Increased molar proportions of propionate, butyrate, isobutyrate, and isovalerate. Potential decrease in protozoa population	Liu et al. (2019)

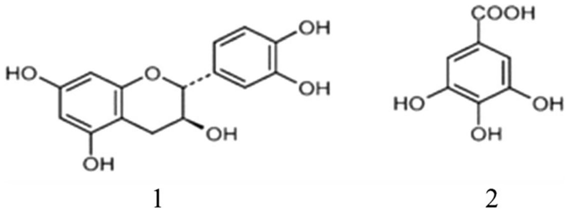


Fig. 1 Chemical structure of tannins: (1) condensed tannins (Catechin) and (2) hydrolysable tannins (Gallic acid)

Several studies showed that molecular weight of condensed tannins promotes an important role on methanogenesis in ruminants (Hariadi and Santoso 2010; Huang et al. 2010, 2011; Saminathana et al. 2016). The potential of methane mitigation by using tannins can range from 2 to 58% in comparison with analyzed control groups (Patra and Saxena 2010; Bodas et al. 2012; Hristov et al. 2013) and factors responsible for the mitigation are various, for example, tannin type, plant source, and molecular weight. However, it is unknown how PSM affects methanogen diversity and community composition. According to Huang et al. (2011), CT with high molecular weight showed 62% of inhibition compared to control. Methane production had 47% of reduction, with decreased on total methanogens and total protozoa number in diet with inclusion of 15 mg of CT/500 mg dry matter. Nevertheless, a higher level of CT promotes negative effects on dry matter digestibility. Saminathana et al. (2016) reported direct effect on rumen methanogens with higher molecular weight CT fractions showing greater reduction of methanogens.

Tan et al. (2011) verified that inclusion of pure condensed tannin extracts from *Leucaena leucocephala* hybrid-Rendang caused a linear reduction in total methanogens and CH_4 production. Studies showed that CT fractions have negative effect on methanogen, particularly for *Methanobrevibacter* spp., promoting the reduction of ruminal methane production (Tavendale et al. 2005; Min et al. 2014; Saminathana et al. 2016). It may be due to the inhibition of methanogenesis via deactivation of the mcr enzyme (key enzyme in CH_4 production) (Juottonen et al. 2006).

It was suggested that CT has toxic effects that causes inhibition of methanogens growth among other ruminal microorganisms. This is most likely to be due to bacteriostatic and/or bactericidal effects of CT (Tavendale et al. 2005). *Methanobrevibacter* spp. (gram-positive methanogens) has been described with higher susceptibility to tannin inhibition compared to the *Methanomicrobium* and *Methanimicrococcus* (gram-negative) (Field and Lettinga 1992). The capacity of tannins to bind proteins, results in both inhibitions of extracellular enzymes and substrate unavailability for digestion, leading to deactivation and subsequently death of microbes (Smith et al. 2005). Hence, the formation of complexes with proteins and consequently protection of condensed tannins, mainly CT with high molecular weight, from digestion in the rumen, could lead a decrease the ammonia nitrogen level in rumen fluid and limit the supply of available hydrogen from ammonia to methanogens (Chollot et al. 1962).

More effects on rumen by CT have been described such as population and diversity of protozoa (Tan et al. 2011, 2013). Significant reduction on protozoa population was verified in animals supplemented with tannins (Cieslak et al. 2012). There is a symbiotic relationship between rumen methanogens and rumen protozoa, possibly because of the production of H_2 and formate from fermentation of protozoa. Due to the cross feeding of nutrients between two microbes class (Vogels et al. 1980), it is possible that a reduction of the rumen protozoa will conduct a reduction in methanogen population (Saminathana et al. 2016). Reduction in rumen protozoal counts may decrease archeal counts as well indirectly affect methane emission (Cieslak et al. 2012). Tannins can directly suppress methanogenesis by affecting rumen archea by defaunation (Bhatta et al. 2009, 2012b). Due to the complex structure of extracts containing one bioactive compound, even in a predominant concentration, as well as the interactions between individual extract components and feed components becomes difficult to interpret the results obtained (Cieslak et al. 2013). Hence, the methanogenic capacity of plants containing tannins may be related to other factors not only tannin content (Soltan et al. 2012).

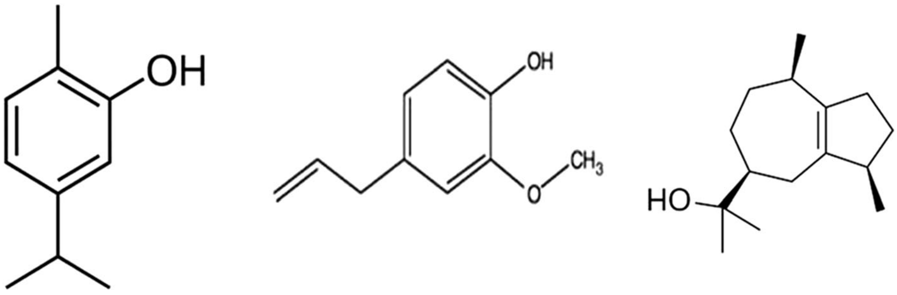
Effect of essential oils on rumen methanogenesis

This group of secondary plant metabolites (Fig. 2) are steam volatile or organic solvent present in flowers, leaves, stems, bark, fruit pulps, roots and seeds (Voon et al. 2012). Humans have used these bioactive compounds for years due to their flavor and specific aroma as well as antimicrobial agents and preservatives. The concentrations of essential oils are influenced by type of plant, stage of growth, plant heath and ambient factors (light, temperature and humidity), and stress (Hart et al. 2008). Based on chemical groups, the essential oils are commonly divided in terpenoids, synthesized through mevalonate and phenylpropanoids, synthesized through shikimic acid metabolic pathways (Gershenzon and Croteau 1991; Calsamiglia et al. 2007). Terpenoids are derived of a basic structure of C_5 isoprene units and are classified depending on the number of these units in its skeleton. Within terpenoids group, the principal components of the majority of plants are monoterpenoids and sesquiterpenoids (Gershenzon and Croteau 1991; Calsamiglia et al. 2007). On the other hand, phenylpropanoids are composed by a side chain of three carbons bound to an aromatic ring of C_6 (Calsamiglia et al. 2007).

Previous investigations showed antimicrobial properties of essential oils against rumen microbes with effect on rumen methanogenesis. Consequently, several researches were conducted using essential oils as feed additive in ruminant nutrition and aiming to identify the essential oil that reduce methane production without a concomitant reduction in feed digestion. Evans and Martin (2000) reported that thymol (essential oil derived from Thymus and Origanum plants) inhibited in vitro methane production. However, there was a decrease in acetate and propionate concentrations. According to Macheboeuf et al. (2008), thymol (from *Origanum vulgare*) at 6 mM concentration caused a suppression of methane to the extent of 99%.

Hundal et al. (2016) conducted an experiment aiming to screen the best, amongst the four essential oils used (cinnamaldehyde, carvacrol, limonene and carvone), and the level/dose at what these should be supplemented to get best response with respect to enteric methane mitigation; with least effect on digestibility of nutrients using wheat straw as a substrate. The results showed that methane production was reduced with the supplement beyond 1% level of carvacrol or limonene, but the digestibility of nutrients was also depressed.

Many investigations also reported that the use of essential oils such as lemon (Castillejos et al. 2006), cinnamon (Fraser et al. 2007), thyme (Castillejos et al. 2008), eucalyptus (Sallam et al. 2010) and peppermint (Agarwal et al. 2009; Ozkan et al. 2015) modified



1 2 3

Fig. 2 Chemical structure of some essential oils: (1) monoterpenoids (Carvacrol), (2) phenylpropanoids (Eugenol), (3) sesquiterpinoids (Guaiol) rumen microbial fermentation. The authors have described that the alteration on rumen fermentation is due to decreased in ammonia nitrogen concentration through their impact on hyper-ammonia producing bacteria resulting in reduced deamination of amino acids, reduce methane emission and protozoa count (Sallam et al. 2011, 2012; Soltan et al. 2011). Authors have described that essential oils stimulated some protozoa species such as *Isotricha* spp. or *Dasytricha* spp. with consequent increasing in *Methanobrevibacter smithii*. However, several studies reported methane mitigation using essential oils without modifications on protozoa population (Evans and Martin 2000; Busquet et al. 2005).

The essential oils act directly on methanogen cells due to structure and properties of the oil used or secondary plant metabolites contained therein (Cieslak et al. 2013). Essential oils and their anti-methanogenic effect in the rumen are related to the presence of terpenoids and phenylpropanoids in oils. The use of essential oils such as carvacrol (phenolic compound) or a cinnamaldehyde (carbonyl compound) demonstrated a stronger antimicrobial activity in the oils that contains monoterpenes. Hence, antimicrobial activity is affected by interactions of different essential oils components (Cobellis et al. 2016). The use of mixtures of essential oils have presented additive, antagonistic and synergistic effects between their components (Burt 2004). Thus, suggests that essential oils combinations of different composition or specific combinations of essential oil secondary metabolites, may result in additive and/or synergetic effects which may enhance efficiency of rumen microbial fermentation (Benchaar and Greathead 2011).

Effect of saponins on rumen methanogenesis

Saponins are a group of glycosides with high molecular weight consisting of a triterpene (triterpene saponins) or steroidal (steroid saponins) sapogenin nucleus with one or more carbohydrate branches. Triterpene saponins (Fig. 3) are more widely distributed in nature than steroidal types in a wide variety of plants (Hostettmann and Marston 1995). The degradability of saponins in the rumen is dependent of its structure among others factors. The majority of researches using this bioactive compound were conducted to exploit the effect on inhibition of rumen ciliate protozoa, which might improve the efficiency of microbial protein synthesis by reducing microbial protein turnover and enhance protein flow to the duodenum and ruminant production (Patra and Saxena 2009). However, saponins may also be exploited for suppressing of rumen methanogenesis. Many studies have reported that saponins or plants rich, both in vitro (Takahashi et al. 2000; Pen et al. 2006, 2008; Holtshausen et al. 2009) and in vivo (Sliwinski et al. 2002; Pen et al. 2007; Wang et al. 2009; Santoso et al. 2004; Holtshausen et al. 2009) have presented reduction on methanogenesis.

In sheep fed sarsaponins ($C_{27}H_{44}O_3$, extract from *Yucca schidigera* under commercial name DK Sarsaponin 35 Organic) for 25 days (35% saponins), there was a reduction on methane production of 7.1% (0.12 g/kg diet) (Santoso et al. 2004) and 15.5% (0.13 g/kg diet) (Wang et al. 2009). Pen et al. (2007) used Yucca extract (containing 8–10% saponins) in their studies relatively at high doses (13.8 g/kg diet) and noted a non-significant decrease (11.7%) in methane release in sheep. On the other hand, investigations reported no influence of saponins on

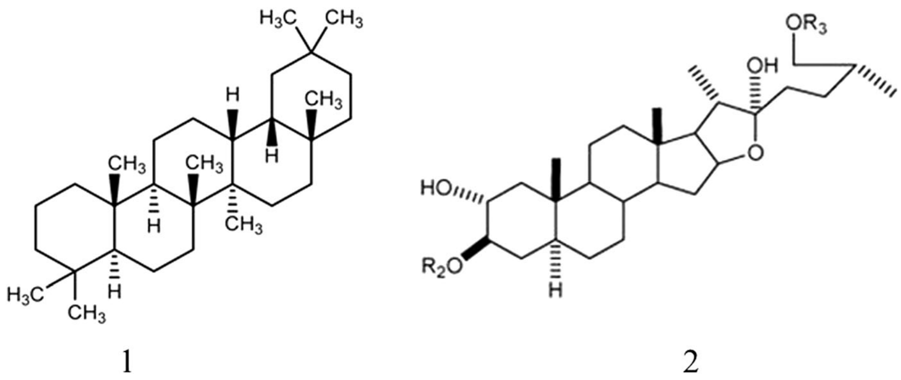


Fig. 3 Chemical structure of saponin: (1) triterpenoid (Oleanane) and (2) steroidal (Furostanol)

methanogenesis of sheep (Sliwinski et al. 2002), and cows (Holtshausen et al. 2009). These authors described that the no effect was due to an inclusion of a low dose of sarsaponins and adaptation of ruminal microbiota to saponins (Wang et al. 1998; Patra and Saxena 2009).

It was reported that saponins might decrease the activities of methane producing genes or rate of methane production in each methanogenic cell (Guo et al. 2008; Hess et al. 2003). This fact suggested that saponins affect methane production due to the reduced rate of methanogenesis via diminished activity of methane producing gene without changing the total methanogen population (Guo et al. 2008). However, the use of saponins may promote defaunation by sterol binding capability of saponins and destruction of protozoal cell membranes (Patra and Saxena 2009) and consequently resulting in decrease methanogenesis (Hostettmann and Marston 1995). The increase on propionate production in ruminants fed saponins favor the channel ling of hydrogen from methanogenesis to propionate production may cause lower methane production.

The capacity of saponins on transfering the digestion of nutrients from the rumen to the hindgut (Lu and Jorgensen 1987) could reduce methane production due to a substantial presence of reductive acetogenesis, reducing fermentation activity and absence of protozoa in the hindgut (Varadyova et al. 2000). In the context of rumen methanogenesis, the microbiological effects of saponins are more significant than your physiological properties (Lu and Jorgensen 1987). However, it should be considered that saponins, in some cases, may increase methane production, once saponins affect the passage rate (Lu and Jorgensen 1987; Klita et al. 1996) and there is a relationship between flow rate of digesta and methane production probably due to increased fiber degradation in the rumen.

Although some studies have showed that saponins have reduced the amount of enteric methane production by up to 50% (Szumacher-Strabel and Cieslak 2010; Patra and Saxena 2010; Bodas et al. 2012). However, more in vivo studies are necessary to confirm these effects and the best level of compound to use in ruminant diet, which promotes positive effects (methane mitigation) without compromise animal performance.

Conclusion

It is important to reduce the CH_4 production from ruminants and also to produce more quantity of food products with lower environmental impact associated with animal production. Therefore, it is well proven that the diet could influence the rumen microbial community and fermented end-products that would led to a greater or smaller enteric CH_4 production. The use of PSM as strategy to mitigate enteric CH_4 by manipulating the rumen microbiota and/or fermentation, especially if using plant extracts would increase the animal productivity, benefiting both the animals and humans without harshening the environment.

References

Abdalla Filho AL, Corrêa PS, Lemos LN, Dineshkumar D, Issakowicz J, Ieda EH, Lima PMT, Barreal M, McManus C, Mui TS, Abdalla AL, Louvandini H (2017) Diets based on plants from Brazilian Caatinga altering ruminal parameters, microbial community and meat fatty acids of Santa Inês lambs. Small Rumin Res 154:70–77

Achakzai AKK, Palwasha A, Ayeesha M, Kayani SA, Tareen RB (2009) Response of plant parts and age on the distribution of secondary metabolites on plants found in Quetta. Pak J Bot 41:2129–2135

Agarwal N, Shekhar C, Kumar R, Chaudhary LC, Kamra DN (2009) Effect of peppermint oil on in vitro methanogensis and fermentation of feed with buffalo rumen liquor. Anim Feed Sci Technol 148:321–327

Agarwal N, Kamra DN, Chaudhary LC (2015) Rumen microbial ecosystem of domesticated ruminants. In: Puniya AK, Singh R, Kamra DN (eds) Rumen microbiology: from evolution to revolution. Springer, New Delhi, pp 17–30

Balandrin MF, Klocke JA, Wurtele ES, Bollinger WH (1985) Natural plant chemicals: sources of industrial and medicinal materials. Science 228:1154

Barton KE, Koricheva J (2010) The ontogeny of plant defense and herbivory: characterizing general patterns using meta-analysis. Am Nat 175:481–493

Beauchemin KA, Mcginn SM, Martinez TF, Mcallister TA (2007) Use of condensed tannin extract from quebracho trees to reduce methane emissions from cattle. J Anim Sci 85:1990–1996

Benchaar C, Greathead H (2011) Essential oils and opportunities to mitigate enteric methane emissions from ruminants. Anim Feed Sci Technol 166:338–355

Bergman EN (1990) Energy contributions of volatile fatty acids from the gastrointestinal tract in various species. Physiol Rev 70:567–590

Bhatta R, Uyeno Y, Tajima K, Takenaka A, Yabumoto Y, Nonaka I, Enishi O, Kurihara M (2009) Difference in the nature of tannins on in vitro ruminal methane and volatile fatty acid production and on methanogenic archaea and protozoal populations. J Dairy Sci 92:5512–5522

Bhatta R, Baruah L, Saravanan M, Suresh KP, Sampath KT (2012a) Effect of medicinal and aromatic plants on rumen fermentation, protozoa population and methanogenesis in vitro. J Anim Physiol Anim Nutr 97:446–456

Bhatta R, Saravanan M, Baruah L, Sampath KT (2012b) Nutrient content, in vitro ruminal fermentation characteristics and methane reduction potential of tropical tannin-containing leaves. J Agric Sci 92:2929–2935

Bodas R, Prieto N, García-González R, Andrés S, Giráldez FJ, López S (2012) Manipulation of rumen fermentation and methane production with plant secondary metabolites. Anim Feed Sci Technol 176:78–93

Brooker JD, O'Donovan L, Skene I, Sellick G (1999) Mechanisms of tannin resistance and detoxification in the rumen. In: Proceedings of the 8th international symposium on microbial ecology

Burt S (2004) Essential oils: their antibacterial properties and potential applications in foods-a review. Int J Food Microbiol 94:223–253

Busquet M, Calsamiglia S, Ferret A, Cordozo PW, Kamel C (2005) Effect of garlic oil and four of its compounds on rumen microbial fermentation. J Dairy Sci 88:4393–4404

Calsamiglia S, Busquet M, Cardozo PW, Castillejos L, Ferret A (2007) Invited review: essential oils as modifiers of rumen microbial fermentation. J Dairy Sci 90:2580–2595

Castillejos L, Calsamiglia S, Ferret A (2006) Effect of essential oils active compounds on rumen microbial fermentation and nutrient flow in in vitro systems. J Dairy Sci 89:2649–2658

Castillejos L, Calsamiglia S, Martín-Tereso J, Wijlen TH (2008) In vitro evaluation of effects of ten essential oils at three doses on ruminal fermentation of high concentrate feedlot-type diets. Anim Feed Sci Technol 145:259–270

Chahaardoli A, Nooriyan Soroor ME, Foroughi A (2018) The effects of Anise (*Pimpinella anisum*) essential oil and extract on in vitro rumen fermentation parameters and protozoa population of sheep. Int J Vet Sci 7:21–27

Chollot B, Chapon L, Urion E (1962) Polyphenolisehe und proteinisehe VorNiufer der Oxydationstriibung. (Nancy, Versuchslab. d. Brauerei-Hochschule.). Brauwiss 15:321–329

Chouchen R, Attia K, Darej C, Moujahed N (2018) Potential of eucalyptus (*Eucalyptus camaldulensis*) essential oil to modify in vitro rumen fermentation in sheep. J Appl Anim Res 46:1220–1225

Cieslak A, Zmora P, Pers-Kamczyc E, Szumacher-Strabel M (2012) Effects of tannins source (*Vaccinium vitis idaea* L.) on rumen microbial fermentation in vivo. Anim Feed Sci Technol 176:102–106

Cieslak A, Szumacher-Strabel M, Stochmal A, Oleszek W (2013) Plant components with specific activities against rumen methanogens. Animal 7:253–265

Cipriano-Salazar M, Rojas-Hernández S, Olivares-Pérez J, Jiménez-Guillén R, Cruz-Lagunas B, Camacho-Díaz LM, Ugbogu AZ (2018) Antibacterial activities of tannic acid against isolated ruminal bacteria from sheep. Microb Pathog 117:255–258

Cobellis G, Trabalza-Marinucci M, Marcotullio MC, Yu Z (2016) Evaluation of different essential oils in modulating methane and ammonia production, rumen fermentation, and rumen bacteria in vitro. Anim Feed Sci Technol 215:25–36

De Sousa RR, Queiroz KC, Souza AC, Gurgueira SA, Augusto AC, Miranda MA, Peppelenbosch MP, Ferreira CV, Aoyama H (2007) Phosphoprotein levels, MAPK activities and NFkappaB expression are affected by fisetin. J Enzyme Inhib Med Chem 22:439–444

Dias Moreira G, Lima PMT, Borges BO, Longo C, Mcmanus C, Abdalla A, Louvandini H (2013) Tropical tanniniferous legumes used as an option to mitigate sheep enteric methane emission. Trop Anim Health Prod 48:879–882

Durmic Z, Moate PJ, Eckard R, Revell DK, Williams R, Vercoe PE (2014) In vitro screening of selected feed additives, plant essential oils and plant extracts for rumen methane mitigation. J Agric Sci 94:1191–1196

European Union. Regulation (EC) No. 1831/2003 of European Parliament and the Council of 22 September 2003 on additives for use in animal nutrition. Official Journal of European Union, Brussels, 18 Oct 2003. p L268/36

Evans JD, Martin SA (2000) Effects of thymol on ruminal micro-organisms. Curr Microbiol 41:336–340

Facchini PJ (2001) Alkaloid biosynthesis in plants: biochemistry, cell biology, molecular regulation, and metabolic engineering applications. Annu Rev Plant Physiol Plant Mol Biol 52:29–66

Faixova Z, Faix S (2005) Manipulation of rumen nitrogen metabolism—a review. Folia Vet 49:215–219

Fang X, Yang CMAQ, Yang L, Chen X (2011) Genomics grand for diversified plant secondary metabolites. Plant Divers Resour 33:53–64

Ferreira D, Brandt EV, Coetzee J, Malan E (1999) Condensed tannins. Prog Chem Org Nat Prod 77:22–59

Field JA, Lettinga G (1992) Biodegradation of tannins. In: Sigel H, Sigel A (eds) Metal ions in biological systems. Degradation of environmental pollutants by microorganisms and their metalloenzymes. Marcel Dekker Inc., New York, pp 61–97

Fraser GR, Chaves AV, Wang Y, McAllister TA, Beauchemin KA (2007) Assessment of the effects of cinnamon leaf oil on rumen microbial fermentation using two continuous culture systems. J Dairy Sci 90:2315–2328

Gea A, Stringano E, Brown HR, Mueller-Harvey I (2011) In situ analysis and structural elucidation of Sainfoin (*Onobrychis viciifolia*) tannins for high-throughput germplasm screening. J Agric Food Chem 59:495–503

Gerber P, Vellinga T, Opio C, Steinfeld H (2011) Productivity gains and greenhouse gas emissions intensity in dairy systems. Livest Sci 139:100–108

Gershenzon J, Croteau R (1991) Terpenoids. In: Rosenthal GA, Berenbaum MR (eds) Herbivores: their interactions with secondary plant metabolites, vol 1. Academic Press, San Diego, CA, pp 165–219

Gouvea DR, Gobbo-Neto L, Sakamoto HT, Lopes NP, Lopes JLC, Meloni F, Amaral JG (2012) Seasonal variation of the major secondary metabolites presents in the extract of Eremanthus mattogrossensis Less (*Asteraceae: Vernonieae*) leaves. Quím Nova 35:2139–2145

Guo YQ, Liu JX, Lu Y, Zhu WY, Denman SE, McSweeney CS (2008) Effect of tea saponin on methanogenesis, microbial community structure and expression of mcrA gene, in cultures of rumen micro-organisms. Lett Appl Microbiol 47:421–426

Guyader J, Eugène M, Doreau M, Morgavi DP, Gérard C, Martin C (2017) Tea saponin reduced methanogenesis in vitro but increased methane yield in lactating dairy cows. J Dairy Sci 3:1845–1855

Hagerman AE, Butler LG (1989) Choosing appropriate methods and standards for assaying tannins. J Chem Ecol 11:1535–1544

Hariadi BT, Santoso B (2010) Evaluation of tropical plants containing tannin on in vitro methanogenesis and fermentation parameters using rumen fluid. J Sci Food Agric 90:456–461

Hart KJ, Yanez-Ruiz DR, Duval SM, McEwan NR, Newbold CJ (2008) Plant extracts to manipulate rumen fermentation. Anim Feed Sci Technol 147:8–35

Hartmann T (2007) From waste products to ecochemicals: fifty years research of plant secondary metabolism. Phytochemistry 68:2831–2846

Haslam E (1989) Plant polyphenols. Cambridge University Press, Cambridge

Henderson G, Cox F, Ganesh S, Jonker A, Young W, Abecia L, Janssen PH (2015) Rumen microbial community composition varies with diet and host, but a core microbiome is found across a wide geographical range. Sci Rep 5:145–167

Hess HD, Monsalve LM, Lascano CE, Carulla JE, Diaz TE, Kreuzer M (2003) Supplementation of a tropical grass diet with forage legumes and *Sapindus saponaria* fruits: effects on in vitro ruminal nitrogen turnover and methanogenesis. Aust J Agric Res 54:703–713

Holtshausen L, Chaves AV, Beauchemin KA, McGinn SM, McAllister TA, Odongo NE, Cheeke PR, Benchaar C (2009) Feeding saponin-containing *Yucca schidigera* and *Quillaja saponaria* to decrease enteric methane production in dairy cows. J Dairy Sci 92:2809–2821

Hostettmann K, Marston A (1995) Saponins. Cambridge University Press, Cambridge

Hristov AN, Firkins JL, Dijkstra J, Kebreab E, Waghorn G, Makkar HPS, Adesogan AT, Yang W, Lee C, Gerber PJ, Henderson B, Tricarico JM (2013) Special topics—mitigation of methane and nitrous oxide emissions from animal operations: I. A review of enteric methane mitigation options. J Anim Sci 91:5045–5069

Huang XD, Liang JB, Tan HY, Yahya R, Khamseekhiew B, Ho YW (2010) Molecular weight and protein binding affinity of Leucaena condensed tannins and their effects on in vitro fermentation parameters. Anim Feed Sci Technol 159:81–87

Huang XD, Liang JB, Tan HY, Yahya R, Ho YW (2011) Effects of Leucaena condensed tannins of differing molecular weights on in vitro CH_4 production. Anim Feed Sci Technol 166:373–376

Hundal JS, Wadhwa M, Bakshi MPS (2016) Effect of supplementing essential oils on the in vitro methane production and digestibility of wheat straw. J Anim Res Nutr 1:1–14

Ingale SL, Lokhande A, Zadbuke S (2013) Nutritional strategies to mitigate greenhouse gases emission from livestock agriculture: a review. Livest Res Intl 1:34–45

Iqbal MF, Cheng Y, Zhu W, Zeshan B (2008) Mitigation of ruminant methane production: current strategies, constraints and future options. World J Microb Biot 24:2747–2755

Jadhav RV, Kannan A, Bhar R, Sharma OP, Gulati A, Rajkumar K, Mal G, Singh B, Verma MR (2018) Effect of tea (*Camellia sinensis*) seed saponins on in vitro rumen fermentation, methane production and true digestibility at different forage to concentrate ratios. J Appl Anim Res 46:118–124

Jahani-Azizabadi H, Durmic Z, Vadhanabhuti J, Vercoe PE (2019) Effect of some australian native shrubs essential oils on in vitro rumen microbial fermentation of a high-concentrate diet. J Anim Plant Sci 29:8–15

Juottonen H, Galand PE, Yrjälä K (2006) Detection of methanogenic Archaea in peat: comparison of PCR primers targeting the mcrA gene. Res Microbiol 157:914–921

Kamra D (2005) Rumen microbial ecosystem. Curr Sci 89:124–135

Khatiwora E, Adsul VB, Kulkarni MM, Deshpande NR, Kashalkar RV (2010) Spectroscopic determination of total phenol and flavonoid contents of *Ipomoea carnea*. Int J ChemTech Res 2:1698–1701

Kliebenstein DJ (2013) Making new molecules—evolution of structures for novel metabolites in plants. Curr Opin Plant Biol 16:112–117

Klita PT, Mathison GW, Fenton TW, Hardin RT (1996) Effects of alfalfa root saponins on digestive function in sheep. J Anim Sci 74:1144–1156

Knapp JR, Laur GL, Vadas PA, Weiss WP, Tricarico JM (2014) Invited review: enteric methane in dairy cattle production: quantifying the opportunities and impact of reducing emissions. J Dairy Sci 97:3231–3261

Lei Z, Zhang K, Li C, Wu J, Davis DI, Casper DP, Jiang H, Jiao T, Wang J, Wang X (2018) Dietary supplementation with essential-oils-cobalt for improving growth performance, meat quality and skin cell capacity of goats. Sci Rep 8:11634

Lei Z, Zhang K, Li C, Jiao T, Wu J, Wei Y, Tian K, Li C, Tang D, Davis DI, Casper DP, Jiang H, Wang X, Wang J (2019) Ruminal metagenomic analyses of goat data reveals potential functional microbiota by supplementation with essential oil-cobalt complexes. BMC Microbiol 19:30

Lima PMT, Moreira GD, Sakita GZ, Natel AS, Mattos WT, Gimenes FMA, Gerdes L, McManus C, Abdalla AL, Louvandini H (2018) Nutritional evaluation of the legume *Macrotyloma axillare* using in vitro and in vivo bioassays in sheep. J Anim Physiol Anim Nutr 102:669–676

Liu C, Qu YH, Guo PT, Xu CC, Ma Y, Luo HL (2018) Effects of dietary supplementation with alfalfa (*Medicago sativa* L.) saponins on lamb growth performance, nutrient digestibility, and plasma parameters. Anim Feed Sci Technol 236:98–106

Liu Y, Ma T, Chen D, Zhang N, Si B, Deng K, Tu Y, Diao Q (2019) Effects of tea saponin supplementation on nutrient digestibility, methanogenesis, and ruminal microbial flora in Dorper crossbred ewe. Animals 9:29

Lopes SG, Barros LBG, Louvandini H, Abdalla AL, Costa Junior LM (2016) Effect of tanniniferous food from *Bauhinia pulchella* on pasture contamination with gastrointestinal nematodes from goats. Parasit Vectors 9:102

Lu CD, Jorgensen NA (1987) Alfalfa saponins affect site and extent of nutrient digestion in ruminants. J Nutr 117:919–927

Macheboeuf D, Morgavi DP, Papon Y, Mousset JL, Arturo-Schaan M (2008) Dose–response effects of essential oils on in vitro fermentation activity of the rumen microbial population. Anim Feed Sci Technol 145:335–350

Makkar HPS (2003) Quantification of tannins in tree and shrub foliage. A laboratory manual. Kluwer Academic Publishers, Dordrecht

Malik PK, Kolte AP, Baruah L, Saravanan M, Bakshi B, Bhatta R (2017) Enteric methane mitigation in sheep through leaves of selected tanniniferous tropical tree species. Livest Sci 200:29–34

Marinoa R, Atzori AS, D'andrea M, Iovane G, Trabalza-Marinucci M, Rinald L (2015) Climate change: production performance, health issues, greenhouse gas emissions and mitigation strategies in sheep and goat farming. Small Rumin Res 135:50–59

McAllister TA, Newbold CJ (2008) Redirecting rumen fermentation to reduce methanogenesis. Aust J Exp Agric 48:7–13

McCann JC, Wickersham TA, Loor JJ (2014) High-throughput methods redefine the rumen microbiome and its relationship with nutrition and metabolism. Bioinform Biol Insights 8:109–125

McSweeney C, Mackie R (2012) Commission on genetic resources for food and agriculture. Micro-organisms and ruminant digestion: state of knowledge, trends and future prospects. Backgr Study Paper (FAO) 61:1–62

Min BR, Salaiman S, Shange R, Eun JS (2014) Gastrointestinal bacterial and methanogenic archaea diversity dynamics associated with condensed tannin-containing pine bark diet in goats using 16S rDNA amplicon pyrosequencing. Int J Microbiol Hindawi Publishing Corporation, Archaea, Article ID 141909. https://doi.org/10.1155/2014/141909

Morgavi DP, Forano E, Martin C, Newbold CJ, Anderson RC, Rasmussen MA, Morrison M (2010) Microbial ecosystem and methanogenesis in ruminants. Animal 4:1024–1036

Mueller-Harvey I (2006) Unravelling the conundrum of tannins in animal nutrition and health. J Sci Food Agric 86(13):2010–2037

Naghiloo S, Movafeghi A, Delazar A, Nazemiyeh H, Asnaashari S, Dadpour MR (2012) Ontogenetic variation of total phenolics and antioxidant activity in roots, leaves and flowers of *Astragalus compactus Lam.* (Fabaceae). BioImpacts 2:105–109

Ozkan CO, Kamalak A, Atalay AI, Tatliyer A, Kaya E (2015) Effect of peppermint (*Mentha piperita*) essential oil on rumen microbial fermentation of barley grain. J Appl Anim Res 43:287–290

Patra AK (2012) Enteric methane mitigation technologies for ruminant livestock: a synthesis of current research and future directions. Environ Monit Assess 184:1929–1952

Patra AK (2014) Trends and projected estimates of GHG emissions from Indian livestock in comparisons with GHG emissions from world and developing countries. Asian-Australas J Anim Sci 27:592–599

Patra AK, Saxena J (2009) A review of the effect and mode of action of saponins on microbial population and fermentation in the rumen and ruminant production. Nutr Res Rev 22:204–219

Patra AK, Saxena J (2010) A new perspective on the use of plant secondary metabolites to inhibit methanogenesis in the rumen. Phytochemistry 71:1198–1222

Pellikaan WF, Stringano E, Leenaars J, Bongers DJGM, Van Laar-van Schuppen S, Plant J, Mueller-Harvey I (2011) Evaluating effects of tannins on extent and rate of in vitro gas and CH_4 production using an automated pressure evaluation system (APES). Anim Feed Sci Technol 166–167:377–390

Pen B, Sar C, Mwenya B, Kuwaki K, Morikawa R, Takahashi J (2006) Effects of *Yucca schidigera* and *Quillaja saponaria* extracts on in vitro ruminal fermentation and methane emission. Anim Feed Sci Technol 129:175–186

Pen B, Takaura K, Yamaguchi S, Asa R, Takahashi J (2007) Effects of *Yucca schidigera* and *Quillaja saponaria* with or without b-1, 4 galacto oligosaccharides on ruminal fermentation, methane production and nitrogen utilization in sheep. Anim Feed Sci Technol 138:75–88

Pen B, Sar C, Mwenya B, Takahashi J (2008) Effects of *Quillaja saponaria* extract alone or in combination with *Yucca schidigera* extract on ruminal fermentation and methanogenesis in vitro. J Anim Sci 79:193–199

Qi M, Jakober KD, McAllister TA (2010) Rumen microbiology. In: Hudson RJ (ed) Animal and plant productivity. Encyclopedia of Life Support Systems (EOLSS), Oxford, p 462

Ramakrishna A, Ravishankar GA (2011) Influence of abiotic stress signals on secondary metabolites in plants. Plant Signal Behav 6:1720–1731

Ramírez-Restrepo CA, Tan C, O'Neill CJ, López-Villalobos N, Padmanabha J, Wang J, McSweeney CS (2016) Methane production, fermentation characteristics, and microbial profiles in the rumen of tropical cattle fed tea seed saponin supplementation. Anim Feed Sci Technol 216:58–67

Righi F, Simoni M, Foskolos A, Beretti V, Sabbioni A, Quarantelli A (2017) In vitro ruminal dry matter and neutral detergent fibre digestibility of common feedstuffs as affected by the addition of essential oils and their active compounds. J Anim Feed Sci 26:204–212

Sallam SMA, Bueno ICS, Nasser ME, Abdalla AL (2010) Effect of eucalyptus (*Eucalyptus citriodora*) fresh or residue leaves on methane emission in vitro. Ital J Anim Sci 9:299–303

Sallam SMA, Abdelgaleil SAM, Bueno ICS, Nasser MEA, Araujo RC (2011) Effect of some essential oils on in vitro methane emission. Arch Anim Nutr 3:203–214

Sallam SMA, Morsy AS, Soltan YA, Alencar SM, Abdalla AL (2012) Antimethanogenic activity of commercial essential oils products. In: Proceedings of 14th international seminar of FAO-CIHEAM sub-network on sheep and goat nutrition and 2nd symposium low input breeds. Feeding and management strategies to improve livestock productivity, welfare and product quality under climate changes

Samal L, Chaudhary LC, Agarwal N, Kamra DN (2016) Effects of plants containing secondary metabolites as feed additives on rumen metabolites and methanogen diversity of buffaloes. Anim Prod Sci 56:472–481

Saminathana M, Sieoa CC, Ganc HM, Abdullahb N, Wong CMVL, Ho YW (2016) Effects of condensed tannin fractions of different molecular weights on population and diversity of bovine rumen methanogenic archaea in vitro, as determined by high-throughput sequencing. Anim Feed Sci Technol 216:146–160

Santoso B, Mwenya B, Sar C, Gamo Y, Kobayashi T, Morikawa R, Kimura K, Mizukoshi H, Takahashi J (2004) Effects of supplementing galacto oligosaccharides, *Yucca schidigera* and nisin on rumen methanogenesis, nitrogen and energy metabolism in sheep. Livest Prod Sci 91:209–217

Sharma AK, Gangwar M, Kumar D, Nath G, Kumar Sinha AS, Tripathi YB (2016) Phytochemical characterization, antimicrobial activity and reducing potential of seed oil, latex, machine oil and press cake of *Jatropha curcas*. Avicenna J Phytomed 6:366–375

Siddiqui ZS, Arif UZ (2004) Effects of benlate systemic fungicide on seed germination, seedling growth, biomass and phenolic contents in two cultivars of *Zea mays L.* Pak J Bot 36:577–582

Skuce PJ, Morgan ER, Van Dijk J, Mitchell M (2013) Animal health aspects of adaptation to climate change: beating the heat and parasites in a warming Europe. Animal 7:333–345

Sliwinski BJ, Kreuzer M, Wettstein HR, Machmuller A (2002) Rumen fermentation and nitrogen balance of lambs fed diets containing plant extracts rich in tannins and saponins and associated emissions of nitrogen and methane. Arch Anim Nutr 56:379–392

Smith AH, Zoetendal E, Mackie RI (2005) Bacterial mechanisms to overcome inhibitory effects of dietary tannins. Microbiol Ecol 50:197–205

Soltan YA, Morsy AS, Araujo RC, Elziat HM, Sallam SMA (2011) Carvacrol and eugenol as modifiers of rumen microbial fermentation and methane production in vitro. In: Proceedings of 4th animal wealth research conference in the Middle East and North Africa, pp 354–364

Soltan YA, Morsy AS, Sallam SMA, Louvandini H, Abdalla AL (2012) Comparative in vitro evaluation of forage legumes (*prosopis, acacia, atriplex,* and *leucaena*) on ruminal fermentation and methanogenesis. J Anim Feed Sci 21:759–772

Strack D (1997) In: Dey PM, Harborne JB (eds) Phenolic metabolism: plant biochemistry. Harcourt Asia PTE Ltd, Noida, pp 387–390

Szumacher-Strabel M, Cieslak A (2010) Potential of phytofactors to mitigate rumen ammonia and methane production. J Anim Feed Sci 19:319–337

Taiz L, Zeiger E (2006) Secondary metabolites and plant defense. Plant Physiol 4:315–344

Takahashi J, Miyagawa T, Kojima Y, Umetsu K (2000) Effects of *Yucca schidigera* extract, probiotics, monensin and L-cysteine on rumen methanogenesis. Asian Aust J Anim Sci 13:499–501

Tan HY, Sieo CC, Abdullah N, Liang JB, Huang XD, Ho YW (2011) Effects of condensed tannins from *Leucaena* on methane production, rumen fermentation and populations of methanogens and protozoa in vitro. Anim Feed Sci Technol 169:185–193

Tan HY, Sieo CC, Abdullah N, Liang JB, Huang XD, Ho YW (2013) Effect of condensed tannins on bovine rumen protist diversity based on 18S rRNA gene sequences. J Euk Microbiol 60:98–100

Tavendale MH, Meagher IP, Pacheco D, Walker N, Atwood GT, Subathira S (2005) Methane production from in vitro rumen incubations with *Lotus pedunculatus* and *Medicago sativa* and effects of extractable condensed tannin fractions on methanogenesis. Anim Feed Sci Technol 123(124):403–419

Varadyova Z, Zelenak I, Sirka P (2000) In vitro study of the rumen and hindgut fermentation of fibrous materials (meadow hay, beech sawdust, wheat straw) in sheep. Anim Feed Sci Technol 83:127–138

Verma N, Shukla S (2015) Impact of various factors responsible for fluctuation in plant secondary metabolites. J Appl Res Med Arom Plants 2:105–113

Vogels GD, Hoppe WF, Stumm CK (1980) Association of methanogenic bacteria with rumen ciliates. Appl Environ Microbiol 40:608–612

Voon HC, Bhat R, Gulam R (2012) Flower extracts and their essential oils as potential antimicrobial agents for food uses and pharmaceutical applications. Compr Rev Food Sci Food Saf 11:34–55

Wadhwa M, Bakshi MPS, Makkar HPS (2016) Modifying gut microbiomes in large ruminants: opportunities in non-intensive husbandry systems. Anim Front 6:27

Wang Y, McAllister TA, Newbold CJ, Rode LM, Cheeke PR, Cheng KJ (1998) Effect of *Yucca schidigera* extract on fermentation and degradation of steroidal saponins in the rumen simulation technique (RUSITEC). Anim Feed Sci Technol 74:143–153

Wang CJ, Wang SP, Zhou H (2009) Influences of flavomycin, ropadiar, and saponin on nutrient digestibility, rumen fermentation, and methane emission from sheep. Anim Feed Sci Technol 148:157–166

Wang B, Tu Y, Zhao SP, Hao YH, Liu JX, Liu FH, Xiong BH, Jiang LS (2017) Effect of tea saponins on milk performance, milk fatty acids, and immune function in dairy cow. J Dairy Sci 100:8043–8052

Weimer PJ (2015) Redundancy, resilience, and host specificity of the ruminal microbiota: implications for engineering improved ruminal fermentations. Front Microbiol 6:296

Yatoo MI, Kumar P, Dimri U, Sharma MC (2012) Effects of climate change on animal health and diseases. Int J Livest Res 2:15–24