

Review

The potential impacts of dietary plant natural products on the sustainable mitigation of methane emission from livestock farming



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ABSTRACT

Livestock production is one of the major contributors of greenhouse gases such as methane (CH_4) and carbon dioxide (CO_2). These gases contribute greatly to global warming, environmental degradation and pollution. Livestock production is responsible for 18% CH_4 and 9% CO_2 productions of all greenhouse gases emissions. Methane has a greater global warming effect (about 23 times) more than CO_2 . Currently, livestock production faces a great challenge of increasing production to meet global demand for agricultural products and at the same time reduces environmental impact. Many researchers have reported the effects of substituting phytoconstituents such as tannins, saponins and essential oil as chemical feed additives to modify rumen fermentation. These modifications are aimed at reducing loss of feed energy, improving animal productivity and mitigating CH_4 and CO_2 emitted during livestock production. This present review is aimed at providing information on the influence of plant natural products or secondary metabolites (PNP) such as tannins, saponins and essential oils on ruminal microflora and their potentials to mitigate biogases during livestock production. This work will also review purported anti-microbial activities of plant secondary metabolites and its ability to improve animal health and enhance productivity. From the findings of this review, PNP have the potential to improve rumen fermentation, reduce loss of feed energy, improve animal health and productivity, increase animal lifetime performance, and reduce greenhouse gases production- CH_4 and CO_2 during animal production. This review also revealed that supplementation of saponin, tannins or essential oils at low to moderate doses have more potentials and are the promising natural feed additives suitable to manipulate microbial ecosystems, inhibit pathogenic bacteria proliferation in gastrointestinal tract, improve rumen fermentations, mitigate rumen CH_4 production and reduce environmental impact of livestock production. However, further research is required to establish the effective daily doses of plant natural products to animals without any detrimental effect.

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Contents

1. Introduction	916
2. Effects of saponins on the ruminant microflora and CH_4 production	916
3. Effects of tannins on the ruminant microflora and CH_4 production	919
4. Effects of essential oil on the ruminant microflora and CH_4 production	921
5. Conclusion	922
6. Implications and recommendations	922

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Acknowledgements	923
References	923

1. Introduction

In the past two decades, there have been emerging and growing worries about the significant increase in greenhouse gases emissions. These gases- CH₄, NO₂ and CO₂ have detrimental impact on the environment and causes global warming which leads to climate change and environmental degradation (IPCC, 2007, Patra and Sexena, 2010). Currently, agro-food based industries such as livestock production is among the leading contributors of the anthropogenic source of greenhouse gases- CH₄ and CO₂ (Audsley and Wilkinson, 2014). Slade et al. (2016) in their recent investigation observed that two-third of these direct emissions is due to livestock production. According to the report of FAO (2006), animal production is responsible for 18% CH₄ and 9% CO₂ productions of all gases emissions. Methane has a greater global warming effects (about 23 times) more than CO₂ (Rira et al., 2015) and accounts for 50–60% emitted gases during ruminant production (Mirzaei-Aghsaghali et al., 2012). The main constraints in livestock production are nutrient wastage caused by excess excretion and inefficient or poor digestibility of feeds, CO₂ and CH₄ emissions that causes 2–12% loss of feed energy (Hristov et al., 2015). Because of these challenges, animal nutritionists, biochemists and microbiologists have focused their attention on the application of PNP (Elghandour et al., 2018a), enzymes (Hernández et al., 2017a,b; Vallejo-Hernández et al., 2018) and yeasts (Shurson, 2018) as feed additives to modify or manipulate microbial ecosystems and fermentation kinetics of ruminants. The basic aim of these modifications is to improve animal feed utilization, enhance digestibility of fibrous feeds, reduce protein degradability (Salem et al., 2012), inhibits pathogenic bacteria proliferation in gastrointestinal tract (Arowolo and He, 2018), increase animal performance, minimize loss of dietary energy during rumen fermentation, and also reduce CH₄ and CO₂ productions for eco-friendly animal production. Recently, researchers have demonstrated that PNP are exploitable natural and safer feed additives that can play essential role to reduce CH₄ and CO₂ productions during ruminant production without adversely affecting rumen fermentation (Patra and Saxena, 2010). Elghandour et al. (2017) reported that the leaves of *Pistacia vera*, *Dalbergia retusa*, *Crescentia alata*, *Azadirachta indica*, *Eichhornia crassipes*, *Cnidoscolus chayamansa*, *Guazuma ulmifolia*, *Vitex mollis* and *Moringa oleifera* decreased CH₄ and CO₂ emissions in dairy calves. Elghandour et al. (2018b) also reported that Prickly cactus and *Moringa oleifera* extract in ruminant diets significantly decreased CH₄ and CO₂ production. Halmemies-Beauchet-Filleau et al. (2018) reported that Lipid-rich camelina (*Camelina sativa*) has potential to enrich ruminant milk and meat fat with bioactive trans-11 18:1 and cis-9,trans-11 18:2 fatty acids and also mitigate CH₄ emissions. These significant reductions are likely due to PNP present in the plant leaves (see Table 1).

Plant natural products (i.e., PNP) are non-nutritive plant metabolites that play vital roles such as protection of plants against herbivorous organisms, microorganisms and pests (Bodas et al., 2012). The term refers to a large group of biological compounds that are resident in plants and confers several biochemical potentials relating to growth and reproduction (Patra and Sexena, 2010). These group of large molecular weight compounds, do not only possess phytopotentials, but also present important benefits in healing and managing of diseases and infections. Several classes of

PNP have already been screened over the years with the aid of high profile techniques, and they include saponins, tannins, terpenoids, flavonoids, glycosides, alkaloids, phenols and essential oils. These natural products emanate from a common metabolic pathway (Fig. 1). The bioactivity of these compounds is influenced greatly by geographical location coupled with weather condition, time/period of collection, method used to process or store them (Bodas et al., 2008). The feeds of ruminant animals contain bulk of complex molecules that are degraded by microbes during fermentation to release energy and other chemical compounds (IPCC, 2007). The incorporation of PNP as biological additives in the feed of ruminants has been observed over the year to reduce loss of feed energy to metabolisable energy (Johnson et al., 1991), thus decreasing the energy loss and emission of CH₄ and CO₂ into the atmosphere. This review report will provide insight on the use of few selected PNP like saponins, tannins and essential oils as feed additives to modify or manipulate ruminal microflora and fermentation kinetics in order to reduce CH₄ and CO₂ during ruminant production. It will also evaluate the anti-microbial activities of PNP and their ability to improve animal health and enhance productivity. The review will draw conclusions on whether and to what extent PNP have beneficial effects, and recommend more *in vitro* and *in vivo* practical studies to be carried out on PNP as an alternative feed additive.

2. Effects of saponins on the ruminant microflora and CH₄ production

Structurally, saponins (Fig. 2) are supra molecular glycosides of steroids and triterpenoids abundantly present in plants (Vincken et al., 2007). Chemically, saponins are complex organic compounds consisting of saccharide chain backbone bound to either triterpene or steroid aglycone moiety called sapogenin (Petra and Sexena, 2010). The triterpene are more abundant in nature and consist of about 30 carbon atoms whereas the steroid saponins contain 27-carbon atoms linked to either 6-ring spirostane or 5-ring furostane structure and belong to the class of Liliopsida (Petra and Sexena, 2010). Saponins are mainly found in angiospermous plants and they protect plants against the attack of bacteria and fungi diseases (Szumacher-Strabel and Cieślak, 2012). In nature, spirostanol is monodesmosidic and furostanol bidesmosidic. The aglycone moiety links with different sugars which are integral in the determination and derivation of a large number of saponin.

Several research works have been documented on the interaction of saponins with rumen methanogens. Presently, there is paucity of information on the inhibitory activity of saponins on rumen methanogens. For example, in cattle, an *in vitro* fermentation of rumen liquor, saponin from the extracts of leaves of *Sesbania sesban*, seeds of fenugreek and leaves of *Knautia* reduced methanogen populations by 78, 22 and 21%, respectively (Goel et al., 2008). The efficacy of these phytoconstituent is directly proportional to the concentrations in the ruminal diet. At 2 mg/mL of methanolic fruit extract of *Sapindus rarak*, the level of archaeal RNA methanogens as determined by the method of membrane hybridization, was not affected but reduced significantly at the highest dose of 4 mg/mL (Wina et al., 2005). However, at lower doses of 0.4 mg/mL, tea saponin had no inhibitory effect on the growth of rumen methanogens present in the ruminal fluid from sheep (Guo

Table 1Effects of plant natural products (PNP) on methane (CH_4) and rumen fermentation parameters.

Plant sources and (PNP)	Doses	Animals	Effect on CH_4	Effect on fermentation parameters	References
<i>Acacia mearnsii</i> (Condensed tannin)	0.615 g/g CT/kg of DM	Sheep	Reduced CH_4 production (13%)	Decreased ruminal ammonia concentration	Carulla et al. (2005)
<i>Leucaena leucocephala</i> (Condensed tannin)	40 g CT/kg of DM	Sheep	Reduced CH_4 production (25.7%)	Not detected	Dias-Moreira et al. (2013)
<i>Castanea sativa</i> (Condensed tannin)	68.6%	Sheep	No alteration in CH_4 production	Had effects on rumen fermentation	Wischer et al. (2014)
<i>Quercus valonea</i> (Condensed tannin)	63.3%	Sheep	No alteration in CH_4 production	Had effects on rumen fermentation	Wischer et al. (2014)
<i>Terminalia chebula</i> (Condensed tannin)	47.2 g DM/kg	Sheep	Reduced CH_4 production (24%)	Increased in digestibility	Patra et al. (2011)
<i>Ficus benghalensis</i> (Condensed tannin)	272 g/kg DM	Sheep	20.4%	No influence dry matter and digestibility	Malik et al. (2017)
<i>Artocarpus heterophyllus</i> (Condensed tannin)	179 g/kg DM	Sheep	20.8%	No influence dry matter and digestibility	Malik et al. (2017)
<i>Azadirachta indica</i> (Condensed tannin)	184 g/kg DM	Sheep	26.1%)	No influence dry matter and digestibility	Malik et al. (2017)
<i>Salix spp.</i> (Condensed tannin)	12 g/kg diet	Sheep	No effect	No effect	Ramirez-Restrepo et al. (2009)
<i>C. sativa</i> wood (Hydrolysed tannin)	20%	Sheep	Increased CH_4 (21.5%)	Digestibility, TVFA, acetate to propionate ratio, protozoa numbers unaffected	Sliwinski et al. (2002)
<i>Calliandra calothyrsus</i> (Condensed tannin)	11.5%	Lamb	Reduced CH_4 (21.5%)	Decreased digestibility	Tiemann et al. (2008)
<i>Lespedeza striata</i> (Condensed tannin)	151 g CT/kg of DM	Goats	Decreased CH_4 production (54.8%)	Reduced protozoa	Animut et al. (2008a)
<i>Lespedeza cuneata</i> (Condensed tannin)	153 g CT/kg of DM	Goat	Reduced CH_4 production (46.3%)	Reduced protozoa	Puchala et al. (2012a)
<i>Lespedeza cuneata</i> (Condensed tannin)	20% of CT/kg of DM	Goat	Reduced CH_4 production (40.9%)	Reduced protozoa	Puchala et al. (2012b)
<i>Lespedeza cuneata</i> (Condensed tannin)	17.7%	Goat	Reduced CH_4 production (50.2%)	TVFA and acetate to propionate ratio unaffected	Puchala et al. (2005)
<i>Lespedeza cuneata</i> (Condensed tannin)	14%	Goat	Reduced CH_4 production (43.1%)	Digestibility and protozoa numbers decreased, TVFA and acetate to propionate ratio unaffected	Animut et al. (2008b)
<i>Lespedeza cuneata</i> (Condensed tannin)	2.6%	Steer cattle	Decreased CH_4 production	No effect on total gas production	Naumann et al. (2015)
<i>Desmodium paniculatum</i> (Condensed tannin)	9%	Steer cattle	Decreased CH_4 production	No effect on total gas production	Naumann et al. (2015)
<i>Acacia mearnsii</i> black wattle (mimoso); 700 g/kg DM CT; <i>Castanea sativa</i> Mill (chestnut); 800 g/kg DM HT	14.9 mg/kg DM	Steer cattle	no effect on CH_4	No effect on nutrient intake, digestibility	Krueger et al. (2010)
<i>Acacia mearnsii</i> (Condensed tannin)	603 g CT/kg of DM	Cattle	Reduced CH_4 production (29.0%)	Decreased digestibility	Grainger et al. (2009)
<i>Vaccinium vitis idaea</i> (Condensed tannin)	2 g CT/kg of DM	Cattle	Reduced CH_4 production (11.3%)	Reduced protozoa	Cieslak et al. (2012)
<i>Schinopsis quebracho-colorado</i> (Condensed tannin)	2%	Cattle	No alteration in CH_4 production	Not detected	Beauchemin et al. (2007)
<i>Acacia mearnsii</i> (Condensed tannin)	0.6%	Cattle	Reduced CH_4 production (8%)	Reduced relative energy loss	Junior et al. (2017)
Tea (saponin)	0.50 g/L	Cow	Reduced CH_4 (29%)	Reduced protozoa concentration	Guyader et al. (2016)
<i>Yucca schidigera</i> (saponin)	10 g/kg of DM	Cow	No effect	No effect on TVFA, protozoal number, ammonia, propionate	Holtshausen et al. (2009)
<i>Quillaja saponaria</i>	10 g/kg of DM	Cow	No alteration in CH_4 production	No effect on TVFA, protozoal number, ammonia, propionate	Holtshausen et al. (2009)
Tea saponins	4.1 g/kg diet	Lamb	Reduced CH_4 (28.3%)	TVFA increased; acetate to propionate ratio unaffected; protozoa number decreased	Mao et al. (2010)
<i>Quillaja saponaria</i> (saponin)	13.5 g/kg of diet	Sheep	Reduced CH_4 (21.7%)	TVFA decreased, Digestibility, acetate to propionate ratio and protozoa numbers unaffected	Pen et al. (2007)
<i>Yucca schidigera</i>	13.8 g/kg of diet	Sheep	Reduced CH_4 (15.6%)	TVFA decreased, digestibility, acetate to propionate ratio and protozoal numbers unaffected	Pen et al. (2007)
Tea saponins	5 g/kg diet	Sheep	No effect	TVFA and acetate to propionate ratio unaffected	Yuan et al. (2007)
<i>S. saponaria</i> fruits (saponin)	5 g/kg BW	Sheep			

(continued on next page)

Table 1 (continued)

Plant sources and (PNP)	Doses	Animals	Effect on CH ₄	Effect on fermentation parameters	References
Tea (saponin)	0.24 g/L	Sheep	Reduced CH ₄ (7.8%) Reduced CH ₄ (14%)	Digestibility, acetate to propionate ratio and protozoa decreased; TVFA increased. Reduced protozoa	Hess et al. (2004) Guo et al. (2008)
Lucerne saponins (saponin)	27.8%	Sheep	No effect	TVFA and acetate to propionate ratio; unaffected; digestibility and Protozoa decreased	Klita et al. (1996)
<i>Medicago sativa</i> (saponin)	20.4 g/kg DM	Sheep	Reduced CH ₄ (7.1%)	TVFA and acetate to propionate ratio; unaffected	Goel et al. (2008)
Tea seed (saponin)	30 g/day	Cattle	Reduced CH ₄ (22%)	TVFA, acetate and propionate were not affected	Ramírez-Restrepo et al. (2016)
Tea seed (saponin)	0.8%	Steer cattle	Reduced CH ₄ (32.5%)	Protozoa count, ammonia-N production decreased	Jadhav et al. (2016)
<i>Quillaja saponaria</i> (saponin)	50–70 g/kg	Cow	No effect	decreased protozoa numbers, ammonia production, No effect on TVFA	Pen et al. (2006)
<i>Yucca schidigera</i> (Sarsaponin)	5 g/day	Cow	Decreased CH ₄	Increased gas production, and VFA production	Singer et al. (2008)
<i>Trifolium alexandrinum</i> (Berseem fodder) saponin	45% of the diet	Cattle	Decreased CH ₄ (17%)	No effect	Malik et al. (2010a)
<i>Medicago sativa</i> (Lucerne fodder) saponin	45% of the diet	Cattle	Reduced on CH ₄	Decreased protozoa number	Malik et al. (2010b)

CH₄: methane, TVFA: total volatile fatty acid, CT: condensed tannin, HT: hydrolysed tannin, DM: dry matter.

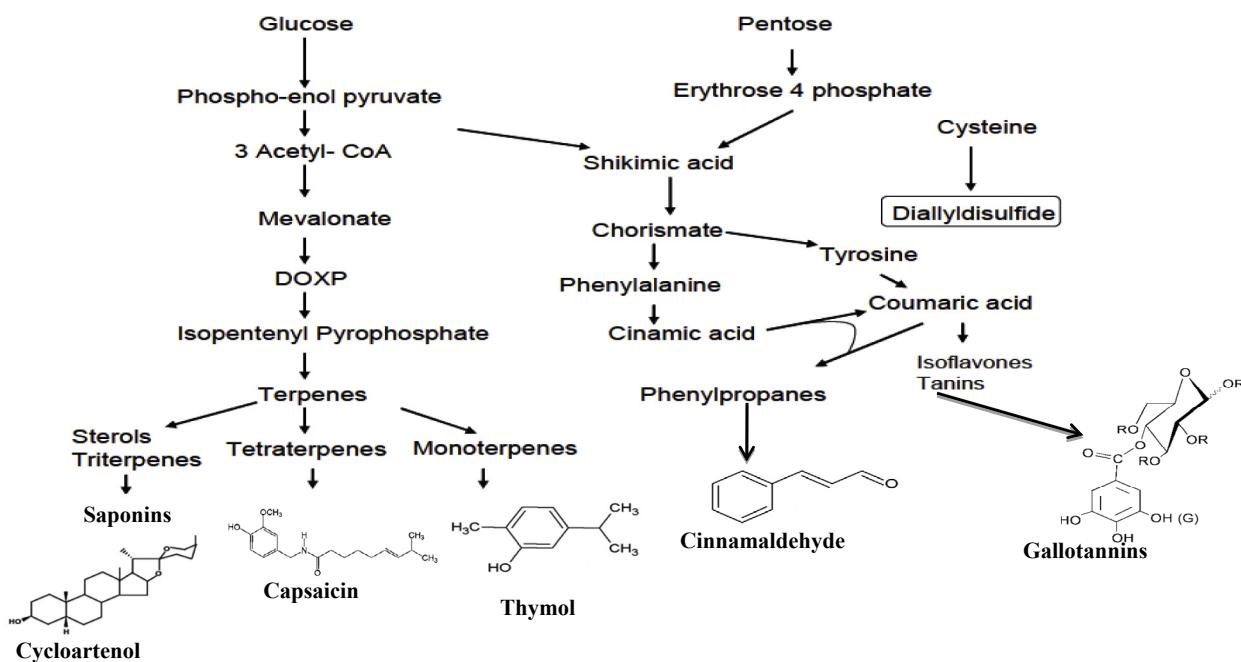


Fig. 1. Generalized pathway for the biosynthesis of PNP (saponins, tannins and essential oils (modified from Calsamiglia et al., 2007).

et al., 2008). Zhou et al. (2012) documented that addition of tea saponin at the concentrations ranging from 400 to 800 mg/kg had no influence on nutrient digestibility and rumen fermentation in goats. Ramírez-Restrepo et al. (2016) opined that saponin containing tea seed from *Camellia sinensis* L. supplemented to the diet of cattle neither decrease population of protozoa nor reduce CH₄ emissions. Goel et al. (2008) also reported that inclusion of *Trigonella foenumgraecum* seeds extract containing 34.5% at the concentration of 0.14 and 0.29 g/L did not decrease methanogen populations. Klita et al. (1996) reported that the doses of 800 and 1600 mg/kg saponin from the root extract of alfalfa reduced the population of ruminal protozoa and decreased ruminal digestibility. Patra and Yu (2012) established that the combination of 0.6 and 1.2 g/L of *Quillaja* saponin and nitrate (NO₃) increased

cellulolytic bacteria and feed degradability. Hu et al. (2005) observed that the ability of tea saponins to modify rumen fermentation through inhibition of CH₄ and NH₃-N release is integral in the utilization of nutrients *in vitro*. Guyader et al. (2016) stated that 0.5 g/L of added saponin caused 29% reduction in CH₄ while Hu et al. (2005) reported a similar findings *in vitro* study and reported 14% CH₄ reduction (mL/g) for 0.24 g/L of added saponin.

Sarsaponin and steroid saponins from the *Yucca schidigera* as well as triterpenoids from *Quillaja saponaria* had anti-methanogenic effect in *in vitro* study (Takahashi et al., 2000) and also in *in vivo* studies (Pen et al., 2007; Holtshausen et al., 2009). Inclusion of 35% saponins from sarsaponins for 25 days in the sheep diet of 0.12 and 0.13 g/kg diet) decreased CH₄ production by 7.1 and 15.5%, respectively (Santoso et al., 2004; Wang et al., 2009). Pen

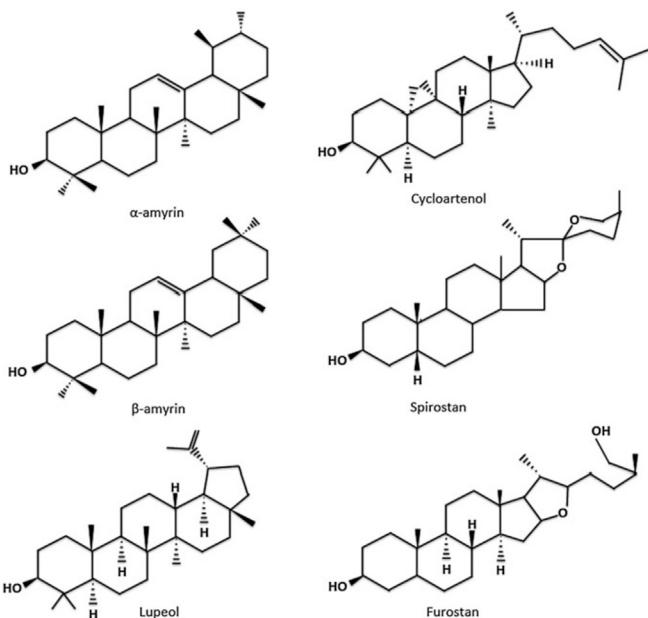


Fig. 2. Chemical structures of triterpenoids (α -amyrin, β -amyrin, lupeol) and steroids (cycloartenol, spirostan and furostan) (Faizal and Geelen, 2013).

et al. (2007) also reported that *Yucca schidigera* extract containing 8–10% saponins had 11.7% decrease in CH_4 production. In contrast, Sliwinski et al. (2002) reported that there is no influence on methanogens as a result of addition of low doses of saponins in sheep diet. Supplementation of *Y. schidigera* plant extract containing 6% saponins to diet of dairy cows and fed for 28 days had no effect on CH_4 production (Holtshausen et al., 2009). However, the decrease in the production of CH_4 has been also linked to the suppression of genes that control methanogenesis without changing the population of methanogens (Hess et al., 2003; Guo et al., 2008). Hostettmann and Marston (1995) stated that the inhibition of the growth of protozoa may be through destruction of cell membrane of protozoa which occurs as a result of sterol-saponin binding capacity. Another study reported that saponin inclusion in the diet favours the synthesis of higher proportion of propionates which may result to decrease CH_4 production. Immig (1996) and Varadyova et al. (2000), found that saponins have the ability to shift or move the breakdown of animal nutrients in rumen to the hindgut, thus lowering methanogenesis due to reductive acetogenesis, decrease in ruminal fermentation and no or lack of protozoa in the hindgut. However, rapid digestibility of feed diets has the ability to cause a manifold increase in methanogenesis owing to significant increase in bacterial and fungal population (Pen et al., 2007). In addition, the reverse correlation found amidst of digesta passage rate and CH_4 emission may be because of an increase in degradation of fiber in the rumen; however, saponins have been reported to lower the rate of digesta passage (Klita et al., 1996). The rate of methanogenesis may increase following the interaction of saponins with passage rate. However, Lu and Jorgensen (1987) reported that the physiological influence of saponin may be non-significant compared to the microbiological effects. Wallace (2004) reported that saponin containing extract has the potential to suppress the bacterial activities, and therefore enhance microbial protein in rumen fluid collected from cattle and sheep. Based on the available information, it can be inferred that saponins might exert substantial inhibitory effect at higher doses on the proliferation of methanogens.

3. Effects of tannins on the ruminant microflora and CH_4 production

Tannins are supra molecular weight hydrophilic compounds capable of forming tannin-protein complex because of the presence of large proportion of phenolic hydroxyl groups. They are classified into three groups according to their chemical structures. There are two main class of tannins; hydrolysable tannins (HT), and condensed tannins (CT). While the HT are substituted from a carbohydrate core (usually glucose) esterified with gallic acid (gallo-tannin) or ellagic acid (ellagitannin), CT are polymeric unit of flavonol (flavan-3-ol) commonly joined by carbon-carbon bonds in the 4/6 or 4/6 position (Ferreira et al., 1999; Le Bourvellec and Ranarda, 2012). Complex tannins on the other hand, are tannins in which a catechin unit is linked glycosidically to either gallo-tannin or ellagitannin units and are partially hydrolysable owing to carbon–carbon coupling of their catechin unit (Fig. 3).

Tannins as a naturally occurring plant secondary metabolite that can be easily accessed and suitably use as natural alternative source of feed additives to improve digestive utilization of dietary protein (Hernandez et al., 2014; Salem et al., 2014), mitigate CH_4 and CO_2 productions and improve animal productivity in agro-based industries (Huang et al., 2018). Tannins also have anti-microbial, anti-oxidant and anti-parasitic activities which are useful in ruminant animal production. Cipriano-Salazar et al. (2018) established that tannic acid has the potential to inhibit ruminal bacteria from sheep. They reported that tannic acid $\leq 1.25 \text{ mg/L}$ could be efficiently used to manipulate ruminal microbial activities and improve animal production by enhancing feed utilization. Tannins-containing forage can adequately bind to excess plant proteins, precipitating them out of rumen fluid and in the process prevent the formation of stable foam's characteristic of pasture bloat. This non-bloating tendency and inhibition of internal parasites are exquisite traits of tannins to grazing ruminants (Hoste et al., 2006). The capacity of tannins to influence methanogens and rumen fermentation solely depends on the vast structural diversity of tannins, its sources, dosage, chemical structure, types and the species of rumen microorganisms. Tannins are known to exert anti-methanogenic activities by direct inhibition of methanogens or indirect interference with the proliferation of protozoa, which leads to restriction of inter-species H_2 transfer (Bhatta et al., 2009). Recently, Jayanegara et al. (2015) in an *in vitro* study established that hydrolysable and condensed tannins have positive effects on CH_4 emission, microbial protein and rumen fermentation. They reported that hydrolysable tannins have the capacity to decrease CH_4 production and less adverse effects on nutrient digestion than condensed tannins. Addition of low to medium ($<50 \text{ g/kg DM}$) concentration of CT in temperate forage regions improves the utilization of polypeptides in the rumen of microorganisms with no possible alteration in feed intake and nutrient degradation (Barry and Mcnabb, 1999; Waghorn, 2008). This is because CT reduces protein degradation and elevates the amount of dietary protein reaching the intestinal lumen for absorption (Wang et al., 1996). A reduction in enteric CH_4 production (20–26%) was achieved at higher concentrations of CT obtained from the leaf extracts of tropical tree of *F. benghalensis* (272 g/kg DM), *A. heterophyllus* (179 g/kg DM) and *A. indica* (184 g/kg DM) at 4% concentration in feeds of sheep. The degree of methanogenesis was in the order: *Ficus benghalensis* (20.4%) <*Artocarpus heterophyllus* (20.8%) <*Azadirachta indica* (26.1%) (Malik et al., 2017). These findings suggest that CT has the ability to lower CH_4 emission without detrimental effects to relevant fermentation indices. Beauchemin et al. (2007) reported that 0, 1 or 2% of CT obtained from red quebracho (*Schinopsis quebracho-colorado*) did not decrease enteric CH_4 production in beef cattle. Carulla et al. (2005) opined that CH_4 production from sheep decreased only

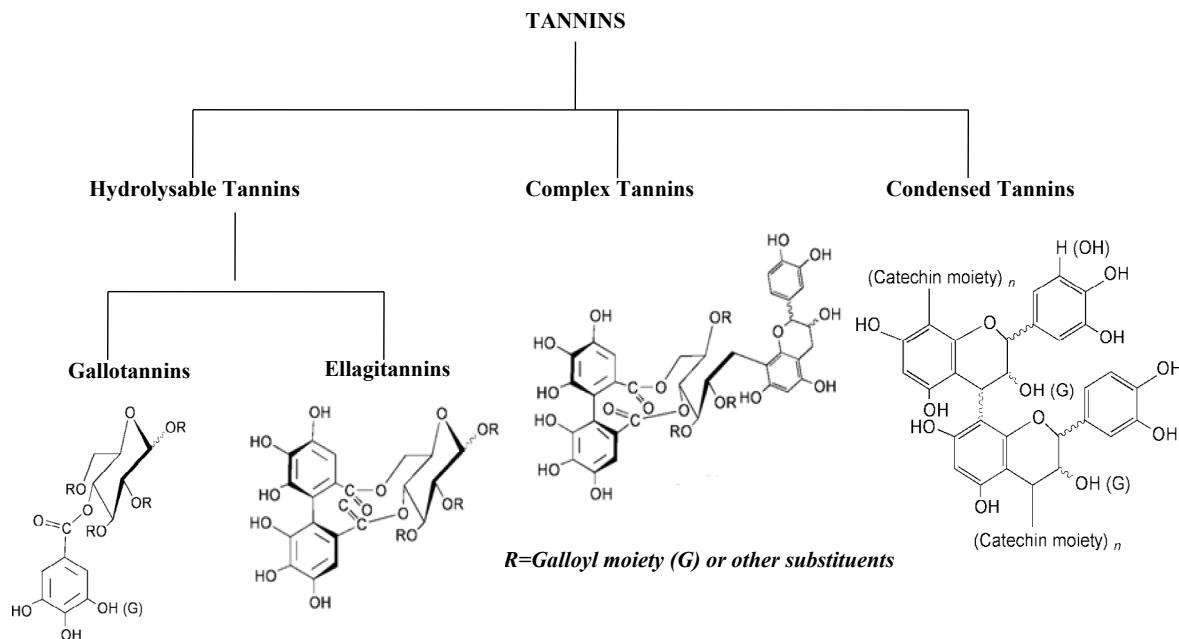


Fig. 3. Classification of tannins (Khanbabae and van Ree, 2001).

by 12% when 2.5% CT extracts of *A. mearnsii* were added to animal diet. Percentage reductions of 14% and 29% of CH₄ emissions were observed when cow fed with 0.9 and 1.8% DM respectively of tannin extract from *A. mearnsii* (Grainger et al., 2009).

In another *in vitro* assay, Pham et al. (2017) reported that supplementation of tannin (0.3%) to the diet of steer significantly lowered methanogenesis and enhanced animal productivity. A significant reduction in protozoa and methanogen numbers with simultaneous decrease in rumen CH₄ production was reported by Szczechowiak et al. (2016) with the incorporation of mixed diets containing *Vaccinium vitisidaea* dried leaves extract with 4.83 g/kg DM of CT and 32.2 g/kg DM of blended fish-soybean oils. Waghorn (2008) opined that inclusion of 30 g CT/kg DM of *L. corniculatus* has beneficial effects on ruminant production. Huang et al. (2018) reported that incorporation of CT at higher concentrations have the tendency of impeding animal feed intake because of their astringent nature, thus reducing protein and nutrients digestion by overprotecting proteins. This leads to decrease rumen microbial activity and inhibition of the activities of endogenous digestive enzymes which negatively affects animal performance and productions. Li et al. (1996) stated that 1.0 mg CT/g DM prevents pasture bloat. Wang et al. (2006) and Sottie et al. (2014) reported that incorporating CT-containing forage is an effective method that could be used to control pasture bloat.

Tannins from mimosa (hydrolysed tannin), chestnut (hydrolysed tannin) and quebracho (Condensed tannin) are used to control several intestinal parasites in ruminant (Min and Hart, 2003; Min et al., 2005, 2015). Jin et al. (2015) and Huang et al. (2015) opined that in ruminant's digestive tract system, the growth of *E. coli* O157:H7, one of the known deadly food borne pathogenic bacteria was significantly inhibited by purple prairie clover forage containing CT. However, Huang et al. (2015) in their study observed that lambs challenged with pathogenic bacteria *E. coli* O157:H7 and subsequently fed with diets comprising of 36 g CT/kg DM purple prairie clover had less *E. coli* O157:H7 compared to lambs fed without CT purple prairie diets. Jin et al. (2015) in their own study demonstrated that grazing pasture consisting of 16–20 g CT/kg DM had a reduced *E. coli* fecal shedding when compared to cattle

fed without CT. Min et al. (2007) also opined that inclusion of 15 g/kg DM chestnut tannin had a decreased fecal shedding effect of *E. coli* for cattle fed hay diets (Min et al., 2007). However, Lee et al. (2009a,b) and Berard et al. (2009) opined that at lower doses of <13.5 g CT/kg DM that sainfoin and *S. lespedeza* had no influence on fecal *E. coli* shedding. In addition, a reduction in feed intake and body weight were observed when different doses of *Mimosa pudica* tannin extract (*i.e.*, CT) 0.5, 1.5, 2.0 and 2.5% were supplemented to broiler diets (Iji et al., 2004). A negative effect was documented in birds fed with tannin-supplemented diets, which resulted in reduced ileal digestibilities of energy, protein and amino acids (Huang et al., 2018). In addition, they observed that inclusion of 10% quebracho tannins extract caused increase in body weight of challenged birds, increase in crypt:villi ratio of the intestine and a decrease in oocyst excretion. They suggested that quebracho CT could be used as an effective potential prophylactic anticoccidials agent. In addition, a significant improvement in weight gain was observed by Zotte and Cossu (2009) in a 6-week feeding trial when 1% and 3% of red quebracho tannins-supplemented diet of rabbits. Ebrahim et al. (2015) established that tannic acid (1%) has the potential to decrease body weight and feed intake of broiler under stress. However, Huang et al. (2018) observed an improvement in fatty acid profile of breast. In general, the activity of ruminal microflora can be reduced by addition of CT (Priolo et al., 2000; Cieslak et al., 2014). Vasta et al. (2009a,b) documented in an *in vitro* study that dietary tannins reduced ruminal biohydrogenation and also increased muscle Δ9-desaturase protein expression in sheep. In their *in vitro* study in 2009, they stated that the suppression of ruminal biohydrogenation was through inhibition of ruminal microbial proliferation and not by direct interaction of tannins with the operating enzymes in the biohydrogenation pathway.

Furthermore, Ramírez-Restrepo et al. (2016) observed that supplementing (30 g/day) dietary tea seed saponins decreased dry matter intake in steers. Francisco et al. (2015) also stated that addition of different doses of CT ranging from 2.7 to 15.0 g/kg DM from *Cistus ladanifer* in combination with different doses of vegetable oil (0, 40 and 80 g/kg DM) had no observable effect on

conjugated linoleic acid content in intramuscular fat. Kamel et al. (2018) reported that lamb diets supplemented with 20 g/kg sunflower oil and 40 g/kg quebracho tannins increased conjugated linoleic acid content in the intramuscular fat of lambs.

4. Effects of essential oil on the ruminant microflora and CH₄ production

Essential oils are collection of natural products derived from the plant volatile fractions by different analytical methods. Based on the route of biosynthesis, they are classified into two chemical groups: terpenoids and phenylpropanoids (Fig. 4). Terpenoids are derived from an isoprenoid structure (C₅H₈) via the mevalonate metabolic pathway with monoterpenoids and sesquiterpenoids as most abundant representatives. The phenylpropanoids consist of three side chain linked to six carbon aromatic ring and are synthesized through schikimic acid metabolic pathway (Calsamiglia et al., 2007). They exist as volatile or ethereal oils. They are aromatic oily compounds in liquid form that can be sourced from leaves, stems, roots, flowers, seeds and fruits of plants.

Essential oils are one of the most promising bioactive substances that can be used to minimize the environmental impact of ruminant production because they can be used to improve rumen fermentations, ruminants' lifetime performances and mitigate CH₄ emissions (Cobellis et al., 2016; McGrath et al., 2018; Omonijo et al., 2018). Essential oils are known to have beneficial effect such as antioxidant, anti-inflammatory and antimicrobial properties, ability to enhance digestive secretion, improve blood circulation and immune status (Acamovic and Brooker, 2005; Brenes and Roura, 2010) and are also used to inhibit odour and NH₃-N. It has been reported that genetic and environmental factors affect the composition of essential oil in plants. Other factors such as geographical location, species, parts of plant used, time of harvest and method of extraction also greatly affect the composition of the essential oil (Faleiro et al., 2002).

Dorman and Deans (2000) postulated that terpenoids and

phenylpropanoids exert their antimicrobial actions through interaction of cell membrane. This interaction is triggered by a conformational change in the cell membrane, thus leading to escape of ions across the cell membrane. Cox et al. (2001) suggested that the alterations in microbial energy utilization may impact negatively on the growth of the rumen microflora thus leading to microbial death. The major positive effects of essential oil in ruminants include; increasing propionate, decreasing CH₄, acetate and NH₃-N without negatively influencing volatile fatty acid (Busquet et al., 2005a; Gunal et al., 2014). The effectiveness of essential to inhibit the growth of rumen microorganisms depend on their concentrations, type, doses, the species of microbes in the ruminal fluid. Wu et al. (2018) reported that citrus essential oils inhibit rumen fermentation, reduces volatile fatty acid and rumen ammonia without any adverse effects on body weight, dry matter intake, and total nutrient digestibility in Hu sheep. Busquet et al. (2005a) reported that 2.2 mg/L of carvacrol significantly reduced peptide-N and increased NH₃-Nafter 2 h of feeding; indicating an inhibition of proteolysis or stimulation of peptide lyses (Busquet et al., 2005a). They stated that higher doses of ≥300 mg/L carvacrol significantly increased the pH and butyrate but reduced proportion of acetate, propionate and volatile fatty acid. Antimicrobial activities of thymol have also been documented. Evans and Martins, (2000) reported the effects of thymol on the *Streptococcus bovis* and *Selenomonas ruminantium* in relation to energy utilization. The results showed that the compound inhibited microbial metabolism through reduction of CH₄ and lactate concentrations. At higher dose of 400 mg/L, there were significant reductions in nutrient digestion and total volatile fatty acids (*i.e.*, VFA) production. However, moderate concentrations led to an elevation in acetate to propionate ratio. Moreover, susceptibility index of thymol on *S. ruminantium* was greater compared to *S. bovis*, thus resulting in marked accumulation of lactate. Castillejos et al. (2006) documented that 50 mg/L thymol had no influence on rumen microbes. However, at 500 mg/L dose, TVFA and NH₃-N decreased and also increase in acetate to propionate ratio was recorded. Cardozo et al. (2005)

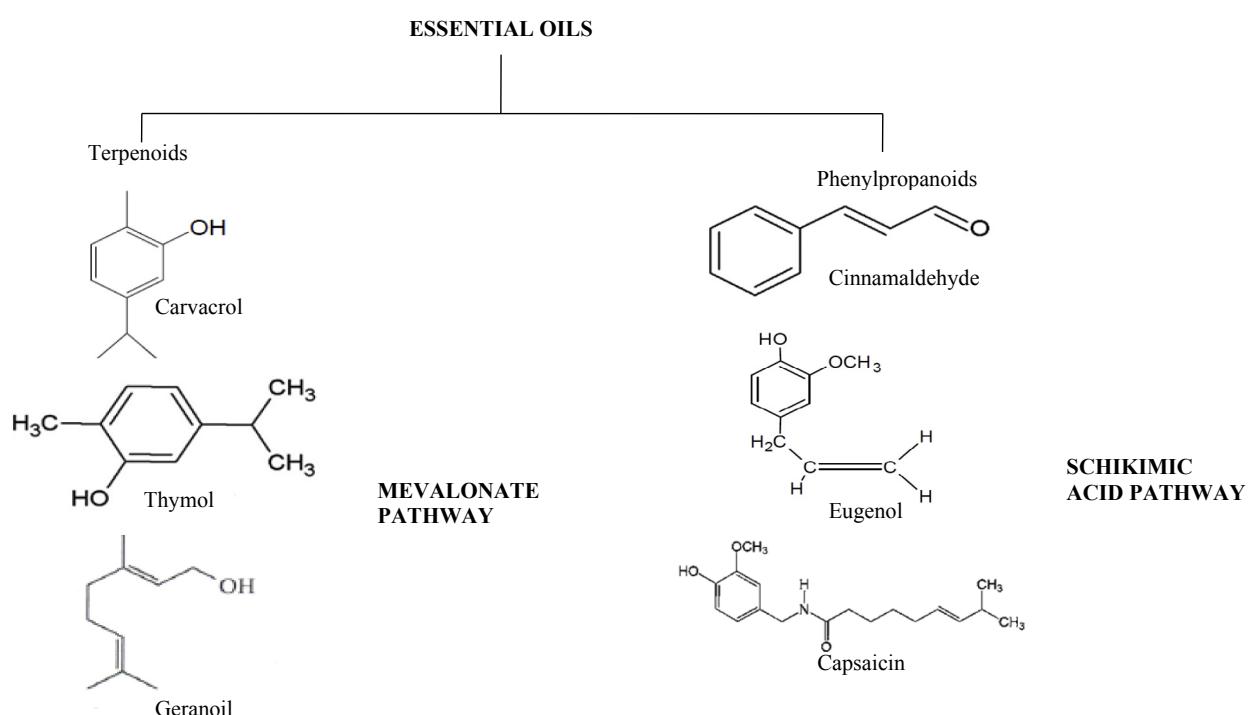


Fig. 4. Chemical structures of selected essential oils (Calsamiglia et al., 2007).

found that thymol has the capacity to reduce the ratio of acetate to propionate in rumen fluid from cattle. The effectiveness of carvacrol and thymol as potential antimicrobial agents may be due to the presence of hydroxyl groups (OH^-) (Ultee et al., 2002; Benchaar et al., 2007) and lower molecular weight compounds in tannin structures (Calsamiglia et al., 2007).

The antimicrobial activities of cinnamaldehyde, eugenol and anethol against gram-positive and gram-negative bacteria have been demonstrated long before now. Cinnamaldehyde, an active ingredient of cinnamon oil has the ability to modify N-metabolism of rumen microflora by inhibition of peptidolysis, but presented no negative effect on total VFA proportions (Cardozo et al., 2004). Decreased in total VFA was recorded at higher doses of cinnamaldehyde with greater antimicrobial activity (Busquet et al., 2003). The effects of cinnamon oil and cinnamaldehyde on the proportion of individual VFA (acetate, propionate and butyrate) have been documented. Calsamiglia et al. (2007) reported that cinnamon oil had increasing effects on acetate with no influence on propionate and butyrate proportions while cinnamaldehyde increases propionate with no effect on acetate and butyrate proportions. Busquet et al. (2005a, b) stated that at low doses, cinnamaldehyde in a long term, revealed a non-significant difference in the proportion of the individual VFA but at higher concentrations of 31.2 and 312 mg/L, cinnamaldehyde significant decreased proportion of acetate and increased propionate and butyrate proportions (Busquet et al., 2005b).

Patra and Yu (2012) reported 1.0 g/L dose of essential oil from oregano had 87% reduction in CH_4 production. Pawar et al. (2014) in their *in vitro* study observed dose-dependent inhibition of CH_4 by Ceylon cinnamon bark essential oil and reported complete inhibition of CH_4 at higher dose of 833 mL/L. Roy et al. (2014) reported 5.3% decreased in CH_4 emissions using cinnamon oil. Macheboeuf et al. (2008) reported 98% decrease in CH_4 emissions when 5 mM oregano essential oil or cinnamon essential oil was administered but only 12% inhibition were observed when dill essential oil at the same dose. However, they observed that carvacrol and trans-cinnamaldehyde at the concentration of 5 mM showed decrease mitigation efficiency when compared to oregano essential oil and cinnamon essential oil. Wang et al. (2009) demonstrated that combination of essential oils obtained from oregano (0.25 g/d) to sheep for 15 days decreased CH_4 production while Beauchemin and McGinn (2006) and Tomkins et al. (2015) reported no effect in CH_4 emission from cattle fed with a commercial blended essential oil. According to Agarwal et al. (2009) 0.33 mL/L of peppermint oil elevated the level of rumen methanogens and reduced CH_4 production by 20%. Joch et al. (2016) opined that the dose of 900 mg/L of geraniol decreased CH_4 emissions by 97.9% when compared to the control. However, total VFA and dry matter digestibility were reduced. Lin et al. (2012) in an *in vitro* experiment evaluated the ability of mixtures of essential oils from thyme, oregano, cinnamon, and lemon. They observed that the essential oils from thyme decreased CH_4 production than those from cinnamon and lemon.

Eugenol is the main active ingredients of clove bud and cinnamon oil (Davidson and Naidu, 2000). Cardozo et al. (2006) found that the mixture of cinnamaldehyde (180 mg/day) and eugenol (90 mg/day) decreased total digestibility matter as well as water intake in beef cattle. Busquet et al. (2003) also reported reduced digestibility matter intake of dairy cattle supplemented with 500 mg/day of cinnamaldehyde. Kung et al. (2008) showed that inclusion of essential oil at the concentration of 1.2 g/cow/day to cow had an increased digestibility matter intake. Tager and Krause (2011) reported that dairy cattle fed 10 g/day of essential oil did not influence nutrient digestibility and milk production. In another study, where the concentration of essential oil was reduced to 0.85 g/day, there was no interference in the degradation of organic

matter, crude protein and neutral detergent fiber (Santos et al., 2004). Tager and Krause (2011) found that essential oil at the dose of 10 g/day administered to dairy cow negatively influenced rumen fermentation while utilization of nutrient was not affected. Lin et al. (2013) found that inclusion of 1 g/day essential oil from clove or mixture of eugenol, carvacrol, citral, and cinnamaldehyde did not produce any negative influence on nutrient digestibility of sheep but they observed that inclusion of mixture of essential oils inhibited the growth of methanogens such as *Butyrivibrio fibrisolvens* and *Fibrobacter succinogenes*. Inclusion of eugenol from clove oil increased protein utilization and improved energy efficiency of ruminants (Calsamiglia et al., 2007). Cobellis et al. (2016) found that essential oil that is composed of phenolic (carvacrol) or carbonyl (cinnamaldehyde) compounds exhibited greater antimicrobial activities than those of monoterpenes. Hristov et al. (2008) observed that inclusion of 10 and 100 mg/L citronella oil did not alter total VFA.

Benchaar et al. (2007) established that inclusion of 400 mg/L of carvacrol and 800 mg/L of eugenol had increasing effects on butyrate and decreasing effects on propionate proportions, suggesting that higher concentrations of carvacrol and eugenol inhibited propionate producing bacteria and increased butyrate-producing bacteria. Another component of essential oil with proven antimethanogenic activity is capsaicin, which are a triterpenoid present in pepper (*Capsicum annuum* ssp.). Inclusion of 0.3, 3, 30 and 300 mg/dl capsicum oil in rumen fluid from beef cattle diet affected the proportions of VFA, $\text{NH}_3\text{-N}$ and acetate to propionate ratio at different pH in an *in vitro* study (Cardozo et al., 2005). At pH 7.0, acetate to propionate proportions increased while TVFA and $\text{NH}_3\text{-N}$ proportions decreased. However, at pH 5.5, the acetate to propionate proportions decreased, $\text{NH}_3\text{-N}$ reduced and VFA and propionate proportions increased, thus suggesting an improvement in nutrient utilization. The lower pH appears to move the molecules toward hydrophobic regions, which portend greater antimethanogenic effect (Calsamiglia et al., 2007).

5. Conclusion

In agro-based industries, especially livestock production the major challenges animal nutritionists are facing is how to reduce feed energy loss and mitigate the greenhouse gases- CH_4 and CO_2 without adverse effects to the animal health during ruminant production. Attempt to address this global issue has led to the inclusion of additives in the feeds of ruminants. Plant natural products (*i.e.*, PNP) notably saponin, tannins and essential oils are promising natural substances suitable for manipulating microbial ecosystems and fermentation kinetics of ruminants. It has been established that these PNP have the potentials to improve rumen fermentation, reduce loss of feed energy, increase animal lifetime performance, and also reduce greenhouse gases production- CH_4 and CO_2 during animal production. This review provides strong evidence that the reviewed PNP are effective in modifying rumen fermentation parameters, mitigate CH_4 production and serve as antimicrobial agents without negatively affecting the animal production. However, the mechanism of actions of PNP on rumen methanogenesis is yet to be fully elucidated. Again, detrimental effects of these PNP on the feed intake, nutrient digestibility, total volatile fatty acids and rumen fermentation have been documented. However, these observed positive or negative effects depend on the composition and administered dosage of PNP, dietary composition, pH and methanogen species.

6. Implications and recommendations

The findings from this review show that PNP have great positive

impact in livestock production because they have potentials to improve animal feed utilization, enhance digestibility of fibrous feeds, reduce protein degradability, increase animal performance and productivity, minimize loss of dietary energy during rumen fermentation, and also reduce CH₄ and CO₂ productions. This is a promising means of moving towards eco-friendly cleaner animal production. However, we recommend that more research work should be carried out on the following areas to accelerate the beneficial use of PNP in livestock production; i) to determine in an *in vitro* and *in vivo* experiments, the effective daily doses to be included in animal diets without any detrimental effects to the animals, ii) to identify and characterize their bioactive compounds, iii) to evaluate the mode of action of each PNP, iv) to determine cost implication of using them to modulate ruminant nutrition at the farm level, v) to evaluate the antimethanogenic potentials of the active ingredients after prolonged *in vivo* trials.

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