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Role of tannin-rich plants and brown algae in reducing enteric methane emissions in ruminant livestock

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Abstract Cattle production is a cornerstone of global food security, but it represents a significant source of greenhouse gas emissions, particularly methane (CH_4) resulting from enteric fermentation. This process, mediated by the ruminal microbiota, enables the conversion of fibrous compounds into usable energy; however, it involves considerable energy losses in the form of CH_4. In this context, plant secondary metabolites, particularly tannins, have been proposed as an effective strategy to mitigate these emissions without compromising productivity.This review assesses the effect of hydrolysable tannins (HT), condensed tannins (CT) and phlorotannins (PT) on ruminal fermentation and CH_4 production. The evidence shows that CTs and PTs exhibit more consistent responses, due to their ability to selectively modulate the microbiota, reduce protein degradation and improve nitrogen use efficiency. In contrast, HTs exhibit greater variability and, in some cases, negative effects on digestibility. Of particular note is the potential of phlorotannins, found in brown algae, which have demonstrated significant reductions in CH_4 in in vitro studies, in some cases outperforming terrestrial sources. However, the efficacy of these compounds depends on factors such as dose, source, diet and experimental conditions, which explains the inconsistencies between studies. However, the efficacy of these compounds depends on factors such as dose, source, diet and experimental conditions, which explains the inconsistencies between studies. At moderate levels, tannins can reduce CH_4 without affecting digestibility, whilst high doses tend to impair fermentation. In conclusion, tannins represent a promising tool for more sustainable livestock systems. However, the high variability of data and the limited quantitative evidence under in vivo conditions highlight the need to standardise their use and further investigate their productive evaluation.

Keywords: hydrolysable, condensed, phlorotannins, plants secondary compounds, greenhouse gas emissions

1. Introduction

Livestock farming is a cornerstone of global food security; however, it faces the critical challenge of mitigating its environmental impact, given that it accounts for approximately 14.5% of anthropogenic greenhouse gas (GHG) emissions (Food and Agriculture Organization, 2013). Within this emissions profile, it is estimated that carbon dioxide (CO_2), methane (CH_4) and nitrous oxide (N_2O) account for 75%, 18% and 4% of the total, respectively (Subedi et al., 2022).

In ruminants, the key process is enteric fermentation, carried out by the rumen microbiota (bacteria, archaea, protozoa and fungi). This system enables nutrients to be converted into microbial protein and volatile fatty acids (acetate, propionate and butyrate), which constitute the animal's main source of energy. However, this process is metabolically inefficient, as a significant portion of the ingested energy is not utilised and is lost in the form of methane (CH_4) released into the atmosphere (Sandoval-Pelcastre et al., 2020).

Given the current need to mitigate greenhouse gas emissions in the livestock sector, it has been proposed to incorporate plant species with proven anti-methanogenic properties (Cardoso-Gutierrez et al., 2021; Canul-Solis, 2020; Jayanegara et al., 2011). The ability of these plants to modulate the ruminal environment is centred on their content of plant secondary metabolites (PSMs), which intervene in fermentation pathways and succeed in reducing CH_4 excretion (Piñeiro-Vázquez et al., 2018; El-Zaiat et al., 2020; Montoya-Flores et al., 2020). However, due to the wide diversity of plant species with anti-methanogenic effects, there is a need to assess which have the greatest impact on CH_4 emissions and the quantity that should be included in the diet (Sandoval-Pelcastre et al., 2020).

Within this range of plant compounds, condensed and hydrolysable tannins stand out as one of the most effective biological tools, due to their ability to directly or indirectly inhibit methanogenic archaea and limit the activity of protozoa and other microbial populations responsible for hydrogen synthesis (Patra & Saxena, 2010; Tavendale et al., 2005). However, the use of tannins presents critical variability that has hindered their standardised implementation. This variability is mainly

attributed to the diversity in the molecular weight and chemical structure of these compounds, which dictates their degree of bioactivity in the ruminal ecosystem (Aboagye & Beauchemin, 2019). Given these limitations, there has been growing interest in phlorotannins exclusive to brown algae, which possess a unique molecular architecture based on phloroglucinol units linked by ether or carbon-carbon bonds (Kim et al., 2023). Unlike terrestrial sources, marine species such as *Himanthalia elongata* and *Fucus vesiculosus* contain phlorotannins with a high capacity for enzymatic and membrane interaction, achieving significant reductions in CH_4 in *in vitro* studies (Barnes et al., 2025).

Consequently, the use of these botanical sources and the variability in the concentration and biological activity of tannins require a rigorous evaluation to identify the compounds with the greatest potential to mitigate enteric CH_4 emissions without compromising animal performance (Sandoval-Pelcastre et al., 2020). Although tannins have demonstrated considerable anti-methanogenic potential, the available evidence remains inconsistent due to differences in their chemical structure, inclusion level, animal species, diet composition, and experimental conditions, which has limited the establishment of consistent conclusions regarding their practical application in ruminant systems. In addition, previous reviews have focused mainly on condensed and hydrolysable tannins from terrestrial plants, whereas phlorotannins derived from brown algae have been addressed in a more limited and fragmented manner. Therefore, there is a need for a review that integrates and critically discusses the available evidence on hydrolysable tannins, condensed tannins, and phlorotannins under a comparative framework that considers their mechanisms of action, anti-methanogenic efficacy, and the principal factors associated with the variability of reported responses. In this context, the aim of this review was to provide a comparative and critical assessment of terrestrial and marine tannin sources as nutritional strategies for mitigating enteric CH_4 emissions in ruminants.

2. Review Analyses Methodology

To assess the impact of tannin supplementation on methane (CH_4) emissions in ruminants, a narrative review of the scientific literature was conducted, integrating evidence from both in vivo and in vitro studies. The review followed the recommendations of the SANRA scale for narrative reviews to improve transparency, methodological organization, and quality in the selection and interpretation of evidence (Baethge et al., 2019).

The literature search was conducted between February 3, 2025, and November 30, 2025, using the electronic databases ScienceDirect, Scopus, Dialnet, SciELO, PubMed, Redalyc, and Google Scholar. Publications published between 2000 and 2025 were considered. The search strategy combined the selected keywords using Boolean operators (“AND” and “OR”) according to the requirements of each database. The search included combinations of the following terms: “ruminants”, “cattle”, “sheep”, “goats”, “tannins”, “condensed tannins”, “hydrolysable tannins”, “phlorotannins”, “secondary metabolites”, “methane emission”, “enteric methane”, “CH4”, “digestibility”, “rumen fermentation”, “brown algae”, “*in vitro*”, and “*in vivo*”. In addition, manual searches of the reference lists of relevant articles were performed to identify additional studies of interest.

2.1. Selection of publications

In accordance with methodological recommendations for evidence selection in narrative reviews (Baethge et al., 2019; Lean et al., 2014), explicit inclusion and exclusion criteria were established before the screening process. Studies were included when they were original peer-reviewed research articles evaluating the effects of tannins or phlorotannins on methane production in ruminants using in vivo or in vitro experimental approaches, and when they reported methane production data, dietary inclusion levels, sample size, and measures of variability. Only studies published in English or Spanish were considered. Review articles, conference abstracts, editorials, theses, duplicate publications, studies lacking quantitative methane emission data, studies without clear information regarding tannin source or inclusion level, and studies not involving ruminant species were excluded.

The study identification and screening process followed a structured selection procedure. A total of 1,589 records were initially identified through database searches. After duplicate removal, 1,349 records were screened based on title and abstract evaluation. Subsequently, 49 full-text articles were assessed for eligibility, and 17 articles were excluded because they did not meet the established inclusion criteria. Finally, 32 studies were included in the narrative synthesis.

To facilitate comparison among studies, methane data from in vitro experiments were reported as mL/g dry matter or mL/day, whereas methane emissions from in vivo studies were expressed as g CH_4/day whenever possible. A narrative and descriptive synthesis of the selected studies was performed, prioritizing the interpretation of biological trends and consistency of evidence rather than quantitative statistical integration. The effects of tannins and phlorotannins were compared according to their biological origin, chemical class, source type, dietary inclusion level, and impact on methane mitigation and digestibility.

Although a structured search and screening strategy was applied to improve transparency and reproducibility, this work should be interpreted as a narrative review rather than a systematic review or meta-analysis. Therefore, no formal risk-of-bias assessment, effect-size estimation, statistical heterogeneity analysis, or quantitative meta-analytical procedures were performed.

3. Results and Discussion

3.1. Secondary metabolites

To understand secondary metabolites, it is first necessary to consider the primary metabolites of plants, which are essential compounds required for growth, development, reproduction and the maintenance of cellular functions. These metabolites are mainly synthesised during the exponential growth phase and their concentration generally increases in parallel with plant development. As they are directly involved in central metabolic processes, they are also referred to as 'central metabolites' (Salam et al., 2023). Among the most representative examples are ethanol, citric acid, lactic acid, acetic acid, vitamins, amino acids and nucleotides (Bhatla & Lal, 2023).

In contrast, secondary metabolites are not essential for the plant's basic survival; however, they play a key role in adaptation and ecological interactions. Their synthesis is typically associated with later stages of plant development, particularly when growth slows and environmental pressures become more significant. Consequently, the production of these compounds is strongly influenced by external stimuli such as abiotic stress, nutrient limitation or biotic interactions (Salam et al., 2023; Bhatla & Lal, 2023). Through these mechanisms, secondary metabolites contribute to plant defence, signalling and adaptation to changing environmental conditions.

The biosynthesis of secondary metabolites involves highly interconnected metabolic pathways derived from primary carbon metabolism (Figure 1a). Importantly, plants can simultaneously synthesize multiple secondary compounds depending on physiological status and environmental conditions. As a result, the concentration and composition of these metabolites may vary considerably in response to stress factors such as temperature, ultraviolet radiation, drought, salinity, and nutrient availability (Figure 1b) (Bhattacharya & Pal, 2025).

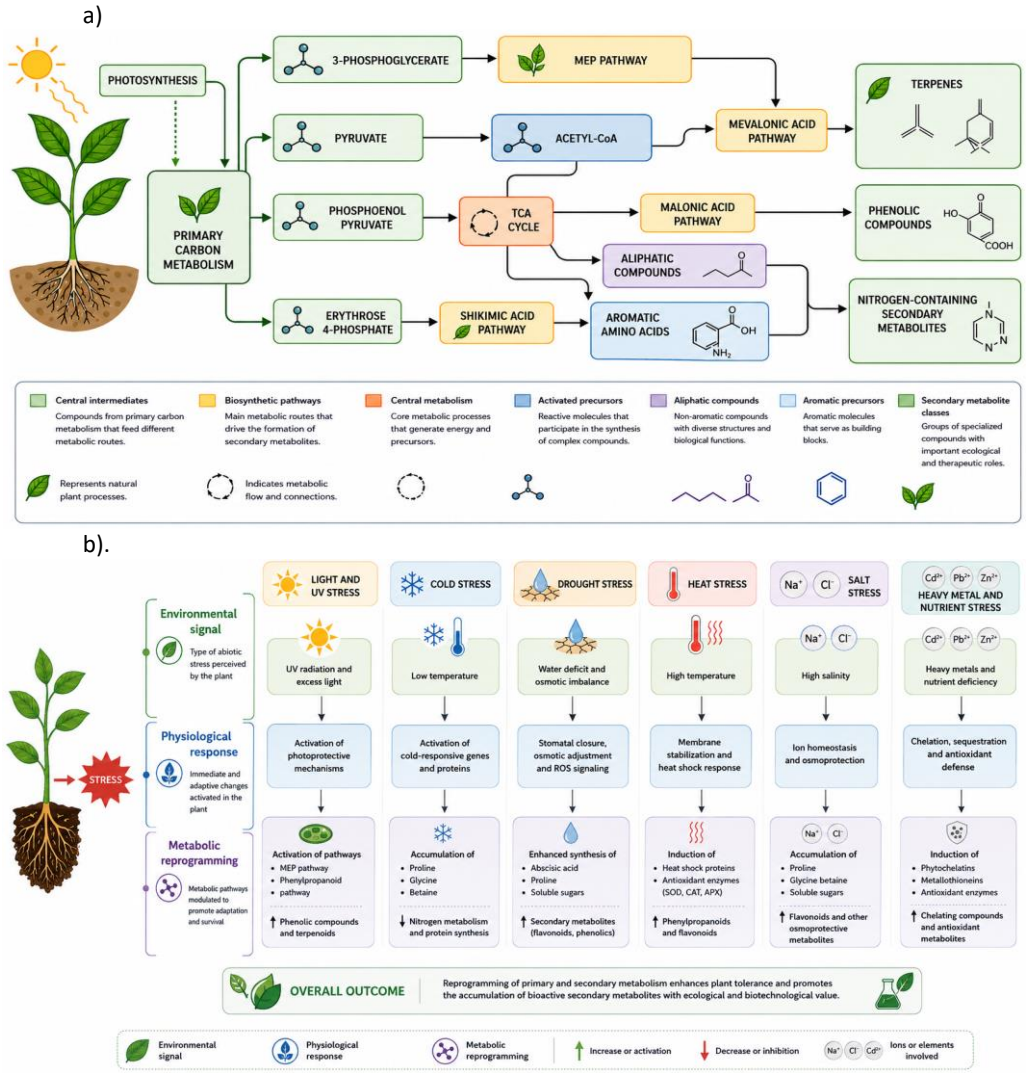


Figure 1 Formation of secondary metabolites in plants (a) and environmental factors affecting their concentration (b). This figure was originally designed by the authors using BioRender and graphically enhanced using artificial intelligence-assisted visualization tools.

Secondary metabolites are commonly classified according to their chemical structure, biosynthetic origin, solubility and chemical composition, including the presence of nitrogen or sugars (Nørskov et al., 2023). Among the main classes described in plants are terpenes, nitrogenous compounds and phenolic compounds.

Terpenes constitute a highly diverse group that includes hormones, pigments, essential oils, steroids and rubber. Nitrogenous compounds include alkaloids, glucosinolates, cyanogenic glycosides, cardiac glycosides, saponins and non-protein amino acids such as canavanine and mimosine. Phenolic compounds, for their part, comprise coumarins, flavonoids, lignin and tannins, which stand out among the most studied secondary metabolites due to their antioxidant and antimicrobial properties (Nørskov et al., 2023).

Within this broad group, phenolic compounds can be subdivided into flavonoids and non-flavonoids (Figure 2). Non-flavonoid compounds mainly include phenolic acids, such as gallic and salicylic acids, as well as tannins, which may occur in hydrolysable or condensed forms. This structural diversity largely determines their biological activity and their role in plant defence and animal nutrition (Nørskov et al., 2023).

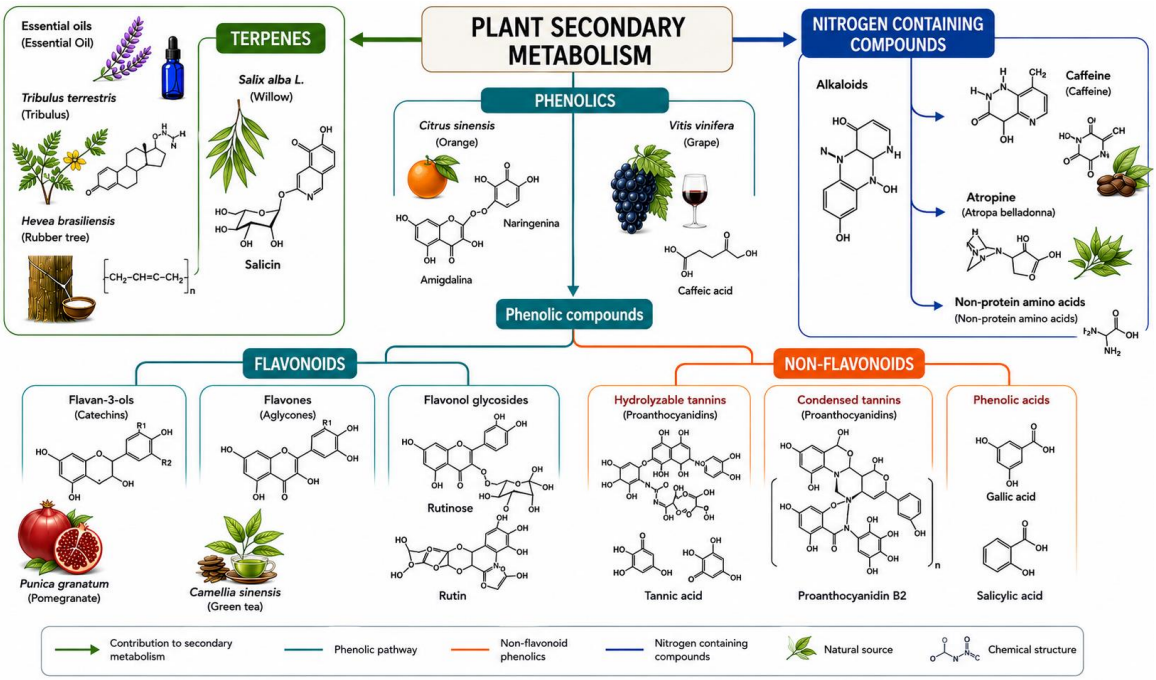


Figure 2 Classification of phenolic compounds. This figure was originally designed by the authors using BioRender and graphically enhanced using artificial intelligence-assisted visualization tools.

3.2. Tannins

Among the phenolic secondary metabolites, tannins have received particular attention due to their widespread distribution in plants and their multiple biological functions. These polyphenolic compounds occur naturally in numerous fruits, legumes, shrubs and trees, including species such as *Quercus robur*, *Schinopsis spp.*, *Castanea sativa*, *Acacia farnesiana* and *Prosopis juliflora* (Haslam, 1998). In plants, tannins play a role in defence mechanisms against herbivores and pathogenic microorganisms, as well as contributing to the response to environmental stress (Bhatla & Lal, 2023).

Beyond their ecological function, tannins have attracted growing interest in animal nutrition due to their antimicrobial, antioxidant and protein-binding properties (Bhatla & Lal, 2023). However, their biological effects depend largely on their chemical structure and molecular weight. Consequently, tannins are primarily classified into condensed tannins (CT) and hydrolysable tannins (HT), which differ in stability, protein affinity, degradability and ruminal activity (Vasta et al., 2019).

This structural differentiation is particularly relevant because it directly influences their nutritional and physiological effects in ruminants. Condensed tannins are generally more resistant to degradation and can reduce the ruminal breakdown of proteins, whilst hydrolysable tannins often exhibit greater antioxidant activity and broader antimicrobial effects (Vasta et al., 2019). In this context, hydrolysable tannins derived from chestnut (*Castanea sativa*) have shown promising results in dairy cattle, including improvements in oxidative status and parameters related to immune response during the transition period. These findings highlight the potential of tannins not only as plant defence compounds, but also as functional additives capable of modulating ruminal fermentation and contributing to animal health (Prodanović et al., 2023; Prodanović et al., 2024).

In recent years, interest in these compounds has increased because of their potential use in reducing enteric CH_4 emissions in ruminants. However, CH_4 production is a normal part of ruminal fermentation and plays an important role in removing excess hydrogen generated during carbohydrate degradation (Paul et al., 2012; Poulsen et al., 2013). Ruminants have

evolved for millions of years relying on microorganisms capable of degrading cellulose and other structural carbohydrates through fermentative processes associated with CH_4 formation (Waters et al., 2025). Therefore, although decreasing emissions may represent an improvement in energy utilization, excessive reduction of methanogenesis may also negatively affect fiber digestion and ruminal fermentation stability. In addition, CH_4 production is closely related to feed intake and ruminal passage rate, since higher intake levels generally decrease proportional energy losses as CH_4 due to changes in the volatile fatty acid profile, particularly increased propionate and reduced acetate production (Knapp et al., 2014). This may explain why some studies report substantial CH_4 reductions without negative effects on animal performance, whereas others show decreases in digestibility and nutrient utilization (Aboagye & Beauchemin, 2019).

Differences between CT and HT help explain part of this variability. CT generally act by forming complexes with dietary proteins, thereby decreasing protein degradation in the rumen and improving nitrogen utilization (Reggi et al., 2020). In addition, these compounds can modify certain microbial groups associated with hydrogen production, including methanogenic archaea and protozoa, reducing CH_4 formation without severely altering fermentation (Min et al., 2020). In contrast, HT exert a more direct antimicrobial effect on methanogenic archaea and other ruminal microorganisms, which in some cases increases CH_4 reduction, although it may also negatively affect digestibility when high doses are used (Jayanegara et al., 2015). The main differences between HT and CT regarding ruminal stability, protein interaction, and effects on microbiota are summarized in Table 1.

Table 1 Effect of the inclusion of tannins (condensed, hydrolyzable tannins and phlorotannins) in ruminants, regarding ruminal function.

Rumen Function	Hydrolyzable Tannins (HT)	Condensed Tannins (CT)	Phlorotannins
Stability in the rumen	Low – easily hydrolyzed	High – resistant to degradation	High – generally stable
Interaction with proteins	Moderate	High	High
Protection of dietary protein (bypass protein)	Limited	Very efficient	Very efficient
Reduction of protein degradation	Moderate	High	High
Reduction of ammonia (NH_3) production	Moderate	High	High
Effect on microbiota	Variable, may be toxic	Selective modulation	Selective modulation with stronger antimicrobial effect
Effect on protozoa	May reduce them	Reduces populations	Reduces populations
Effect on cellulolytic bacteria	May strongly inhibit	Slight inhibition at high doses	Variable, depends on dose and algae species
Effect on methanogenic archaea	Indirect inhibition	Direct and indirect inhibition	Direct and indirect inhibition
Reduction of CH_4 production	Moderate	High	High (potentially greater in some cases)
Effect on fiber digestibility	May considerably reduce it	May decrease at high doses	May decrease at high levels
Impact on fermentation patterns	May negatively alter them	Promotes propionate production	Promotes propionate and energy efficiency
Risk of toxicity	High (release of phenolic metabolites)	Low	Low to moderate
Antioxidant activity	Moderate	Moderate	High
Effect on nitrogen use efficiency	Moderate	High	High

Besides tannins present in terrestrial plants, phlorotannins (PT), characteristic compounds of brown macroalgae, have recently received attention. PT are phloroglucinol polymers structurally similar to other tannins and are found in species such as *Durvillaea antarctica*, *Laminaria japonica*, *Undaria pinnatifida*, *Pelvetia siliquosa*, *Hizikia fusiforme*, *Ecklonia kurome*, *Chorda filum*, and *Scytosiphon lomentaria* (Künzel et al., 2022; Robles-Jimenez et al., 2024). These compounds have attracted interest because of the high CH_4 reductions observed in *in vitro* studies. Figure 3 summarizes the main mechanisms through which HT, CT, and PT may modify ruminal fermentation and CH_4 production, showing important differences in chemical stability and action on ruminal microorganisms (Vasta et al., 2019; Reggi et al., 2020).

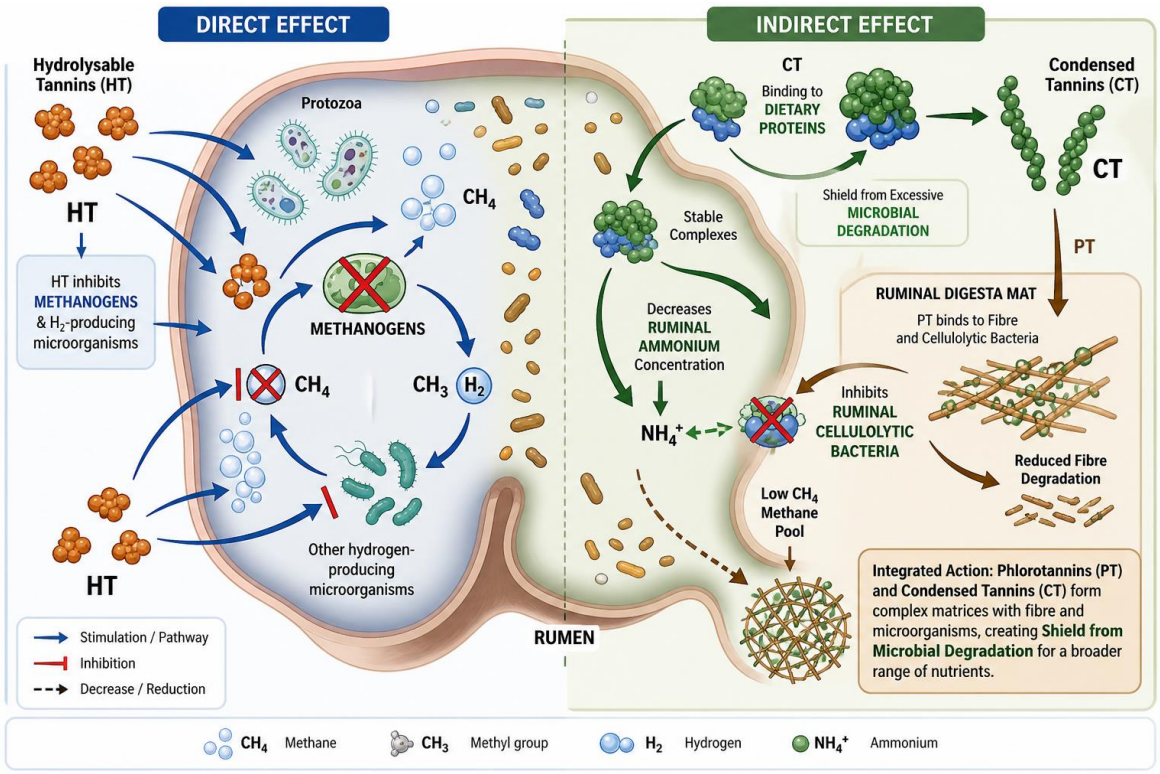


Figure 3 Mode of action of hydrolysable tannins (HT), condensed tannins (CT), and Phlorotannins (PT) in the rumen. This figure was originally designed by the authors using BioRender and graphically enhanced using artificial intelligence-assisted visualization tools.

Ruminal microbiota plays a central role in these responses. Ruminal protozoa, mainly ciliates and flagellates, represent between 20 and 50% of the total ruminal microbiota (Williams & Coleman, 1997; Williams et al., 2020). These microorganisms actively participate in hydrogen production, which is subsequently used by methanogenic archaea to produce CH_4 through the hydrogenotrophic pathway (Morgavi et al., 2015; Solomon et al., 2022). For this reason, several studies suggest that partial reduction of protozoa and hydrogen-producing microorganisms may decrease CH_4 emissions (Newbold et al., 2015). However, methanogenesis also contributes to maintaining stable and efficient fermentation. Therefore, when high tannin concentrations are used, especially HT or certain CT, CH_4 reductions are often accompanied by decreases in digestibility and feed utilization (Tan et al., 2011; Hassanat & Benchaar, 2012).

The *in vitro* studies summarized in Table 2 show that the response to tannins varies considerably among plant sources and extract types. In studies using *Schinopsis* spp. extracts, some authors reported moderate CH_4 reductions together with improvements in nitrogen utilization (Aboagye et al., 2018), whereas others observed no major changes in emissions but reported decreases in dry matter and fiber digestibility as the dose increased (Beauchemin et al., 2007; Norris et al., 2020). Similarly, Bhatta et al. (2009) and Chen et al. (2021) observed that quebracho extracts generated variable CH_4 reductions depending on the concentration used, although accompanied by reductions in ruminal degradability. These differences are probably related to variations in extract chemical composition, tannin polymerization degree, and diet composition used in each study (Waghorn, 2008; Vasta et al., 2019). Similar inconsistencies have been observed with commercial tannin extracts, where some studies showed improvements in nitrogen metabolism without affecting digestibility (Martello et al., 2020), whereas others reported lower protein and dry matter degradability (Mezzomo et al., 2011). Furthermore, some studies reported inconsistent responses or even absence of CH_4 reduction when low concentrations of commercial extracts were used (Min et al., 2021; Muñoz-Grein et al., 2026).

In contrast, forages naturally rich in tannins, such as *Leucaena leucocephala*, *Lotus corniculatus*, and *Hedysarum coronarium*, generally show more stable responses. In these systems, CH_4 reductions are usually moderate, while digestibility and animal performance are maintained (Woodward et al., 2002; Woodward et al., 2004). This suggests that the rumen may adapt more efficiently when tannins are naturally present in the diet rather than supplied as concentrated extracts. Nevertheless, several studies show that high inclusion levels may still negatively affect fiber digestion (Tan et al., 2011; Hess et al., 2008; Rira et al., 2015). Similarly, de Oliveira Pereira et al. (2007) observed that tannin-rich sorghum silages reduced CH_4 emissions, although the response depended on dietary conditions and inclusion level.

Table 2 Effect of tannins on methane production in ruminants *in in vitro* studies.

Specific origin	Source type	Tannin type	Inclusion (% DM tannins)	Methane reduction vs control (%)	Digestibility effect (reported units)	Reference
Schinopsis quebracho	Tannin extract	HT + CT	Variable (~1–3 %)	CH_4 ↓ 0.6–5.5 %	Not quantified	(Bhatta et al., 2009)
Schinopsis quebracho	Tannin extract	HT + CT	1–2 % each	CH_4 ↓ 8–10 %	DM degradability ↓	(Chen et al., 2021)
Quercus aegilops, Schinopsis balansae	Tannin extract	HT or CT	≥5 %	CH_4 ↓ up to 40 %	Fermentation efficiency ↓ at high levels	(Hassanat & Benchaar, 2012)
Schinopsis *quebracho* extract	Tannin extract	CT	~0.7 %	CH_4 ↓ (quantitative % not reported)	Digestibility generally unchanged	(Min et al., 2021)
Schinopsis quebracho extract	Tannin extract	CT	~3.7 %	CH_4 ↓ 5.5 %	Digestibility ↓	(Ishlak et al., 2015)
Leucaena leucocephala	Tannin-rich plant	CT	1.7 %	CH_4 ↓ (no % reported)	Digestibility maintained	(Piñeiro-Vázques et al., 2018)
Leucaena leucocephala	Tannin-rich plant	CT	6.2 %	↓ 20–30 % CH_4 production	DM digestibility ↓ significantly	(Tan et al., 2011)
Leucaena leucocephala	Tannin-rich plant	CT	31 %	Not evaluated	OM and CP degradation ↓	(Hess et al., 2008)
Chestnut + quebracho commercial mixture	Tannin extract	HT + CT	0.01–0.03 % (mg/L conversion)	No effect	Not reported	(Muñoz-Grein etal., 2026)
Vaccinium vitis-idaea L. (lingonberry)	Tannin-rich plant	CT	~2–3 % DM (natural plant material)	↓ ~10–15 % CH_4 vs control (reported reduction in methane production and methanogen activity)	No major negative effect on total VFA; slight shift in acetate:propionate ratio	(Cieslak et al., 2012)
Chesnut, Sumach, Mimosa,Quebracho	Tannin extract	HT + CT	0.05–0.1 %	↓ 10–25 % CH_4 (dose response)	OM digestibility ↓	(Jayanegara et al., 2015)
Schinopsis quebracho extract	Tannin extract	CT	~1–3 % DM (dietary supplementation level evaluated)	No significant reduction in CH_4	No negative effect on total tract digestibility; ruminal fermentation parameters minimally affected	(Cieslak et al., 2012)
Lessonia flavicans	Macroalgae	Phlorotannins	Natural concentration	↓ 98.6 % CH_4	Fermentation maintained	(Robles jimenez et al., 2024)
Macrocystis pyrifera	Macroalgae	Phlorotannins	Natural concentration	↓ 99.7 % CH_4	Digestibility variable	(Robles jimenez et al., 2024)
Ascophyllum nodosum	Macroalgae	Phlorotannins	Natural concentration	CH_4 ↓ (not quantified)	Digestibility generally maintained	(Künzel et al., 2022)
Fucus vesiculosus	Macroalgae	Phlorotannins	Natural concentration	CH_4 ↓ (not quantified)	Variable digestibility effects	(Künzel et al., 2022)
Mixed brown algae extracts	Macroalgae	Phlorotannins	Variable	CH_4 ↓ production (not quantified)	Minor fermentation effects	(Barnes et al., 2025)

Ecklonia cava phlorotannin derivatives	Macroalgae compound	Phlorotannins	Extract concentrations	↓ Significant CH_4 inhibition (quantitative % not reported)	Digestibility not evaluated	(Dias Batista et al., 2021)

Note: CT, condensed tannins; HT, hydrolysable tannins; CH_4, Methane; VFA, volatile fatty acids.

Results obtained with PT from brown macroalgae have been particularly remarkable. As shown in Table 2, species such as *Lessonia flavicans* and *Macrocystis pyrifera* achieved CH_4 reductions greater than 90% under *in vitro* conditions (Robles-Jimenez et al., 2024). Other species, such as *Ascophyllum nodosum* and *Fucus vesiculosus*, also showed positive effects on CH_4 mitigation with limited changes in ruminal fermentation (Künzel et al., 2022). Barnes et al. (2025) also reported important CH_4 reductions using PT-rich brown algae extracts. Likewise, Dias Batista et al. (2021) found that PT derivatives obtained from *Ecklonia cava* significantly inhibited CH_4 production. However, these results should be interpreted cautiously because most data come from controlled laboratory studies, and information under commercial production conditions remains limited. In addition, the response varies according to algae species, inclusion level, and diet composition.

The *in vivo* studies summarized in Table 3 show that results observed under laboratory conditions are not always replicated in animal production systems. In general, the greatest CH_4 reductions were obtained with high tannin inclusion levels, although frequently accompanied by decreases in digestibility and feed utilization efficiency. For example, *Leucaena leucocephala* and tropical CT-rich plant mixtures achieved important CH_4 reductions (Piñeiro-Vázquez et al., 2017; Rira et al., 2015), although some studies also reported negative effects on digestibility when dosage increased. Similarly, *Schinopsis* spp. extracts showed variable responses depending on inclusion level and basal diet composition. While some studies reported improvements in nitrogen efficiency and moderate CH_4 reductions (Aboagye et al., 2018), others found no major changes in emissions but observed decreases in digestibility (Beauchemin et al., 2007; Grainger et al., 2009; Norris et al., 2020; Ebert et al., 2017). Even Dschaak et al. (2011) reported that some commercial quebracho extracts did not modify apparent nutrient digestibility. On the other hand, Prodanović et al. (2025) observed that chestnut extracts reduced CH_4 while simultaneously increasing milk production and decreasing somatic cell count, suggesting additional productive and health-related benefits. Furthermore, Jayanegara et al. (2015) reported that chestnut extracts showed greater CH_4 mitigation capacity compared with other plant sources such as *Rhus coriaria*, *Mimosa tenuiflora*, and *Schinopsis* spp.

Overall, the reviewed studies indicate that tannin effects depend on multiple factors, including chemical structure, plant source, dosage, diet composition, and evaluation conditions (Vasta et al., 2019; Min et al., 2020). Therefore, differences observed among studies do not necessarily indicate contradictory results but rather reflect the complexity of interactions between tannins and the ruminal ecosystem. It is also important to consider that tannin concentration may vary even within the same plant species because of environmental conditions, growth stage, and plant fraction used (Waghorn, 2008). McSweeney et al. (2001) observed that species with low HT content did not alter voluntary intake, whereas plants with high HT concentrations significantly reduced intake in sheep. From a practical perspective, this indicates that tannin-based mitigation strategies should focus on carefully selecting both tannin source and inclusion level in order to reduce CH_4 emissions without compromising digestibility or animal productive performance (Patra & Saxena, 2010; Aboagye & Beauchemin, 2019).

Cardoso et al. (2021) reviewed *in vitro* and *in vivo* studies evaluating tropical tannin-rich plants and reported an overall tendency toward reduced CH_4 emissions in ruminants. According to the authors, the strongest responses were observed in diets including *Leucaena leucocephala* and combinations of *Samanea saman* with *Pennisetum purpureum*, which were mainly associated with their CT content. The study also indicated that increasing tannin inclusion levels generally enhanced CH_4 mitigation, although the magnitude of the response varied depending on plant species, diet composition, and experimental conditions. These observations are consistent with the findings of Jayanegara et al. (2015), who suggested that CT can contribute to reducing methane production. However, the variability among studies also highlights that tannin effects are not uniform and depend on factors such as dosage, tannin structure, and the adaptation of the ruminal microbiota.

The evidence analyzed indicates that the anti-methanogenic effects of tannins depend primarily on their molecular structure and their interaction with the ruminal ecosystem, rather than exclusively on their botanical origin. In this context, the present review provides a comparative and critical synthesis of terrestrial and marine tannin sources, highlighting the potential of phlorotannins to modulate methanogenesis and improve ruminal fermentation efficiency. Furthermore, the analysis identified key factors contributing to the variability observed among studies, including tannin type, inclusion level, animal species, diet composition, and experimental conditions, allowing for a more integrated understanding of the mechanisms involved in enteric CH_4 mitigation in ruminants.

Despite these promising findings, the available evidence still presents important limitations associated with methodological heterogeneity, differences in experimental design, and variability in tannin chemical characterization, which complicate direct comparisons among studies and limit extrapolation to commercial production systems. Therefore, future research should prioritize the standardization of tannin classification criteria and inclusion levels, as well as the development of in vivo studies under diverse production conditions and feeding strategies. In addition, strengthening comparative and meta-analytic approaches through the incorporation of more detailed information on tannin chemical structure, dietary composition,

and animal productive responses will be essential to identify more consistent and applicable supplementation strategies capable of mitigating enteric CH_4 emissions without adversely affecting digestibility or productive performance.

Table 3 Effect of the inclusion of tannins in in vivo studies on diets for ruminants.

Species	Source type	Tannin type	Inclusion (% tannins DM)	Methane reduction vs control (%)	Digestibility effect (reported units)	Reference
Schinopsis quebracho	Tannin extract	CT	1–2 %	No significant change	CP digestibility ↓ 5–15%; DM, NDF, ADF unchanged	(Beauchemin et al., 2007)
Schinopsis quebracho	Tannin extract	CT	Up to 6 %	Not evaluated	NDF digestibility ↓ from 0.718 to 0.590; ADF ↓ from 0.626 to 0.493	(Ahnert et al., 2015)
Schinopsis quebracho	Tannin extract	CT	1.5 %	↓ ≈12 %	Nitrogen utilization improved	(Aboagye et al., 2018)
Schinopsis balansae	Tannin extract	CT	1.5–4.5 %	↓ 9–20 % (dose-dependent)	DM, NDF digestibility ↓ linearly with dose	(Norris et al., 2020)
Commercial condensed tannin extract (*Schinopsis quebracho* extract)	Tannin extract	CT	0.2–3 %	Not reported	Improved nitrogen utilization efficiency; reduced ruminal ammonia-N; no negative effect on apparent DM digestibility (%)	(Martello et al., 2020)
Commercial condensed tannin extract (*Schinopsis quebracho* extract)	Tannin extract	CT	0.2–3 %	Not reported	Reduced DM and CP digestibility (%); improved efficiency of protein utilization; reduced ruminal ammonia-N concentration	(Mezzomo et al., 2011)
Leucaena leucocephala	Tannin-rich plant	CT	≈4–6 %	↓ 31–47 % CH_4 energy losses	DM digestibility slightly ↓	(Piñeiro-Vázquez et al., 2017)
Lotus corniculatus (birdsfoot trefoil)	Tannin-rich forage	CT	Natural plant level (≈2–3 %)	↓ 12–16 %	Protein utilization ↑	(Woodward et al., 2004)
Hedysarum coronarium (sulla)	Tannin-rich forage	CT	Natural plant level (≈2–4 %)	↓ ≈13 %	Digestibility maintained or slightly improved	(Woodward et al., 2002)
Acacia mearnsii extract	Tannin extract	CT	Up to 1.8 % DM equivalent	↓ 13–29 %	Slight reduction in fiber digestibility at high dose	(Grainger et al., 2009)
Castanea sativa extract (chestnut)	Tannin extract	HT	1.9–3.7 %	↓ 12–21 %	DM digestibility unchanged or slightly reduced	(Prodanović et al., 2025)
Mangosteen peel + *Sapindus saponaria*	Plant mixture (tannin + saponin)	CT, HT and saponinin	≈0.48 % tannins equivalent	↓ 10–12.4 %	Fermentation efficiency improved	(Poungchompu et al., 2009)
Sorghum bicolor silage	Tannin-containing plant	CT	0.2–1 % equivalent	↓ 12–54 % (diet dependent)	Digestibility variably affected	(de Oliveira Pereira et al., 2007)
Mixed tropical tannin plants (*Gliricidia, Leucaena, Manihot*)	Tannin-rich plants	CT	3.9–9.2 %	↓ 22–68 % (species dependent)	Fiber digestibility often ↓ at high levels	(Rira et al., 2015)

Schinopsis quebracho	Commercial extract	CT	3%	Not reported (methane not measured)	No significant effect on DM, OM, CP, or NDF digestibility (% of DM basis)	(Dschaak et al., 2011)
Commercial condensed tannin extract (unknown species) (finishing diet)	Extract	CT	0.5–1.0%	No significant effect (≈0% reduction)	Phase 1: Linear decrease in starch digestibility (%). Phase 2: No significant effect on OM or starch digestibility (%)	(Ebert et al., 2017)

Note: CT, condensed tannins; HT, hydrolysable tannins; DM, dry matter; OM, organic matter; CP, crude protein; NDF, neutral detergent fiber; ADF, acid detergent fiber; CH_4, Methane.

4. Conclusions

The evidence analyzed indicates that the anti-methanogenic effects of tannins depend primarily on their molecular structure and their interaction with the ruminal ecosystem, rather than exclusively on their botanical origin. In this context, the present review provides a comparative and critical synthesis of terrestrial and marine tannin sources, highlighting the potential of phlorotannins to modulate methanogenesis and improve ruminal fermentation efficiency. Furthermore, the analysis identified key factors contributing to the variability observed among studies, including tannin type, inclusion level, animal species, diet composition, and experimental conditions, allowing for a more integrated understanding of the mechanisms involved in enteric CH_4 mitigation in ruminants.

Despite these promising findings, the available evidence still presents important limitations associated with methodological heterogeneity, differences in experimental design, and variability in tannin chemical characterization, which complicate direct comparisons among studies and limit extrapolation to commercial production systems. Therefore, future research should prioritize the standardization of tannin classification criteria and inclusion levels, as well as the development of in vivo studies under diverse production conditions and feeding strategies. In addition, strengthening comparative and meta-analytic approaches through the incorporation of more detailed information on tannin chemical structure, dietary composition, and animal productive responses will be essential to identify more consistent and applicable supplementation strategies capable of mitigating enteric CH_4 emissions without adversely affecting digestibility or productive performance.

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5. Declarations

5.1. Ethical considerations

Not applicable.

5.2. Use of artificial intelligence (AI)

The authors declare that AI (ChatGPT-5.5, OpenAI) was used exclusively to improve the resolution and visual quality of the figures originally created in BioRender. This tool was not used for data analysis, interpretation of results, drawing conclusions, or writing the manuscript. All scientific content, as well as the design, interpretation, and final validation of the figures and the manuscript, were the sole responsibility of the authors.

5.3. Conflict of interest

The authors declare no conflicts of interest.

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