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Methanogenesis and Its Strategic Mitigation through Dietary Intervention and Rumen Manipulation: a Review

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Methanogenesis is the formation of methane facilitated by a group of organisms from the phylum Archaea. There are three types of methanogenic Archaea depending on the substrate they use as input metabolite. The hydrogenotrophic (use H_2), methylotrophic (use methylated compound), and acetoclastic (utilize acetate) methanogens. These are a biological process where rumen methanogens consume a substrate from fermentation mainly H_2 to obtain energy where CH_4 is the by-product. This enteric methane emission from livestock is both an environmental concern (greenhouse gases) and a production inefficiency as methane output is considered an energy loss. This paper reviews an understanding of methanogenesis and the application of approaches that could maximize production and reduce the release of pollutants under animal agriculture. The type and ratio of carbohydrates could alter the number and presence of microbes due to variations in rumen pH and substrates contained, such structural carbohydrates favor the growth of propionate-forming microbes that affect the rate of methanogenesis. An increase in the propionate ratio indicates a low methane emission as H_2 is redirected away from the creation of methane. Phytochemicals from plants (oil, tannins, saponins) have direct and indirect effects on methanogens, while they also lower the numbers of protozoa that play a significant role in transferring molecular hydrogen, which will be utilized for methanogenesis. Novel rumen modulators like 3-nitrooxypropanol inhibit the methyl coenzyme M reductase (MCR) necessary for methane synthesis and have a remarkable potential to mitigate CH_4. Other strategies include breeding performance, food waste minimization, change in diet preferences, housing and culling, *etc*. are also ways to decrease methane output. However, there is still a need to validate its effects on animal performance, residues in food, feasibility, availability, and economic grounds.

Keywords: animal production, greenhouse gas emission, methanogenesis, rumen

INTRODUCTION

Since ancient times, raising ruminants has been an important aspect of human activity all over the world (Pulina *et al*. 2017). It contributes significantly to human evolution and development, as well as to the maintenance of social order and the improvement of livelihoods by providing agricultural products, wool, draft power, and protein for food. The practice and management of livestock farming differ depending on location, environmental conditions, resource availability, access to technologies, cultural and traditional food preferences, market channels, and demand potentials (Wanapat *et al*. 2015). However, the human race's quest for a sufficient supply of food had an unfavorable impact on environmental health that is not long-term sustainable. The dire warning about climate change and global warming is caused collectively by several human activities, including animal agriculture (Pragna *et al*. 2018). The population trend continues to

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rise and is expected to continue in the following years. This indicates a strain on the food industry and a high demand for protein-rich foods produced by the livestock sector (Godfray *et al*. 2010). Science investigation efforts regarding methane production and mitigation in ruminants have been at the forefront, particularly for countries that rely heavily on animal farming (Buddle *et al*. 2011). Satisfying the increased demand for animal-based protein caused by a stretching global population while tapering the GHG intensity of ruminant production would, thus, be difficult for the livestock sector and the scientific community. Given the significance of ruminant animals, it is critical to identify techniques and approaches that can be economically implemented on farms to reduce ruminant CH_4 generation while increasing productivity. A complete system analysis must be performed in order to choose the best combination of tactics or cutting-edge technology to use in longstanding field settings (Shibata and Terada 2010). Hence, this paper provides a review of methanogenesis and its strategic techniques for mitigating methane output in ruminant production through various dietary interventions and rumen manipulation.

The Growing Methane Emissions Issue in Animal Agriculture

The production of methane gas by animals is a notable source of greenhouse gas (GHG) emissions that has been linked to climate change (Min *et al*. 2020). Enteric anaerobic fermentation is a digestive activity in which a diverse population of microorganisms found in the reticulo-rumen of ruminants convert plant matter into nutrients that the animal can use to produce high-value proteins such as milk, meat, and leather goods (Doyle *et al*. 2019). Agriculture is accountable for approximately 55% of global methane emissions, two-thirds of this are distributed in the animal industry (Wanapat *et al*. 2015). According to the comprehensive review of Twine (2021), with more recent data on emissions, the lowest estimate of GHGs contributed by animal agriculture should really be increased to 16.5% as a new minimum figure. The current global outlook for milk and meat demand is anticipated to quadruple over the succeeding 30 years. Even so, it is not possible to reduce the number of animals raised because this would jeopardize the production (Buddle *et al*. 2011). All things considered, methane emissions from animal agriculture contribute significantly to GHG output. The increasing demand for animal products necessitates innovative ways to reduce emissions while maintaining the rate of production of animal-derived proteins.

Greenhouse Gases (GHG) and Its Implication

Carbon dioxide is the leading GHG source, followed by methane with a 40% increase in atmospheric accumulation. Although agriculture only makes up a small portion of global GHG emissions, cattle enteric fermentation is the single greatest contributor, accounting for 30% of the total (Shibata and Terada 2010). Between 1960–2017, the global population of ruminants increased by 66%, whereas the population of non-ruminants increased by 435% (FAO 2022). Pig and poultry production account for only 9 and 8% of the sector's direct emissions, respectively, whereas beef and dairy production is liable for the mass portion of emissions, accounting for 41 and 20%, respectively (Llonch *et al*. 2017). The effect of pollutants released into the environment as a result of animal production is not limited to agricultural concerns. This increases the concentration of GHGs, which further warms the planet and contributes to climate change. Agriculture, forestry, and land use were responsible for 23% of all human GHG emissions worldwide, according to the Food and Agriculture Organization’s (FAO 2022) assessment made in 2017 using a one-century global warming potential. The livestock industry's share of GHG emissions varies by location and is influenced by the size of other economic sectors, particularly the energy sector. As an end product of anaerobic fermentation, methane gas contributes to GHG emissions and is regarded as an energy loss for the animal (He *et al*. 2021). Small-scale livestock owners, fishermen, and pastoralists are particularly vulnerable to the climate crisis. Furthermore, 14.5% of all man-made animal supply networks emit GHGs. It amounts to an astonishing 7.1 gigatons of CO_2 equivalent annually. The main cause of emissions is methane produced during ruminant digestion and feed formulation and processing (FAO 2016). Methane emissions from livestock are influenced by a variety of factors – including the amount of feed consumed, the type of nutritional component in the diet, the type of feed, the diet pattern, the environment, genetic make-up of the animal, host adaptability, changes in ruminal microbiota, and rumen ecology (Johnson and Johnson 1995; Shibata and Terada 2010). That is why various strategies for reducing animal methane output have been demonstrated in years (Smith *et al*. 2022), which improved nutritional management, modifying ruminal fermentation by changing the composition of the feed, adding methane modulators, and defaunation (Shibata and Terada 2010). The use of cutting-edge biotechnological tools, managerial techniques, and nutritional intervention (Pragna *et al*. 2018). The utilization of plant metabolites, immunization, VFA’s enhancer, probiotics, breeding efficiency, and genetic preference of low methane emitting animals are some of the technological methods for reducing CH_4 emissions from ruminants (Patra 2012).

Methane Generation in Rumen

Methanogenesis is the generation of methane by methanogens of the kingdom Archaea, a specific subset of microorganisms that live in the rumen under anaerobic conditions. This methanogen primarily uses molecular hydrogen and carbon dioxide as metabolites to synthesize its own energy, serving an important ecological function. Other microorganisms, aside from methanogens, have an impact on methane generation, either by participating in hydrogen uptake or by influencing the population of methanogens or other microbes in the rumen community (Morgavi *et al*. 2010). The rumen microbiota – which comprises bacteria, fungi, and protozoa in ruminant animals – is primarily in charge of digestive processes such as carbohydrate fermentation, protein breakdown, and synthesis of microbial protein (Enjalbert *et al*. 2017). The rumen is the first compartment of the ruminant's gut where microbial fermentation occurs (Sauer *et al*. 2012). Ruminants may use a variety of food substrates that are different from monogastric animals and are not digested by mammals due to this specialized feature in their gastrointestinal tract (Malmuthuge and Guan 2017; Buddle *et al*. 2011). The intricate network of symbioses in the rumen is responsible for the host ruminant's maintenance, immune system, and overall production effectiveness (Cammack *et al*. 2018). Carbohydrates are the primary energy source of ruminants. These polymeric carbohydrates and proteins are digested by a diverse microbial population in a regularly functioning rumen to produce volatile fatty acids (VFAs) and other metabolic compounds *via* several complex metabolic pathways (Janssen and Kirs 2008). The function of the ruminant's gastrointestinal gut accounts for 40% of the ATP used by the entire body (Baldwin and Connor 2017).

Rumen microorganisms are classified into a variety of functional categories – which include cellulolytics (degrade cellulose), amylolytics (degrade starch), proteolytics (degrade proteins), and others that further degrade some of the products synthesized by other microorganisms or break down a different feed component (Henderson *et al*. 2015). Rumen microbes aided in the hydrolysis, degradation, and conversion of polysaccharides – primarily cellulose, hemicellulose, and starch – into glucose, hexoses, and pentoses under anaerobic conditions. Carbon dioxide (CO_2), ammonia (NH_4), and molecular hydrogen (H_2) are formed as a result of the further metabolism of these monosaccharides (Beauchemin *et al.* 2020). The VFAs are absorbed by the host and used as primary sources of energy and carbon for the ruminant (Calsamiglia *et al*. 2007), whereas excess compounds such as CO_2 and molecular hydrogen were consumed by the microbial community in order for them to grow and survive. It is obvious that the final phase of fermenting this ingested feed produces molecular hydrogen, which the rumen methanogens use and reduce to produce CH_4 (Patra 2012). Rumen methanogens were able to generate ATP and obtain energy through this chain of metabolic events, where CO_2 is used as a carbon source and H_2 is the primary electron donor (Ku-Vera *et al*. 2020a; Jeyanathan *et al*. 2014; Llonch *et al*. 2017). Various rumen methanogenic Archaea species use hydrogen and methyl-containing chemicals to obtain energy, producing CH_4 as a waste by-product. This gas output, which serves no other purpose, will exit the animal's gut *via* respiration and be expelled into the environment (Doyle *et al*. 2019). This condition not only has the potential to accelerate global warming by emitting methane as a GHG, but it also has the potential to waste protein and energy invested in animals, potentially limiting the potential of animal livestock production (Calsamiglia *et al*. 2007). The bottom line is that there is a need to redirect the molecular hydrogen away from methanogenesis to energy generation to be used by the host animal.

The Methanogens

Methanogens are organisms from the phylum Archaea – unlike the Eukarya, which includes the bacteria, fungi, and protozoa that comprise the majority of the rumen microbe-host symbiosis (Buddle *et al*. 2011). Methanogenic Archaea comprise 1–4% percent of the microbial biomass with 107–109 cells/mL of rumen fluid and are roughly divided in half between the genera *Methanobrevibacter* and *Methanosarcina* (Ku-Vera *et al*. 2020a; Buddle *et al*. 2011). Moraïs and Mizrahi (2019) define methanogenesis as a process that occurs near the end of the rumen's electron flux and is executed by a taxonomic genus that is remarkably coherent and belongs to the same phylum of Archaea – Euryarchaeota. They classified methanogens based on the metabolites they used as inputs, establishing at most three distinct functioning groups spread across massive phylogenetic gaps between various orders. The first type of methanogen is hydrogenotrophic methanogen, which uses H_2 and CO_2 as input metabolites. The second type of methanogen is methylotrophic methanogen, which uses methylated compounds as a metabolite. Finally, there is acetoclastic methanogen, which uses an acetate compound as an input metabolite.

The initial fermentation of feed by rumen bacteria, fungi, and protozoa produces hydrogen and possibly formate, both of which are used as energy sources by the majority of rumen Archaea. Non-methanogens provide methanogenic substrates during feed fermentation (Pitta *et al*. 2022b). It is reasonable to predict that diet will have an effect on methanogens due to pH variations that may alter methanogen activity and the presence of harmful substances that may directly affect methanogens (Janssen and Kirs 2008). Ruminant methane emissions account for 2–12% loss of feed energy and 16% of world GHG gas emissions (Lan and Yang 2018; Beauchemin *et al*. 2020), which could be used to increase productivity instead (Tseten *et al*. 2022). Aceticlastic/methylotrophic methanogens account for a small proportion of the rumen archaeal population in sheep, whereas hydrogenotrophic methanogens predominate in the rumen (Malik *et al*. 2022a). Furthermore, methylotrophic methanogens may contribute more to CH_4 output in the rumen (Pitta *et al*. 2022b). To reiterate, methane generation is facilitated by the microbes under the phylum Archaea. Yet, diet interventions do not directly target these methanogens but the fate of hydrogen ions after fermentation.

Type and Ratio of Carbohydrates

Forages make up the majority of the diet of domestic cattle because ruminants can utilize fiber breakdown *via* rumen microbial fermentation. Due to the high structural carbohydrate content of forages such as fresh or stored grasses, it can be regarded as completely inedible by humans (Klevenhusen and Zebeli 2021). Diet was found to be more influential than animal type in determining the composition of rumen microbial populations (Henderson *et al*. 2015). A large venue of increasing performance could be attainable by modifying the types of feedstuffs fed to the animals, with consideration of the appropriate mixtures of these carbohydrates and the feasibility of the application in farms. Carbohydrates of various types can have a direct impact on the physiological, chemical, and biological processes of the rumen (Sun *et al*. 2022). A variety of forages are high in cellulose and hemicellulose, structural carbohydrates that may have a better rumen function response than energy-rich concentrates high in non-structural carbohydrates like starch and sugars (Wanapat *et al*. 2015). According to della Rosa *et al.* (2022), a sheep given a 100% forage rape (*Brassica napus*) compared to ryegrass (*Lolium perenne*) based pasture reduces methane yield by about 33%, whereas a 15-wk diet of forage (*Brassica napus* L.) in lamb decreases CH_4 emission by an average of 26% than a ryegrass (*Lolium perenne* L.) (Sun *et al*. 2015), and when alfalfa (*Medicago sativa*) silage is substituted with paulownia (*Paulownia tomentosa*) leaves silage, the methane output can be reduced by 12% in rumen simulation technique (Huang *et al*. 2022). The inclusion of structural carbohydrates in the aforementioned treatments may have a significant impact on the rumen fermentation process. Due to increased propionate-forming microbes, forage rape lowers the acetate ratio while increasing the molar concentration of fermentation products such as valerate, succinate, and propionate (della Rosa *et al*. 2022; Sun *et al*. 2015). This points to a low hydrogen yield and, as a result, lower methane production (Sun *et al*. 2015). Changes in fermentation to produce propionate, succinate, and valerate rather than acetate plus hydrogen resulted in reduced methane generation (della Rosa *et al*. 2022).

In contrast to the improved rumen action caused by structural carbohydrates, concentrate-based diets can have a beneficial effect on metabolism when combined with the appropriate amount of forage. As long as rumen function is not impaired, adding 40% concentrates in terms of dry matter intake to a diet containing medium to poor quality forages reduces methane output (Hristov *et al*. 2013). Cows fed starch-rich diets compared to grass silage-based diets, contained conjugated linoleic acid and saturated fatty acids had fewer protozoa, and shifted their rumen fermentation toward propionate rather than butyrate (Bougouin *et al*. 2018), owing to the fermented substrate switching from fiber to starch, which results in a diminished in methane output (Pragna *et al*. 2018). The rapid breakdown of easily fermentable carbohydrates lowers the rumen's pH, which inhibits metabolic activity and, thus, prevents the growth of methanogens due to the acidic environment in which metabolic activity is inhibited, which further lowers CH_4 emissions (Sun *et al*. 2022). The Archaea and protozoa in the rumen are linked because the protozoa consume hemicellulose, pectin, and soluble carbohydrates to produce the metabolic H_2 and VFA that the Archaea require to obtain the energy necessary for growth (Ku-Vera *et al*. 2020a). Ultimately, by altering rumen fermentation patterns, diets can be modified to incorporate particular forages that are high in structural carbs or balanced with concentrates. Hence, methane emissions can be greatly reduced in this way.

Plant Secondary Metabolite

Antibiotic residues in animal products can result from haphazard antibiotic administration (Bharanidharan *et al*. 2021). As a result, using plant-based metabolites may be an effective way to modify the makeup and function of the rumen microbiome (Ku-Vera *et al*. 2020b). The term "plant secondary metabolite," presumably coined by Albrecht Kossel in 1891, refers to a wide range of chemical substances found in plants that do not participate in the biochemical processes of plant development and growth [Hartmann (2007), as cited by Patra and Saxena (2010)]. The *in vivo* and *in vitro* experiments have revealed the potential of plant-derived substances like essential oils, tannins, and saponins to inhibit the growth, development, and activity of methanogen populations (Cieslak *et al*. 2013; Joch *et al*. 2018). Shrubs, tropical trees, and their foliage and pods at 10% incorporation in cattle ration decreased CH_4 output by 10–25%, depending on plant species and level of intake (Ku-Vera *et al*. 2020b), linseed oil (LSO) at 2% supplementation DMI also 20% reduced methane output (Hassanat and Benchaar 2021; van Gastelen *et al*. 2017), whereas extract of solvent canola meal decreased methane yield in dairy cows (Benchaar *et al*. 2021). In addition, decreased enteric CH_4 yield by 6–20% when vegetable oils and nitrates are added to the diet (Ku-Vera *et al*. 2020b), and mootral – a mixture of garlic plus citrus extract in a 15% corn silage-based diet in commercial feedlot – reduce methane generation and improved carcass leanness (Bitsie *et al*. 2022). These treatments alter the fermentation route that favors propionate production at the expense of butyrate and acetate synthesis (Hassanat and Benchaar 2021; van Gastelen *et al*. 2017; Benchaar *et al*. 2021). Acetate generation is linked to the production of hydrogen gas, which is used as an input metabolite and then transformed into methane in the rumen (della Rosa *et al*. 2022). Here, it is feasible to control the destiny of molecular hydrogen and divert it away from CH_4 formation and toward propionic acid synthesis, by incorporation of plants that contain phytochemicals (Ku-Vera *et al*. 2020b). Furthermore, anise oil, garlic oil, cinnamaldehyde, and eugenol may boost the formation of propionate and reduce the creation of acetate and methane (Calsamiglia *et al*. 2017). The excellent ability of oil supplementation to control the rumen and reduce CH_4 production must be balanced by the risk that an excessive dosage or rate of supplementation will have on DMI, rumen metabolism, and animal performance (Hristov *et al*. 2022), and only certain circumstances and production processes may make its utilization effective (Calsamiglia *et al*. 2007). To recap, phytometabolites may be able to reduce methane emissions in ruminants by altering the pathways involved in rumen fermentation. Propionate production is successfully favored over acetate and methane, although careful dose is required to avoid negative effects on intake, metabolism, and overall animal performance.

Other Modulators

Recent exploration of novel diet incorporation had also a remarkable potential to mitigate methane. Application of silkworm pupae oil (SWPO) at 2–3% DMI in sheep feed results in a 24% reduction in methane output (Thirumalaisamy *et al*. 2022), and addition of native rumen microbes (NRM; *Chordicoccus furentiruminis*, *Succinivibrio dextrinosolvens*, and *Prevotella albensis*) lower a 20% methane yield in cattle (Pittaluga *et al*. 2023). Moreover, red macroalgae (*Asparagopsis taxiformis*) when mixed with rhodes grass hay (*Chloris gayana*) has the potential to reduce CH_4 emission from cattle by up to 95% (Roque *et al*. 2019), whereas red seaweed extracts favor the population of *Anaeroplasma*, Succinivibrionaceae, and Ruminococcaceae, which are connected to increased propionate synthesis, starch breakdown, and methane-reducing amylase activity (Choi *et al*. 2022). Recently, the use of seaweeds as an anti-methanogenic feed additive has gained popularity recently. The recommended species is *Asparagopsis taxiformis* due to its comparatively greater bromoform content. The ruminal methanogenesis can be prevented by the specific inhibition of coenzyme M methyltransferase activity by bromoform, a type of halogenated methane analog found in *A. taxiformis* (Liu *et al.* 2024). *Asparagopsis* is a feed additive that may be easily added to any mixed ration formulation for dairy and feedlot animals. However, techniques must be developed to guarantee that *Asparagopsis's* bioactivity is maintained when it is mixed into a diet (Black *et al.* 2021). In the Philippines, there is approximately 1.5 million metric tons of seaweed were produced in 2022. With over half of the nation's seaweed production in that year, BARMM was the leading producer (Statista 2022). The significant production capacity, particularly in regions such as the Bangsamoro Autonomous Region in Muslim Mindanao, presents an opportunity to establish scalable supply chains for red seaweed-derived goods like *Asparagopsis*. Utilizing this resource could help the Philippines' seaweed farming communities economically and contribute to the global effort to lower methane emissions. Additionally, the infrastructure now in place for seaweed production positions the country as a viable player in this emerging industry.

Rumen Manipulation

Methane emissions may be effectively reduced by altering the ruminal microbiota through a variety of dietary treatments (Min *et al*. 2020). There are three ways to reduce enteric CH_4, including diverting the end product of digestion to propionate formation, rechanneling H_2 away from methanogenesis, and selectively inhibiting the activity of rumen methanogens (Pragna *et al*. 2018). Lower numbers of fibrolytic bacteria and protozoa were observed in 90% of barley silage with the inclusion of canola oil (OIL) in the cattle's diet resulting in 24% reduced CH_4 emission (Gruninger *et al*. 2022), a combination of condensed and hydrolyzable tannin at 1.5% DMI in cattle also lower CH_4 output (Aboagye *et al*. 2018); after linseed oil (SLO) is added to cattle, total protozoa decreases, which increases the fraction of propionate generation and a decrease in CH_4 yield of up to 20% (Hassanat and Benchaar 2021), whereas *Pharbitis nil* and its extract from the seeds had a 37% mitigation in methane yield and decreased the numbers of ciliated protozoa (Bharanidharan *et al*. 2021). Furthermore, the isolated rumen bacteria, *Streptococcus bovis* can reduce CH_4 production by 53% (Garsa *et al*. 2019); when anti-methanogenic (Harit Dhara-HD) is added to sheep at 5% DMI, propionate concentration increases, whereas ammonia nitrogen levels decrease (Malik *et al*. 2022a). Corn oil supplement at 4% DMI incorporation in goats reduces enteric emission by 15% and subsequently decreases in the genus of methanogens (Zhang *et al*. 2019) and essential oils that reduce methanogenic population reduce methane by 23% (Ku-Vera *et al*. 2020b).

Lipid and feeds concentrate augmentation of the diet, processing of feeds, and specific additives of feeds all contribute to improve forage digestibility, and digestible forage consumption (Hristov *et al*. 2013)

Table 1. Dietary intervention to reduce methane output and effects on ruminants.

Diet supplemented	Diet ratio	Animal	Body weight	Methane reduction	Other positive effects	Reference
Forage rape pasture substituted with ryegrass-based pasture	100% on a dry matter basis	Sheep	–	34% less	Decrease in acetate and increase proportion of propionate and succinate. Enhances rumen pH.	della Rosa *et al*. (2022)
Corn silage-based diets with linseed oil (LSO)	2%-3% inclusion of LSO	Lactating Holstein cow	–	20% decrease	Less proportion of acetate than propionate	Hassanat and Benchaar (2021)
Soybean meal substituted with canola meal	24% ratio DMR	Lactating Holstein cow	692 ± 60 kg BW	10% decrease in CH_4 compared to 0% inclusion of CM	Increase DMI and proportion of propionate.	Benchaar *et al*. (2021)
Combination of hydrolyzable tannin (HT) and condensed tannin (CT)	1.5% per dietary DM	Beef cattle	292 ± 4.1 kg	2% less than other treatment	Decrease ruminal NH3 ratio in beef-type cattle fed a high-protein diet without adverse effects on animal performance	Aboagye *et al*. (2018)
3-nitrooxypropanol (3-NOP)	60 mg/kg of feed dry matter	Holstein cows	Average of 601.5 kg BW	26% decrease in methane yield	Improve feed efficiency	Melgar *et al*. (2020)
Red macroalgae *(Asparagopsis taxiformis*)	5% OM inclusion rate	Beef cattle	–	95% reduction in methane	VFAs production not compromised	Roque *et al*. (2019)
Rapeseed (*Brassica napus L.*) compared to perennial ryegrass (*Lolium perenne L.*)	Sole diet within 15 weeks	Sheep	–	22–30% less emission of rapeseed rather than ryegrass	Significant increase in propionate-forming bacteria with less H_2 output. Thus, less methane production during fermentation. Lower rumen pH.	Sun *et al*. (2015)
Ruminal probiotics-native rumen microbes (NRM; *Succinivibrio dextrinosolven*s, *Prevotella albensis,* and *Chordicoccus furentiruminis*)	Inclusion in a 15% corn silage diet	Cattle	353 ± 64 kg	Decreased in 20% CH_4 yield (g/kg DMI)	Improve rumen digestion	Pittaluga *et al*. (2023)
3-nitrooxypropanol (3-NOP)	125 mg/kg DM	Crossbred steers	421 ± 11 kg	76% less CH_4 yield	Acetate: propionate ratio in rumen fluid decreased	Alemu *et al*. (2020)
Silkworm pupae oil (SWPO)	2% of dry matter intake	Sheep	–	23-25% reduction	Increased body weight gain	Thirumalaisamy *et al*. (2022)
3-nitrooxypropanol (3-NOP)	2 mg/g dry matter	Dairy cows *in vitro*	–	11.48% decrease in methane emission	No negative influence on dry matter digestibility and increase proportion of propionate	Liu *et al*. (2022)

that favors efficient rumen fermentation (Gruninger *et al*. 2022) decreased protozoal number – particularly *Methanocaldococcus* and *Methanococcoides methanogens* (Malik *et al*. 2022b; Bharanidharan *et al*. 2021), increased propionate synthesis, and decreased NH_3-N formation (Bharanidharan *et al*. 2021) without having a detrimental impact on animal performance (Aboagye *et al*. 2018). Chemical inhibitors as a viable methanogenesis reduction strategy are not practical due to their toxic effects on ruminants and impairment in the function of rumen (Garsa *et al*. 2019). Hence, plant chemicals may be more effective alternative sources for reducing methane (CH_4) generation since they are more ecologically benign, consumer-friendly, and practical (Bharanidharan *et al*. 2021). In short, by increasing the production of propionate, diverting hydrogen, and inhibiting methanogens, plant-based oils, and additives can reduce methane emissions in ruminants. These methods provide a sustainable alternative to chemical inhibitors while maintaining rumen function and animal performance.

Potential of 3-Nitrooxypropanol (3-NOP)

The 3-nitrooxypropanol was developed to boost the potency of calcium channel modulator, but it was later found that this compound inhibits the active substrate of methyl coenzyme M reductase, essential for mediating CoM reduction and methane production by ruminal Archaea (Schilde *et al*. 2021). Haisan *et al*. (2016) observed a reduction in 23–37% CH_4 yield in cows after the incorporation of 1259 and 2500 mg/d of 3-nitroxypropanol in cattle, whereas there is the synergistic effect of fumarate and 3-NOP that decreased methane yield to 11% in dairy cows at a dosage of 100 mg/DMI (Liu *et al*. 2022). Moreover, 125 mg/kg DMI is an effective CH_4 mitigation strategy in intensive beef feedlot farms with about 76% reduction (Alemu *et al*. 2020) and a 60 mg/kg DMI reduces CO_2 by 5% and lowers CH_4 emission by 26% (Melgar *et al*. 2020).

Reportedly, 3-NOP decreases the abundance of the major genus of methanogens, which is the *Methanobrevibacter*, and increases *Bacteroidetes* (Gruninger *et al*. 2022), *Prevotella*, and *Succiniclasticum* (Liu *et al*. 2022). 3-NOP works by targeting and blocking the enzyme that produces methane, methyl-coenzyme M reductase (MCR) (Pitta *et al*. 2022a; Alemu *et al*. 2020) and partly inactivating the hydrogenotropic methanogenesis (Gruninger *et al*. 2022), which results in an increase concentration ratio of propionate to acetate (Melgar *et al*. 2020) without compromising intake of dry matter (Haisan *et al*. 2016; Liu *et al*. 2022). Recently, this 3-NOP with the commercial name Bovaer® was developed as one effective additive to mitigate methane emissions from livestock. Developed from 3-NOP is Bovaer®, formerly known as 3-nitrooxypropanol (Gadzama 2024). The European Food Safety Authority has authorized the use of its patented product, Bovaer (DSM-Firmenich Nutrition Products Ltd., Kaiseraugst, Switzerland), in dairy cow diets and for all ruminants, including beef and dairy, in numerous countries (Ma *et al.* 2024). This synthetic, non-toxic material functions by inhibiting methyl-coenzyme M reductase, an enzyme responsible for the last step of CH_4 production in ruminant stomachs. When added to animal feed, Bovaer® effectively lowers CH_4 emissions because it inhibits the main enzyme responsible for ruminant CH_4 formation (Gadzama 2024). The effectiveness of Bovaer® depends on the dosage and diet composition. Higher dosages are more effective, however excessive dietary fiber can decrease its effects. Additionally, the effectiveness of Bovaer® varies by geographic location and animal production system (Gadzama 2024). Thus, 3-nitrooxypropanol (3-NOP), which is currently marketed under the name Bovaer®, has become a powerful methane mitigation technique for the livestock sector. Even if there are still issues like dosage optimization for various diets and production systems, adding 3-NOP to ruminant diets is a big step toward reaching worldwide methane reduction goals.

Reduction in Microbes Associated with Methane Generation

The majority (75%) of the energy in carbohydrates comes through VFA synthesis, with the remaining 25% either going to microbial development or being lost as H_2 and CH_4 (Melgar *et al*. 2020). Numerous investigations have shown that pure extracts of tannins and saponins have inhibitory effects on protozoa either indirectly through defaunation or directly by reducing the amount and activity of methanogens (Patra and Saxena 2009; Aboagye *et al*. 2018). While ionophores transform the bacterial colony from gram-positive to Gram-negative microorganisms with a concurrent shift in the fermentation to a more propionate than acetate formation, despite the fact that they do not influence the number and variety of methanogens (Patra 2012), protozoa and fibrolytic bacteria were much less prevalent in the rumen following the addition of oil (Gruninger *et al*. 2022). This fermentation change reduces the amount of H_2 that methanogens may use to produce CH_4 (Patra 2012). While using 3-nitroxypropanol has the potential to significantly lower CH_4 emissions by inhibiting MCR during methanogenesis (Pitta *et al*. 2022a).

As discussed earlier, rumen protozoa are symbiotic with methanogens and participate in interspecies H_2 transfer to provide methanogens the molecular hydrogen they require to convert CO_2 to methane. According to estimates, the methanogens connected to ciliate protozoa produce between 9–37% of the rumen's methane both intracellularly and extracellularly (Wanapat *et al*. 2015). Because of this, the protozoal population in the rumen is decreased by dietary modulators, leading to reduced methane production (Patra and Saxena 2009). However, a fall in CH_4 synthesis is not necessarily accompanied by a decline in protozoa, as certain phytochemicals may reduce methanogens unrelated to protozoa (Aboagye *et al*. 2018). The major causes of fiber breakdown in the rumen are bacterial cellulolytic populations; some like *Ruminococcus spp.* dominantly create acetate, which stimulates the synthesis of additional H_2. On the other hand, the main cellulolytic bacteria, *F. succinogenes* predominantly creates succinate, which causes less H_2 to develop during the formation of propionate (Jeyanathan *et al*. 2014). The generation of methane can be controlled by ruminal microorganisms involved in hydrogen metabolism, particularly hydrogen-utilizing bacteria that create less H_2 (Lan and Yang 2018), notably in forage-fed animals, without impeding fiber breakdown (Jeyanathan *et al*. 2014). Although methanogens share the objective of obtaining energy by producing methane, discrete methanogenic lineages have varying metabolic and physiological capabilities, as well as host genotypic structure, diet ratio, and ambient factors with subsequent effects in H_2 settling and CH_4 generation (Pitta *et al*.

Table 2. Mitigation strategy and its anti-methanogenic mechanism to reduce methane output in ruminants.

Mitigation strategy	Animal	Reduction in CH_4	Anti-methanogenic mechanism	Effect on rumen microbes	Limitation	Reference
Extract from the seeds of *Pharbitis nil*	–	37% reduction	Contained polyunsaturated fatty acids dominated by linoleic acid with a ratio of 18:2	Decrease populations of ciliated protozoa and H_2-producing *Ruminococcus flavefaciens* and increase concentration of propionate rather than acetate	Resource availability	Bharanidharan *et al*. (2021)
Bovicin (type AII antibiotic)	Cattle	50% reduction	Comprising 2 β-methyllanthionine and a disulfide bridge encoded by *bovA* gene hitherto	Inhibited many rumens Gram-positive bacteria including *Lactobacilli*, *Bacillus subtilis*, and *L. monocytogenes*	Not specific response of methanogenesis and yet to be understood	Garsa *et al*. (2019)
3-nitrooxypropanol (3-NOP)	Beef cattle	24–28.2% decrease in methane yield	Disabling the enzyme methyl-coenzyme M reductase used by Archaea (methanogens)	Decreasing of *Methanobrevibacter* and increasing of *Bacteroidetes*	Not yet approved for commercial use	Gruninger *et al*. (2022)
Corn oil supplement	Goat	15% reduction in methane generation	> 50% polyunsaturated fatty acids (PUFA)	Increased population of family *Rikenellaceae*, genus *Lachnospiraceae*, and genus *Butyrivibrio*. Decreased in the order of Methanomicrobiales, and of genus *Methanomicrobium*	Investigation over a long period is needed to validate its effects	Zhang *et al*. (2019)
Linseed oil	Cattle	4% DMI		Decreased in total number and genera of protozoa	Availability of resources	Hassanat and Benchaar (2021)
3-nitrooxypropanol (3-NOP)	Dairy cow	11.48% decrease in methane yield	Disabling the enzyme methyl-coenzyme M reductase used by Archaea (methanogens)	Reduced *Ruminococcus* and Lachnospiraceae_NK3A20_group and increased *Prevotella* and *Succiniclasticum*	Not yet approved for commercial use	Liu *et al*. (2022)
Starch rich diet *vs*. fiber rich diet	Holstein cow	–18% CH_4 g/d	Starch-rich diet has a higher concentration of conjugated linoleic acid and saturated fatty acid	Reduce protozoal population and alter in rumen fermentation process toward propionate formation	–	Bougouin *et al*. (2018)
Red seaweed extracts	*In vitro* batch culture	4.6–35.0% less compared to control	Tended to reduce the acetate-to-propionate ratio while increasing the molar percentage of propionate	Reduction in the abundance of genus *Methanobrevibacter* and total methanogens	–	Choi *et al*. (2022)
Anti-methanogenic supplement (Harit Dhara-HD)	Sheep	22%	Containing 22.1% tannic acid in a ratio of 3: 1 hydrolyzable and condensed tannins	Decreased ruminal protozoa Reduction in *Proteobacteria* whereas increased in *Lentisphaerae*; decrease of *Methanocaldococcus*, *Methanococcoides*, *Methanocella*, and *Methanoregula* methanogens	Determining the impact of this supplement on the overall performance of the rumen is not fully understood	Malik *et al*. (2022a)

2022b). In other words, because these phytochemicals have direct or indirect impacts on the activities of methanogens unrelated to protozoa, a decrease in methane emission does not always coincide with a decrease in protozoa.

Management Approaches to Reduce Enteric Methane Emission

Aside from investigating rumen ecology and how to change it to successfully reduce methane. Additionally, there are several ways to establish sustainable animal farming. Bellarby *et al*. (2012) suggested that waste minimization in food, a shift to plant-based protein source food, regeneration of forest lands, and encouragement of growing livestock to grazing land rather than intensive feedlots could reduce

GHG emissions. In more economically developed nations, the culling of inefficient and low-producing livestock is frequently recommended to reduce the CH_4 budget (Patra 2012; Pragna *et al*. 2018). Enhancing dietary digestibility, effective housing management, animal health interventions and breeding for higher performance (Llonch *et al*. 2017), early life programming (Styles *et al*. 2018), and quality forage and efficient pasture management reduce environmental impact and improved animal production (Pragna *et al*. 2018).

Conclusion and Recommendation

Globally, climate change has a serious direct impact on the agriculture sector, affecting our food system and the livelihood of the people particularly in countries that are on the brink of poverty. An adequate supply of food is predicted to feed the growing population. Thus, collective effort from individuals across nations is significant to curb the outstanding volume of GHG. One of which could come from the agriculture industry, on how we rear animals and produce protein food supply. Animal agriculture contributes to a 16% methane emission. After a thorough review, it is possible to curtail the emission of methane from ruminants by understanding the complexity of enteric methanogenesis including its metabolic process by incorporating strategic methods without compromising animal performance. These include the right proportion and type of forages (structural and non-structural carbohydrates) in feeding the animals, the inclusion of range of races of plants that are rich in phytochemicals (oil, saponins, tannins) that inhibit, alter, and shift the fermentation process, novel approaches (use of seaweed extract, fed microbials) and the use of 3-nitrooxypropanol have a consistent potential in reducing CH_4 output in animals. Moreover, non-diet intervention involving breeding efficiency, housing management, culling, quality of feedstuff, and health regulation could contribute to controlling the CH_4 budget. However, the presented techniques to agitate CH_4 emission need further investigation to validate and scrutinize their effects on animal performance, animal health, and food safety in animal products, as well as the feasibility of the application at the farm level, availability of the resources, and its economic grounds.

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