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Review

The Use of Temperate Tannin Containing Forage Legumes to Improve Sustainability in Forage–Livestock Production

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Abstract: Greenhouse gas emissions from ruminant livestock production systems contribute significantly to the environmental footprint of agriculture. Emissions are lower for feedlot systems than for grass-based systems primarily because of the extra time required for grass-finished cattle to reach slaughter weight. In contrast, legume forages are of greater quality than grasses, which enhances intake and food conversion efficiencies, leading to improvements in production and reductions in environmental impacts compared with forage grasses. In addition, the presence of certain bioactives in legumes such as condensed tannins (CT) enhance the efficiency of energy and protein use in ruminants relative to grasses and other feeds and forages. Grazing tannin-containing legumes also reduce the incidence of bloat and improve meat quality. Synergies among nutrients and bioactives when animals graze diverse legume pastures have the potential to enhance these benefits. Thus, a diversity of legumes in feeding systems may lead to more economically, environmentally, and socially sustainable beef production than grass monocultures or feedlot rations.

Keywords: grass-fed beef; sustainable agriculture; forage diversity; tannin-containing legumes; alfalfa; sainfoin; birdsfoot trefoil; condensed tannins; nitrogen excretion; methane emissions

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1. Introduction

Emissions of greenhouse gases (GHG) from ruminants include methane (CH_4), nitrous oxide (N_2O), and carbon dioxide (CO_2) [1]. In a recent life cycle assessment of the beef cattle industry in the United States, Rotz et al. [1] estimated that the GHG emissions, considering animal outputs and direct emissions from soil (cultivated pastures, range, and cropland) and the manufacturing of the operation's inputs (fertilizers, pesticides, electricity), were equivalent to 242.6 Tg CO_2eq, which represent 3.8% of the 6457 Tg CO_2eq of total anthropogenic GHG emissions for the US in recent years [2]. Approximately, 142 Tg CO_2eq are directly emitted from cattle systems (CH_4 and N_2O from enteric fermentation and manure management), which is nearly 60% of the total GHG emitted for beef cattle production [1], or 2.1% of the total US anthropogenic GHG emissions [2]. When GHG emissions are expressed per unit of product (GHG intensity), the US average for 2019 was approximately 21 kg CO_2eq/kg carcass weight. In beef production, the cow–calf phase is the biggest contributor, contributing 70% of total GHG emissions [1]. These GHG intensity values are in line with previous values reported by Beauchemin et al. [3] for Canadian beef cattle systems of 22 kg CO_2eq/kg BW, with the cow–calf system contributing approximately 80% of total GHG emissions.

The largest contributing source of GHG emissions from beef cattle production is enteric CH_4, accounting for 56% [1] to 63% [3] of all GHG from beef industry and 39% of all GHG emissions from the livestock sector [4]; thus, reducing emissions from this source would have the most impact. Methane is a byproduct of the microbial fermentation of feeds in the rumen and may also represent an energy loss to the animal that ranges between 2 to 12% of the gross energy consumed with the diet [5]. The reduction of CO_2 to CH_4 by methanogenic archaea acts as a hydrogen (H_2) sink, removing H_2 from the rumen and avoiding the negative effects of H_2 accumulation on microbial enzymatic activity and degradation of plant material [6]. Methanogens use H_2 as their main energy source, producing CH_4 in the process. Methane is accumulated in the rumen and eructated by the ruminant to the atmosphere [7], resulting in negative implications for the environmental sustainability of ruminant production systems.

Several comprehensive reviews have described different strategies proposed by the scientific community to reduce enteric methane production and mitigate methane emissions [8–12], but in order to be adopted by beef cattle producers, they should be cost-effective and socially acceptable. Rumen defaunation, for instance, has been shown to reduce CH_4 emissions from ruminants by 50%, due to the fact that protozoans are large producers of H_2 with many methanogens among these microorganisms [13]; however, the lack of persistent response due to rapid adaptation and recovery of protozoal numbers along with impractical defaunation methods has limited its use [14]. On the other hand, antimethanogen vaccines have reduced CH_4 emissions up to 8% in sheep [15], but changes in methanogen populations do not always lead to CH_4 reductions [16]. In addition, the development of a successful wide-spectrum immunization is still on the far horizon for CH_4 abatement programs, limiting the application of such strategies as alternatives to reduce CH_4 emissions. Selection of "low-CH_4"-producing animals might also represent a promising strategy for CH_4 mitigation options [17], but the approach is still in an early stage of development. The use of ionophores that inhibit protozoan growth [18], halogenated methane analogues that inhibit growth and enzymatic activity of archaea in the rumen [19], or nitrate salts that have a greater affinity for H_2 than CO_2 [20] have been discouraged due to consumer perception and potential negative effects on animal health, as well as on the environment [21].

Finally, dietary manipulations such as feeding highly digestible feed components such as grains [22] or feeding organic acids such as fumarate [23] or malate [24], which promote propionate production in the rumen and redirect H_2 to other reductive bacteria, may reduce CH_4 emissions from ruminants. The addition of lipids [25], condensed tannin (CT) extracts [26,27], essential oils [28], exogenous enzymes and yeasts [29], among others—which can be supplied through total mixed rations for confined livestock—are still the most promising CH_4 mitigation options in terms of practical application and acceptance by farmers and consumers. Nevertheless, many ruminants consume forages as their sole diet in pasture-based livestock systems, and the need to supply feed additives in meals might constrain their practical implementation [21]. In this case, CH_4 emissions may be reduced by using highly digestible forage species with a low concentration of fiber [30,31], because forages such as grasses with high fiber concentration reduce passage rate and increase ruminal retention time [32,33], which enhances CH_4 production per unit of forage intake (CH_4 yield). In this situation, the extent of rumen fermentation increases and there is more H_2 to be used as a substrate for methanogenic archaea [34]. In addition, a more fibrous diet usually increases the proportion of acetate to propionate in the rumen, which increases the production and release of CH_4 [5,35].

2. The Use of Forage Legumes for Enteric Methane Abatement in Forage-Based Beef Production Systems

Forage legumes in beef feeding systems can offer economic and environmental advantages relative to grass-fed systems. In contrast to grasses, forage legumes are lower in neutral detergent fiber (NDF), higher in N concentrations [36,37], higher in nonstructural carbohydrates [38,39], and are digested more rapidly by ruminants at similar stages of maturity [37]. These characteristics lead to lower retention times in the rumen; thus, intake and production are greater than in grass-fed systems [40]. This faster rate of digestion of forage legumes is primarily attributed to the faster rates of particle breakdown and quicker fermentation rates in the rumen [41]. An increased passage rate of forage legumes may also favor propionate production, which is considered a competitive pathway for H_2 use in the rumen [34], contributing to reduced CH_4 yield relative to other forages such as grasses [42]. In support of this, Archimède et al. [43], in a meta-analysis of ruminants fed C_3 or C_4 grasses and legumes, identified fiber structure and ruminal retention time as the main factors influencing CH_4 production, with 20% lower CH_4 yields in animals fed warm-season legumes than in those fed C_4 grasses. Similarly, the enteric CH_4 emissions of beef cows grazing the forage legume birdsfoot trefoil (*c*) and cicer milkvetch (*Astragalus cicer*) were approximately half of the emissions reported for the grass meadow brome (*Bromus biebersteinii*) [44].

Alternatively, forages with high concentrations of nonfiber carbohydrates (NFC; soluble carbohydrates plus pectin) that are rapidly fermented in the rumen, and with a low proportion of structural carbohydrates (cellulose and hemicellulose), may yield levels of microbial mass similar to those observed in grain-fed animals, increasing proportions of potentially propionate-forming bacteria and reducing H_2 production and CH_4 emissions, as was observed by Sun et al. [42] feeding forage rape (*Brassica napus* L.) to lambs. Nonfiber carbohydrates represent a readily fermentable source of energy for microorganisms in the rumen, providing energy in synchrony with the high concentrations of protein availability typically observed in forage legumes that contribute to the synthesis of microbial protein [45].

The high nutritional composition of legumes usually leads to greater DM intakes than in animals offered grasses [37], resulting in greater liveweight gains (0.8 to 1.6 kg/d for beef steers) [44,46–48]. For finishing animals, this benefit substantially decreases the number of days to slaughter and the amount of CH_4 emitted over the animal's lifetime relative to grass-fed systems [37]. It has been estimated that the number of cattle required to produce 1 billion kg of beef when finished on pure birdsfoot trefoil pastures is approximately 15% lower than when finished on grass (2.9 vs. 3.4 million animals, respectively; [48]), suggesting that legume-finishing systems represent a realistic strategy to reduce enteric CH_4 emissions.

3. Constraints to the Use of Forage Legumes in Beef Cattle Grazing Systems

Alfalfa (*Medicago sativa* L.) has been one of the most important crops grown in the western US, being the most high-yielding and nutritious forage available for feeding high-producing ruminants [49]. Similarly, white clover (*Trifolium repens*) and red clover (*T. pratense*) have been extensively used for grazing in Australia, New Zealand, and the United Kingdom. However, the direct use of these legumes as grazing forage has been limited due to the high risk of livestock losses caused by pasture bloat [50]. Pasture bloat occurs when ruminants graze fresh, high-protein forages with a high rate of particle breakdown that results in rapid release of plant-soluble proteins and disruption of chloroplasts, providing large quantities of gas and bacterial slime, which create a stable foam that prevents eructation of fermentation gases (CO_2 and CH_4) [51]. Ultimately, the rumen becomes distended, resulting in death from suffocation or cardiac arrest. Subclinical bloat is another significant but often unnoticed cause of reductions in productivity, mostly explained through reductions of intake [52]. Management techniques such as grazing mature bloat-causing legumes might reduce the risk at the expense of reducing the overall nutritive value of legume forages [53]. Grazing grass–legume mixtures still may impose a risk of bloat if animals are able to select and ingest the preferred legume species in high proportions.

A further issue with alfalfa and Trifolium spp. is that the high concentration of rumen-degradable protein in forage legumes usually exceeds the capacity of microorganisms for uptake of NH_3 and synthesis of microbial protein due to a deficient energy supply for N capture [54]. The excess of ruminal NH_3 is absorbed across the rumen wall [55], transformed to urea in the liver, and excreted in the urine with an energy cost for the animal [56]. Consequently, only 10 to 40% of ingested N is retained as animal product (meat or milk) by ruminants [57], and in some cases, when NH_3 detoxification capacity of the liver is surpassed, NH_3 accumulation in blood can be toxic for the ruminant and induce negative internal states that constrain DM intake [58]. In addition, high blood urea levels lead to high urinary N excretions [59] that increase the proportion of N excreted as a highly labile form in the urine, contributing to pollution from agricultural sources that is a major environmental concern [60].

Once urine is excreted and deposited on the soil surface, urea is rapidly hydrolyzed by microbial urease to NH_4^+, which may be nitrified later to nitrite (NO_2^-) and nitrate (NO_3^-) [61]. Greater levels of urinary N excretions are associated with a greater and more rapid NH_3 volatilization and N losses as NO_3^- that may be leached into groundwater or in runoff to waterways [60], contributing to eutrophication [62,63] and the pollution of drinking water. In addition, nitrous oxide (N_2O) is produced as an obligate intermediary during microbial nitrification and denitrification processes [64,65], being one of the most important GHGs with a warming potential 265 times greater than CO_2 in a 100-year time horizon [66]. According to Bao et al. [67], an increment in urinary N excretion of growing beef cattle from 29 to 50 g/d increases the estimated emission of N_2O by 37% from 413 to 565 mg/d. Regardless of these conditions, reductions in the proportion of N partitioned to urine in ruminants will be beneficial for the environment, since urinary N is much more susceptible to gaseous losses than fecal N, which is in the form of covalently bound N and needs a longer time to be mineralized to NH_4^+ before being susceptible to volatilization or available for nitrification [68].

4. Tannin-Containing Legumes in Forage-Based Livestock Systems

To counteract the high urinary N excretion that can result from the grazing of some temperate legumes, legume species that contain moderate concentrations (i.e., 30–60 g/kg DM basis) of the bioactive secondary compounds CT, including sainfoin (*Onobrychis viciifolia*) and birdsfoot trefoil (*Lotus corniculatus*), are used. Sainfoin is a legume species that naturally contains significant concentrations of CT (30 to 80 g CT/kg DM; [69]) distributed throughout the aerial parts of the plant and restricted to the cell's vacuoles [70]. Sainfoin can serve either as an alternative or associate forage crop to alfalfa pastures in climate-adapted environments. The yield and nutritive value of sainfoin are comparable to alfalfa [71], leading to similar performance of sheep and cattle [72–74]. In fact, heifers grazing a 3-way choice among sainfoin, birdsfoot trefoil, and alfalfa selected a varied diet, preferring sainfoin over birdsfoot trefoil or alfalfa in a 46:27:27 ratio, and in a 70:30 ratio when cattle could choose between sainfoin–birdsfoot trefoil or sainfoin–alfalfa, respectively [75].

Birdsfoot trefoil, on the other hand, is a legume species that presents a more prostrate growth habit relative to alfalfa or sainfoin [76], with greater biomass per unit of area and higher bulk density (i.e., herbage weight per unit of canopy volume), which is correlated with a greater leaf area index [77]. It contains 10 to 40 g CT/kg DM [78] and yields approximately two-thirds as much as alfalfa in pure stands in the northern Mountain West [79], with a nutritional value similar to alfalfa [76]. Thus, the use of tanniferous legumes in monocultures or associated with other nontanniferous legumes may reduce ruminal protein degradability and alleviate malaise by inhibiting NH_3 production in the rumen. This strategy will increase the pool of high-quality protein that reaches the small intestine [80], shifting N excretion from urine to feces while improving N utilization [81].

4.1. Condensed Tannin Structure

Condensed tannins are plant secondary compounds (PSCs) also known as proanthocyanidins, consisting of oligomers or polymers of flavan-3-ol monomers that differ due to the hydroxyl groups and the stereochemistry (spatial orientation) of C-2 and C-3 in the C-ring [82]. Most of the CT occurring in forage species are procyanidin (PC) (e.g., catechin and epicatechin) and prodelphinidin (PD) subunits (e.g., gallocatechin and epigallocatechin), which possess an additional hydroxyl group at C-5 of the B-ring [83]. Epicatechin and epigallocatechin have a cisorientation of the C-2 and C-3 in the C-ring, while catechin and gallocatechin possess a transorientation (see Zeller, [83]).

Monomers grow into oligomers and polymers through covalent linkages of the C-4 in the C-ring of a flavan-3-ol to the C-8 or C-6 positions in the C-ring of another monomer [84] (Figure 1). These oligomers and polymers in common forage plants are typically present as mixtures of PC and PD subunits, which are distributed throughout the CT molecule, linked at different positions, leading to many different chemical structures within CT [83]. Molecules of CT also differ in the number of flavan-3-ol subunits they contain (degree of polymerization), resulting in structures that can vary in MW between 1900 and 28,000 Da [82]. Thus, plants' CT vary in degrees of polymerization and the composition of their subunits, and they can differ among plant species, cultivars within the same species, and even organs (leaves, stems, roots) within the same plant [85]. In addition, the concentration of CT varies with phenological stage, declining in concentration as maturity progresses [86]. For instance, leaves of sainfoin have higher CT concentrations and a greater biological activity and PD proportion than stems [87]; therefore, vegetative stages contain higher concentration of CT than mature plants [88], and thus, a greater CT–protein complexation potential [89].

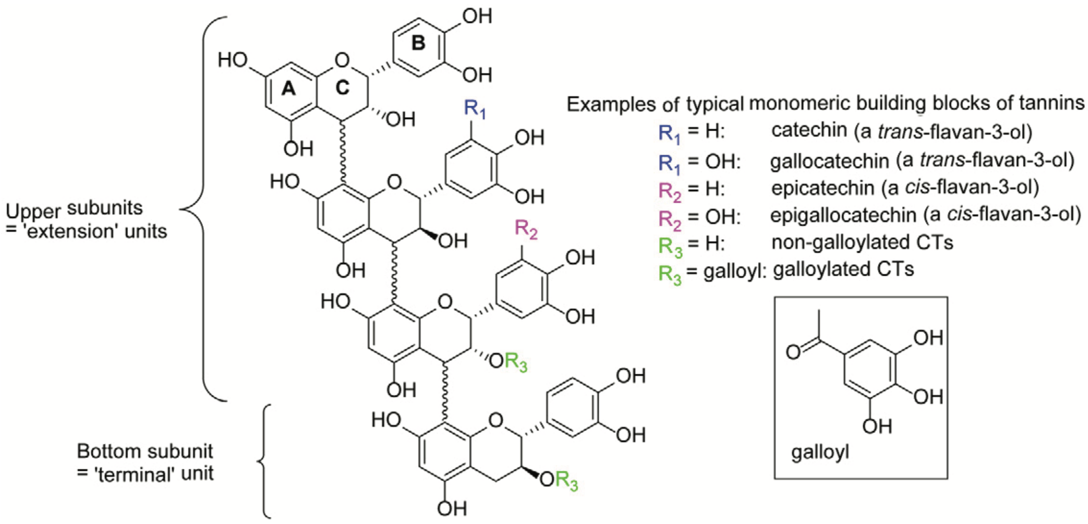

Figure 1. Condensed tannin molecule consisting of four flavan-3-ol monomers. Reproduced with permission from Mueller-Harvey et al. [84], Crop Science; published by John Wiley & Sons, 2019.

4.2. Condensed Tannin–Protein Complexes and Reductions in Urinary N Excretions

Once plant tissues are chewed or degraded during microbial digestion, CT are released from vacuoles and bind to plant salivary and microbial proteins forming insoluble complexes in the rumen [90]. These complexes reduce protein solubilization and protect dietary proteins from microbial hydrolysis and deamination in the rumen, reducing the susceptibility of forage protein to microbial degradation [91]. In addition, CT can form complexes with extracellular and cell coat enzymes of proteolytic bacteria, inhibiting their activity and reducing protein degradation [92]. As a result, there is an increased outflow of undegraded plant protein to the intestines, and reductions in ruminal NH_3 concentrations [93–95]. The CT–protein complexes are stable over the pH range from 3.5 to 7.0 but can dissociate in the abomasum and anterior duodenum at a lower pH [96], releasing proteins for gastric and peptic digestion and increasing the proportion of plant amino acids available for postruminal absorption [97], increasing the efficiency of N utilization by the ruminant.

The formation of the CT–protein complex is due to hydrogen bonding interactions between the hydroxyl groups (–OH) of the CT molecule and the amino group (–NH_2) of peptides (Figure 2), or by hydrophobic interactions between the phenol ring and the carboxyl group (–COOH) of proteins [90]. These are weak associations involving noncovalent CT–macromolecule interactions. The formation of such complexes depends on the structure of both the protein and the specific CT in the plant or plant part, the isoelectric point of the protein, the pH in the gastrointestinal tract, and the tannin–protein molar ratios [85].

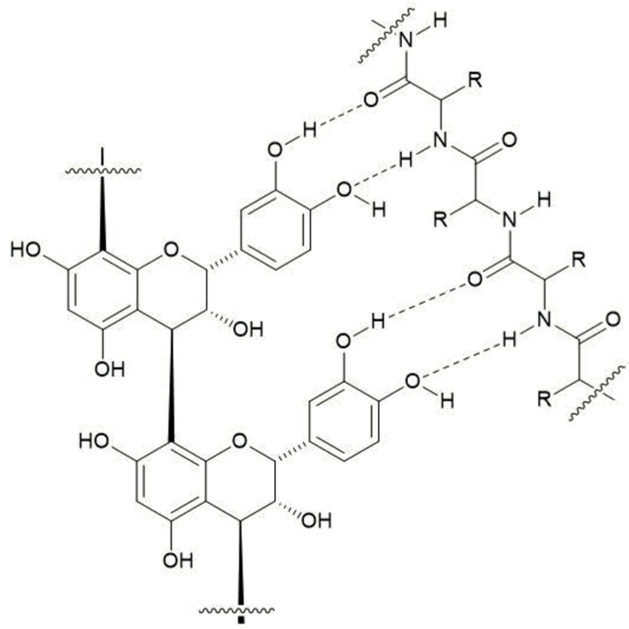

Figure 2. Hydrogen bonding involved in condensed tannin–protein complexation. Reproduced with permission from Zeller [83], Crop Science; published by John Wiley & Sons, 2019.

Different studies have determined that as CT concentration or MW and mean degree of polymerization increase, the protein precipitation capacity of CT also increases [98,99]. AufrèRe et al. [100] found a negative correlation between N solubility and CT concentration, PD/PC ratio, mean degree of polymerization, and cis/trans ratio for three sainfoin varieties at several harvests.

Biochemical mechanisms of bonding between polyphenols and macromolecules also involve irreversible covalent interactions mediated by oxidation of phenolic compounds with the formation of o-quinones or o-semi-quinones, or through the cleavage of proanthocyanidin bonds with the formation of carbocations [101]. Covalent interactions have received less attention than noncovalent interactions, although they have been demonstrated between polyphenols and individual amino-acids [101].

Condensed tannins in birdsfoot trefoil have average molecular weights of 4400 Da [102], with a degree of polymerization in the range of 6 to 14 of predominantly PC type subunits [90], while sainfoin's CTs are predominantly constituted of PD monomers with a mean MW of 5100 Da [102], with polymer sizes that vary between 4–12 subunits [90]. Thus, differences between the molecular structure of CT between birdsfoot trefoil and sainfoin may result in different effects on protein degradability because they differ in binding capacities and affinities for plant, microbial, and mammalian proteins during herbivory. This may explain the higher protein precipitation capacity reported for sainfoin's CT relative to CT from birdsfoot trefoil [102].

Sainfoin has been found to decrease urinary N losses by ruminants [87,103]. Several in vitro [104] and in vivo studies [87,105,106] have reported reductions in ruminal protein degradation, ruminal NH_3 concentrations, and urinary N excretion of substrates incubated with sainfoin or of sheep fed sainfoin relative to animals receiving polyethylene glycol (PEG), a polymer that binds to CT more readily than protein [107]. Condensed tannins in sainfoin may also enhance ruminant nutrition relative to other perennial legumes such as alfalfa [69]. In an in vitro study, Williams et al. [108], found that NH_3 concentrations were lower when sainfoin was incubated in continuous cultures than when alfalfa (a nontanniferous legume) was used as the substrate. However, NH_3 was not different between birdsfoot trefoil and alfalfa in this study. Similar results were obtained later by

Grosse Brinkhaus et al. [109], who observed a 21% reduction in blood urea N and a 38% lower urinary N when dairy cows were fed sainfoin than when they were fed alfalfa pellets; and Lagrange et al. [74] reported that yearlings heifers consuming sainfoin or birdsfoot trefoil showed a 40% reduction in urinary N concentration relative to those grazing alfalfa, diverting more of the N to feces, thereby reducing the loss of N as ammonia into the atmosphere. This study also demonstrated that the partial replacement of alfalfa by sainfoin and birdsfoot trefoil in 2-way or 3-way choices was also effective in reducing the urinary N concentrations of beef heifers. Similarly, Aufrère et al. [110] showed in vitro that mixing sainfoin with alfalfa could be an efficient way to reduce the N solubility of pure alfalfa. Finally, tannin-containing hays have also shown potential to reduce urinary urea N excretion, increase N retention, and reduce enteric CH_4 emissions from beef cattle, suggesting that CTs remain active during the process of forage conservation [111]. Thus, ecoregions around the world where legume supply is limited during certain times of the year, such as spring or winter, could benefit from the provision of CTs through the use of preserved forages.

However, when sainfoin is fed to ruminants, CT–protein complexes may not be completely dissociated in the abomasum and continue intact through the small intestine, preventing amino acid digestion and absorption [97,112]. The potential of these complexes for being reversible is dependent on the type of bonding (noncovalent or covalent) between CT and proteins [101]. Alternatively, CT may still be active under the pH level (5.0) of the proximal small intestine and interfere with endogenous and microbial proteolytic enzymes, increasing the proportion of protein in the feces [94]. In support of this, Lagrange et al. [74] observed that beef cattle grazing sainfoin partitioned more N to feces (30.1% vs. 22.7%, respectively) than animals grazing birdsfoot trefoil, and sheep fed fresh sainfoin showed greater fecal N than sheep fed pure birdsfoot trefoil or alfalfa (31.5% vs. 26.6%, respectively; [113]). This may reduce N retention, as observed for sainfoin diets [114].

The prevalence of PC subunits in birdsfoot trefoil tannin may be associated with a greater protein digestion in the abomasum and small intestine and improved amino acid absorption [81,90]. A greater amino acid absorption has been linked to overall improvements in animal performance, including body weight gain, wool and milk production, reproductive performance, and the ability to cope with gastrointestinal nematode burdens [115]. For instance, Min et al. [116] reported increments of reproduction efficiency and wool production in sheep fed birdsfoot trefoil relative to animals receiving PEG, a polymer that binds and inactivates tannins. This response was produced without increments in voluntary intake, but authors reported a greater concentration of plasma-essential amino acids, suggesting a higher intestinal absorption. The unique CT produced by birdsfoot trefoil, as well as its high fiber digestibility [117–119], also enhance the efficiency of energy and protein use in ruminants relative to other nontanniferous legumes. Sheep grazing birdsfoot trefoil had significantly improved performance compared with sheep grazing alfalfa pastures, resulting in greater ewe and lamb weight gains, carcass dressing-out percentage, and wool growth [120]. Harris et al. [121] found that dairy cows grazing birdsfoot trefoil improved the efficiency of feed utilization and increased milk yield by 10%, with increments in milk protein concentration relative to white clover (another nontanniferous legume), and Lagrange et al. [74] reported 40% greater average daily gains (ADG) in beef heifers grazing birdsfoot trefoil relative to animals grazing alfalfa.

4.3. Effect of Condensed Tannins on Enteric Methane Emissions

Condensed tannins may inhibit CH_4 production in the rumen, which is beneficial for improving nutrient utilization and reducing dietary energy loss and GHG emissions for eco-friendly animal production. Several studies have reported reductions (13–16%) either in the gross emission of CH_4 (g/d) or in CH_4 yield (g/kg dry matter intake), using forages with moderate concentrations of CT (20–50 g/kg DM) [122–124], or CT-containing plant extracts supplied with the feed [125] or drenched directly to the animals [27]. A meta-analysis from

15 in vivo experiments showed that increasing tannin concentration in the diet decreased CH_4 production linearly when expressed relative to dry matter intake (DMI) or digestible OM intake [126]. Thus, low concentrations of CT (<20 g/kg DM) may not affect CH_4 production in ruminants relative to control diets [82].

Chemical structure of CT may also be an important factor affecting enteric CH_4 production, as was demonstrated in vitro by Hatew et al. [127], who found differences in CH_4 emissions among CT extracts from four different sainfoin accessions. Sainfoin is a legume species that has been shown to reduce CH_4 production in in vitro studies [128–130]. As mentioned previously for the protein precipitation capacity of CT, as the degree of polymerization of CT increases, greater reductions in CH_4 production have been reported for in vitro studies [131]. Likewise, higher molecular weight fractions of CT significantly decreased total methanogen numbers in vitro compared with lower molecular weight CT fractions [132].

The effect of CT on enteric CH_4 emissions has been attributed to a direct effect on methanogenic archaea and/or their enzymatic activity [131–133], or more likely, to an indirect effect on fiber digestion, adversely affecting cellulolytic bacteria and consequently reducing the amount of forage substrate fermented in the rumen (reduced digestion) [126,134,135]—a process that may be subsequently compensated in the lower digestive tract by colonic fermentation [40]. The bacteria that digest cellulose produce both acetate and H_2. However, accumulation of H_2 inhibits fermentation, so Archaea dispose of H_2 by using it to reduce CO_2 to CH_4 [34]. Condensed tannins likely inactivate extracellular microbial enzymes through the formation of CT–enzyme complexes, subsequently reduce their digestive activity [136], and/or directly inhibit cellulolytic bacteria [137]. In addition, formation of cell-associated protein–tannin complexes on the cell surface may interfere with microbial attachment to fiber and prevent microbial digestion [138]. In support of this, Wang et al. [69] and Barry and McNabb suggested that concentrations of CT in forages greater than 50 g/kg might decrease DM digestibility in ruminants, and Chung et al. [139] observed a lower NDF digestibility in sainfoin than in alfalfa (45.3 vs. 55.3%), even with CT concentration in sainfoin as low as 2.45%. Reduced fiber digestion due to an increased CT ingestion may also slow clearance of forage residues from the rumen, reducing voluntary DMI [81]; thus, reductions in enteric CH_4 emissions due to a decreased fiber digestibility would not be a viable strategy.

Ciliate protozoa also produce H_2; reducing their numbers with rumen defaunation by supplying CT with the ingestion of tropical legumes [140] could indirectly affect CH_4 emissions, as mentioned previously, either by reducing methanogens symbiotically associated with protozoal populations or by reducing fiber digestion and H_2 supply to methanogenic archaea [141].

Rumen microbiome adaptation to plant secondary compounds is possible, which could influence long-term bioactivity and, thus, enteric CH_4 production, although information on this topic is still limited [142,143]. Such adaptation may be influenced by the specific chemical structure of the phenolic compound in question. For instance, rumen microbes have been reported to adapt to chemicals such as carvacrol and thymol to a greater extent than to phenolics in garlic oil [144]. Further research is needed to determine if the duration of feeding tannin-containing legumes influences the rumen microbiome and if methanogenic adaptation occurs.

5. Other Beneficial Effects of Tanniferous Legumes in Grazing Beef Production Systems

Another advantage of grazing tanniferous legumes is a reduction of the risk of bloat [50], which allows cattle to graze forage legumes at the greatest nutritional value. Tanniferous legumes such as birdsfoot trefoil and sainfoin are nonbloating and can therefore be grazed in pure stands. Complexes between CT and proteins prevent the plant protein from being solubilized into ruminal fluid, inhibiting the formation of proteinaceous, gas-trapping foam [145]. It has been calculated that CT concentrations as little as 1 to 5 g/kg DM should prevent bloat [146]. Adding a source of CT to highly digestible alfalfa could reduce the availability of soluble protein and the rate of gas production and proliferation of ruminal microbial populations, preventing the formation of persistent foam [50]. In support of this, the inclusion of sainfoin into alfalfa pastures has reduced the incidence of bloat [147] and may therefore be a practical and effective means of controlling this disorder. McMahon et al. [128] reported a marked reduction in pasture bloat when as little as 10% sainfoin was included in fresh alfalfa diets.

In addition to their positive effects at attenuating bloat and reducing environmental impacts, the use of forage legumes for finishing beef cattle also results in greater carcass weight, dressing percentage, backfat thickness, and intramuscular fat percentage in the longissimus muscle compared with grass-finished beef (4.4% vs. 2.9%, respectively), approaching values observed for grain-based finishing systems (5.8%; [148]). This outcome might be related to the high concentration of NFC present in forage legumes. Likewise, tenderness, fattiness, juiciness, and overall liking of legume-finished beef did not differ from grain-finished beef, and both types of beef presented greater scores for these characteristics than grass-fed beef [148]. In addition to these results, the omega-6 to omega-3 fatty acid ratio observed in legume-finished beef was much lower than that observed with concentrate diets and similar to grass-fed diets (2.41, 5.74, and 3.44, respectively), with greater omega-3 as well as reduced omega-6 in legume-finished beef [148], maintaining the benefits for human health of the consumption of healthy fatty acids [149–151]. Furthermore, as CTs reduce the activity of specific rumen bacteria responsible for biohydrogenation of dietary fatty acids [152], tanniferous legumes such as sainfoin may promote increments in conjugated linoleic acid and polyunsaturated fatty acids and reductions in saturated fatty acids in meat relative to animals consuming diets without CT [153]. In support of this, beef carcasses from cattle that were fed sainfoin had greater marbling scores, quality grades, and backfat thicknesses than alfalfa-fed cattle, and steaks were redder in color than steaks from cattle finished on alfalfa and contained more unsaturated fatty acids [73].

In contrast to both cereal grains and pasture grasses, perennial legumes form symbiotic associations with soil bacteria (*Rhizobia* spp.) and fix their own N, being productive for multiple years without the need of N fertilization [154,155]. Finishing cattle on N-fixing forages reduces costs and enhances ranch profitability while reducing environmental impact associated with the use of N fertilizers, as they increases nitrate production and water eutrophication [61–63]. Additionally, GHG emissions related to the production, transport, and use of N-based fertilizers [37] decrease in forage legume systems. Moreover, direct emissions of nitrous oxide (N_2O) are negligible from biological N fixation [156].

Therefore, legume-fed beef production systems give producers a sustainable alternative forage-based livestock production program while maintaining high animal performance and high-quality beef that is comparable to grain-finishing programs. In addition, the use of tannin-containing legumes either as pure forages or in association with CT-free legumes offer a feasible solution to the problems of low N utilization and high risk of bloat for cattle grazing nontanniferous legume monocultures, increasing the efficiency of N use and improving the health of ruminants, humans, and the environment.

6. Forage Diversity in Beef Cattle Production Systems

A diversity of forages and biochemicals available in pasturelands may enhance the benefits described above because the complementary relationships among multiple food resources in nature improves the fitness of herbivores [157], which in turn, can reduce environmental impacts. Herbivores have evolved grazing in diverse plant communities, consuming arrays of feeds with different chemical and physical characteristics [158]. Diverse diets offer ruminants a variety of nutrients and PSCs, which allow for a more balanced diet with greater medicinal benefits than single forage species in monocultures [159,160]. In addition, complementarities among nutrients and PSCs may lead to more efficient use of feeds, with improvements in animal welfare and productivity [161], and reduced carbon and N emissions to the environment [115,162]. For instance, the consumption of different forage species with contrasting chemical compositions (different concentrations of NFC, fiber, and proteins) and the presence of CT may lead to associative effects, such as protein degradability lower than the average of the individual forages, as it has been demonstrated in in vitro conditions by Niderkorn et al. [163] for a mixture of sainfoin and cocksfoot (Dactylis glomerata).

Some bioactive secondary metabolites in forage legumes can cause digestive interactions, so that the rumen fermentation pattern of a mixture of forages can differ from the average values of its components [164], resulting in positive (synergistic) or negative (antagonistic) effects on ruminant nutrition. It may therefore be preferable to use more than one CT source so that individual sources are ingested at a lower dosage to avoid potential antinutritional effects of high concentrations of single CT [164]. As described previously, tannins produced by different forage species, cultivars, plants, plant parts, or during different seasons may have contrasting physical and chemical properties that may impact herbivores in different ways [161]. Thus, mixtures between legumes with different CT chemical structures may produce associative effects that enhance the effect relative to a single CT. This was demonstrated by Lagrange et al. [74] in an in vivo study where yearling heifers grazing a choice of tanniferous legumes (birdsfoot trefoil and sainfoin) showed lower levels of urinary N concentration than animals grazing the same legumes in monoculture, suggesting a synergism between different CT sources. In addition, this study showed that heifers grazing the tanniferous legumes (birdsfoot trefoil and sainfoin) in association with a non-tannin-containing legume (alfalfa) reduced urinary N excretion (40.7 vs. 50.6%) and retained more N (36.1 vs. 25.2%) relative to control animals grazing the same species as monocultures on average, respectively [74]. Previously, Aufrère et al. [165] had demonstrated that CT from sainfoin could bind and precipitate protein from alfalfa.

Interactions among CT may also influence the total amount of food a herbivore can ingest [166,167]. It has been observed that the DMI of sheep increases as the number of tanniferous shrubs in the diet increases, relative to single-shrub diets [167]. Food diversity may also provide ruminants a positive stimulus that increases their motivation to eat [168]. A diversity of forages allows animals to incorporate different species into their diets, which may delay the onset of satiety [169]. In contrast, animals constrained to monocultures may reach satiety at lower levels of feed intake due to the nutritional disbalances or excessive orosensory exposure to limited stimuli. In support of this, Lagrange et al. [74] observed a 33% greater dry matter intake (DMI) and 30 to 50% greater ADG in heifers that grazed a 3-way choice among alfalfa, sainfoin, and birdsfoot trefoil relative to the average DMI and ADG from animals grazing the same three species in monocultures, suggesting a synergism among pasture species when these were consumed together. Similarly, sheep that were offered a choice of different legumes and selected 50% alfalfa, 35% sainfoin, and 15% birdsfoot trefoil had 10% greater DMI and DM digestibility than for the average DMI value calculated from the same proportions of these forages when they were fed separately [113]. On the other hand, Wang et al. [147] observed similar feed intakes in beef steers grazing pure alfalfa or mixed alfalfa–sainfoin pastures containing up to 35% sainfoin; Christensen [170], when feeding a mixture of alfalfa–birdsfoot trefoil hays to dairy cows, did not find differences in DMI relative to feeding pure alfalfa.

Animals that are motivated to eat different species (i.e., a choice of legumes) could also incur greater energy expenditures in order to gather different forages and achieve the challenge of building a balanced diet [171]. The spatial aggregation of forage species in contiguous swards as opposed to an intermingled mixture may reduce search time allowing animals being more efficient in diet selection [172]. In a finely intermingled mixed pasture, animals may have a reduced intake rate due to time spent searching for the preferred plant species [173] and reduces daily voluntary intake relative to grazing monocultures. Moreover, some less competitive species such as sainfoin may be outcompeted in a mixture with better adapted species such as alfalfa, or the most preferred herbage species could be overgrazed, leading to resource degradation [174,175]. In contrast, when three different forage legumes were established in side-by-side patches, beef heifers grazing the choice treatments did not invest extra time in walking, searching, or patch switching activities relative to heifers grazing monocultures [75].

Finally, giving choices to ruminants and allowing them to solve problems of nutrient imbalances or excess exposure to a single PSC may elicit positive emotional states and ultimately improve their welfare relative to animals limited to monocultures [176]. Animals exposed to a diverse array of foods have lower indicators of stress relative to animals ingesting single rations [177] and have the opportunity to learn the postingestive consequences of foods and how to meet their needs through selecting a varied diet [178]. Diversity also allows animals to select a diet that is a function of their specific and dynamic needs. In contrast, rations designed for the "average" individual may not satisfy all animals' needs given the inherent individual differences that exist among animals [179].

7. Conclusions

Today's beef producers are challenged by growing consumer demand for environmentally, economically, and socially sustainable food [180,181], and consumer attention to production sources, animal welfare, and human health is on the rise [182,183]. In the US and other beef-producing countries, wetlands and grasslands have been converted to cropland that is used for the production of annual cereal grains, the majority of which are fed to livestock rather than consumed by humans. The ecosystem services of annually cropped farmland are compromised by reduced organic matter, periods of bare soil, and frequent application of inorganic soil nutrients. At the other extreme, grass-finished production systems provide a food source of relatively low quality that reduces productivity, increasing time to slaughter and related environmental impacts. In contrast to grasses, perennial legumes fix their own nitrogen and are digested more rapidly than grasses by ruminants; thus, the intake, production, and efficiency of feed conversion to red meat or milk are higher than for forage grasses, resulting in reduced environmental impacts compared with grass-fed cattle. The unique tannins produced by some legumes such as birdsfoot trefoil and sainfoin, as well as the high fiber digestibility of temperate forage legumes, enhance the efficiency of energy and protein use in ruminants relative to non-tannin-containing legumes such as alfalfa. Synergisms achieved by a diversity of legumes with beneficial PSCs may further enhance the benefits observed for single species, contributing to the development of beef production systems that improve overall sustainability with reduced environmental impacts while satisfying human food needs.

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