



Potential Benefits of Tannins on Ruminant Health, Production and Environmental Sustainability

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Authors' contributions

This work was carried out in collaboration among all authors. All authors read and approved the final manuscript.

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ABSTRACT

Tannins are naturally occurring polyphenolic compounds increasingly recognized for their potential benefits to ruminants. Tannins can be extracted from plants' roots, bark, leaves, and seed husks. Management of plant communities to produce a diverse array of secondary compounds, particularly tannins, is a promising strategy for holistically enhancing agroecosystems on rangelands and benefiting free grazing ruminant animals. Deterioration of rangelands constrains plant diversity, reducing tanniferous forage plants and limiting tannin availability to free-grazing ruminants. Ruminants supplemented with tannin extracts in confined feeding operations have gained several reported benefits. Commercial industries are also expanding to extract and process tannin extracts. The beneficial effects of tannins depend on many factors, including plant species,

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plant part, tannin type (condensed tannins (CTs) or hydrolyzable tannins (HTs), and dose. Tannin binds with proteins, enhances the diversity and abundance of amino acids in the small intestine, and improves overall protein absorption and utilization. Compiled with other mechanisms, tannins can improve the quality, quantity, shelf life, and consumer preference of meat and milk products. Tannins also possess antimicrobial, anti-parasitic, antioxidant, immunomodulatory, and anti-inflammatory properties. CTs also impact rumen microbial populations, decreasing methane production, improving ruminal microbiota diversity, and lowering ammonia nitrogen production. Therefore, the use of tannin from tannin extracts and tanniferous forage plants presents a promising avenue for enhancing confined and free-grazing ruminant animals' health, productivity, and environmental sustainability.

Keywords: *Condensed tannins; hydrolyzable tannin; ruminant health; ruminant production; environmental sustainability.*

1. INTRODUCTION

Plant secondary compounds have traditionally been considered limiters of intake, anti-nutritional factors, and even toxins for ruminant animals [64]. However, recent research has outlined many beneficial effects of plant secondary compounds on ruminants, in addition to the known deleterious effects [61,73]. These studies indicate that relatively small and controllable doses of certain plant secondary compounds, especially tannins, contribute to a ruminant's ability to construct nutritious diets and maintain homeostasis [71]. Tannins are among the most common secondary compounds [53] with potentially the largest evidence base for their beneficial effects in ruminants. Tannins are polyphenolic compounds found in plants that can be extracted from roots, bark, leaves, and seed husks of plants [1]. Tannins are commonly extracted from oaks (*Quercus* spp.), pine (*Pinus* spp.), and eucalyptus (*Eucalyptus* spp.) [3] and can be processed into various animal-consumable forms, including pellets, blocks, liquids, and powders. Common tanniferous forages include legumes, such as birdsfoot trefoil (*Lotus corniculatus*), sainfoin (*Onobrychis viciifolia*), and sericea lespedeza (*Lespedeza cuneata*) [4], and shrubs such as quebracho (*Schinopsis balance*), tamarisk (*Tamarix* spp.), and rhus (*Rhus* spp.) [5-7]. The beneficial effects of tannins are especially pronounced in ruminants, due to their morphological and physiological adaptations [62, 20]. However, the strategic use of dietary tannins is not well understood and not widely adopted by ruminant livestock producers. Intentional incorporation of tannins into ruminant diets is more common in confined animal feeding operations than in free-grazing systems. In the current review paper, we aim to challenge the myopic paradigm that identifies tannins as merely antinutritional

compounds and present the emerging research on the potential of tannins to improve the health, productivity, and sustainability of ruminant production systems.

Supplementation of tannin extracts in confined ruminant feeding operations has shown promising benefits to ruminant health, productivity, and environmental sustainability. Tannins reduce ruminal protein degradation, allowing a greater diversity and abundance of amino acids to reach the small intestines for absorption and utilization by the body. Tannins have been demonstrated to produce a wide range of beneficial outcomes, including decreased ammonia production and increased nitrogen efficiency [26, 12], a more balanced microbiota and prevention of pathogens [13], improved feed efficiency [40,76], growth performance [77-78], gastrointestinal health [35], and meat quality [4]. The improvements highlight the potential for tannins to reduce reliance on in-feed antibiotics, hormonal implants, and feed additives such as ionophores, microbials, or rumen-protected protein [14]. Tannins also modulate carbohydrate fermentation and inhibit the activity of methanogenic archaea, potentially reducing methane emissions and improving energy efficiency in ruminants [17]. These benefits are mostly applicable to ruminants in confined feeding operations. However, free-grazing ruminants may also benefit from access to dietary tannins. Tannin-containing legumes enhance energy and protein use efficiency, especially critical on forage-limited rangelands. Tannins possess anthelmintic, antioxidant, and anti-inflammatory properties [7] that foster long, healthy, productive lives for breeding animals exposed to rangeland conditions. The most cost-efficient method for incorporating tannins into free-grazing ruminant diets is through managing for plant communities that naturally provide

diverse nutrients and tannins. However, this approach may take time and is not always feasible, making tannin extract supplementation a viable alternative for free-grazing ruminants. While more common in confined systems, there is increasing interest in using tannin extracts for free-grazing ruminants. In this review, we highlight these promising new applications to both free-grazing and confined feeding systems. Additionally, we explain mechanisms behind the known effects of tannins on ruminants, and explore the opportunities and challenges associated with using tannins to improve ruminant health, production, and environmental sustainability [21].

2. TANNIN BIOCHEMISTRY

Different plant species produce tannins with varying structures and, accordingly, various functions and properties. The two most common forms of tannins in plants are hydrolysable tannins (HTs) and condensed tannins (CTs) [22]. CTs have a higher relative molecular mass, and the tannin-protein complex is not degraded in the rumen. In contrast, HTs have a relatively low molecular mass, and the tannin-protein complex is more easily degraded [23]. CTs (proanthocyanidins) are non-branched polymers of flavonoid phenol units, primarily catechin, connected by monomers [4,10]. CTs are heterogeneous compounds that can bind proteins in the rumen, which results in the reduction of ruminal protein degradation. Catechin, Epicatechin, Epigallocatechin, and Epigallocatechin are the primary structural components of condensed tannins, and because they contain antibacterial and antiprotozoal activity as well as the ability to bind elements of the diet, mainly protein, the presence of CTs modifies the parameters of ruminal fermentation [2]. Overconsumption of CTs can be especially problematic in ruminants because CTs are not readily broken down by the ruminant digestive system [1-2]. Acute toxicosis from CT is common when ruminant animals have access to plants with unusually high or dynamic concentrations of [81]. In these cases, tannins can cause rupturing of kidneys, abomasum, or small intestines and eventually death [81, 12].

Hydrolysable tannins (HTs) are polyesters made of phenolic acids, primarily gallic acid, and a sugar molecule with a carbohydrate core whose hydroxyl groups are esterified with phenolic acids [2, 61]. HTs have a lower molecular weight and lower binding capacity. HTs are more soluble in

water and are more susceptible to enzymatic and non-enzymatic hydrolysis. As a result, HTs are more readily broken down in the digestive system [60]. HTs can also be toxic to ruminants when administered in high doses without insufficient acclimation [22], though HTs are relatively innocuous compared to CTs. Only dicotyledonous plants contain HTs, while both angiosperms and gymnosperms contain CTs [61]. HTs can form complexes via covalent bonds, ionic bonds, hydrogen bonds, and hydrophobic interactions [58]. Since ionic bonds are created between the phenolate ion and the protein's cationic site, only HTs can form them. The toxic effects of overconsumption of CTs, and to a lesser degree, HTs, have been well recognized, and their mechanism relatively well understood for some time. However, the beneficial effects of consuming small doses of tannins have been underappreciated. The emerging research highlighted in this review documents these benefits and attempts to elucidate the mechanisms behind them.

3. TANNINS AND RUMINANT HEALTH

Health benefits of tannins to ruminants in confined systems: Ruminants in confined feeding operations face a multitude of stressors that significantly impact their health. Pathogen exposure is the primary stressor caused by the proximity of animals, facilitating disease transmission, and creating a constant immune challenge that can compromise their health [13]. Additionally, metabolic stress arises from high-concentrate feed rations, leading to digestive disorders and disrupting normal metabolic functions, resulting in conditions such as postprandial hyperglycemia and elevated cholesterol levels. This metabolic strain is compounded by environmental factors, including limited space and restricted movement, further weakening the immune response, and increasing susceptibility to infections [16]. Furthermore, the overuse of antibiotics to manage these health challenges raises concerns about antibiotic resistance, posing long-term risks to ruminant health [75]. Tannins possess antimicrobial and immunomodulatory properties [27, 74] and can improve metabolic health [60] potential to address these challenges. Their antimicrobial effects arise from their ability to disrupt bacterial cell membranes, inhibit biofilm formation, interfere with quorum-sensing systems, and suppress bacterial growth. Tannin extracts from plants like *Tanfloc* and *Penthorum* mitigate pathogens such as *Staphylococcus aureus* and

Escherichia coli. Tannins also help maintain a balanced gut microbiota by promoting beneficial bacteria like *Prevotella* and *Eubacterium siraeum* while inhibiting harmful pathogens [13;15]. In dairy cows, chestnut hydrolysable tannins (HT) have reduced pathogenic bacteria like *E. coli* in the gut [26]. Similarly, tannins improve digestive health in sheep by inhibiting harmful rumen bacteria [36]. These antibiotic properties make tannins potential alternatives to in-feed antibiotics, minimizing the risk of developing antibiotic-resistant bacteria and supporting sustainable animal production [67, 16].

Tannins also enhance immune responses in ruminants, helping them resist infections. Conditions within confined operations often lead to immunocompromised animals. Beef cattle fed tannin-containing rations retain normal feed intake following an immune challenge, while intake in control cattle is significantly depressed [75]. Tannin-rich leaf meals have been shown to improve cell-mediated immunity in sheep [69], while tannins combined with direct-fed microbials boost average daily gain, feed efficiency, and immune response [59]. Goats fed tannin-rich produced more immunoglobulins after an immune challenge [75]. Although the mechanism remains unclear, tannins may increase amino acid availability for immunoglobulin production. Alternatively, tannin-induced increases in rumen-escape protein may enhance methionine absorption (the most limited in microbial protein), promoting DNA methylation for epigenetic regulation of immune response [70, 53]. Metabolic health is another concern in animal operations, with tannins potentially mitigating negative effects from high-concentrate diets. Persimmon tannins, for instance, inhibit pancreatic α -amylase and intestinal α -glucosidase, reducing postprandial hyperglycemia and metabolic stress [9]. Tannin supplementation has also been shown to lower blood cholesterol in sheep [29] and improve metabolic profiles in dairy cows [30]. In summary, tannin supplementation represents a potentially compelling intervention for addressing challenges of pathogen prevalence, animal immunity, and metabolic health in confined feeding operation.

Health benefits of tannins to ruminants in free-grazing systems: Free-grazing ruminants, such as cows, sheep, and goats, faces health challenges due to their exposure to less controlled and unpredictable rangeland environments. High parasitic loads, particularly

from nematodes like *Haemonchus contortus* [19], lead to severe health issues, including anemia and reduced productivity [66, 69]. The situation is further complicated by growing resistance to anthelmintic drugs, which limits effective treatment options and exacerbates the health risks associated with helminth infections [68]. Additionally, oxidative stress, driven by environmental extremes and poor forage quality, compromises the immune system of these animals, making them more susceptible to infections [52-55]. Nutritional deficiencies are prevalent in rangelands with seasonal forage variability, undermining immune function and growth [54]. Inflammation from infections and physical injuries can impair nutrient absorption, decreasing overall productivity [7]. Collectively, these interconnected factors pose challenges to free-grazing ruminants, necessitating strategies to mitigate their adverse health effects. Hagerman et al. [63] exhibited that tannin-rich plants have emerged as a promising effective strategy to mitigate these health challenges. The tannin-rich plants possess natural anthelmintic properties [31], disrupting nematodes by binding to and damaging their cuticle, which affects their physiological functions such as molting and locomotion [3]. Tannins also bind to endoparasite proteins, causing structural damage and interfering with their metabolism, viability, and reproductive capacity. CT-containing forages reduce fecal egg counts, worm fecundity, egg hatchability, and larvae development of *Haemonchus contortus* in sheep. CTs also decrease fecal egg counts in goats [1]. These effects have been well established in randomized control trials for multiple ruminant species, tannin sources, and endoparasites [66].

Long-term health and resilience are important for free-grazing ruminants to have productive lifespans and withstand the comparatively harsh conditions that characterize rangelands. Tannins' anti-inflammatory and antioxidant properties are especially relevant to ruminant health. Tannins' well-known antioxidant effects protect ruminants from free radicals and oxidative stress [52,54,63]. Tannin supplementation significantly improved antioxidant status in sheep [37] and cows [32,55]. While these studies also observed concomitant health benefits, it is not possible to identify whether the antioxidant properties or some of the other properties discussed were responsible. Still, antioxidants may serve more functions than previously realized, including enhancing acute immune response [37]. The findings above demonstrate that tannins offer

immunomodulatory, antimicrobial, anti-parasitic, and antioxidant benefits, improving overall health, productivity, and disease resistance in ruminant animals in extensive ruminant grazing systems.

4. TANNINS AND RUMINANT PRODUCTION

Benefits of tannins to ruminant animal performance: While promoting animal health will undoubtedly lead to gains in animal production, tannins also directly improve animal production. As discussed in earlier sections, optimal doses of tannins can positively alter the digestion of proteins and the metabolism of carbohydrates, providing a mechanism for the gains in feed or forage efficiency sometimes caused by tannins. Tannins enhance protein utilization and overall animal production efficiency [38]. For instance, a blend of CTs and HTs increase the dry matter digestibility and crude protein in feedstuffs like soybean and cottonseed meal [8]. This pattern is evidenced by the reduction in methane that results from tannin supplementation, as this indicates energy has been partially redirected from methane production towards growth [34]. The balance of experimental trials also reflects this trend. Including quebracho tannins in beef cattle diets improved feed efficiency and average daily weight gain (ADG) [39]. Supplementing beef cattle with tannic acid resulted in a 0.15 kg/day increase in ADG and a 1.60% increase in net meat percentage [83]. While Carvalho et al. [40] reported no effect to growth in steers, they did report an increased carcass weight and dressing percentage, indicating a potential shift towards higher muscle mass and lower fat deposition. Similar results have been recognized in sheep. Lambs fed tannin-rich diets exhibited a 30% reduction in parasite burden and improved weight gain by 15% compared to untreated lambs [35]. Inclusion of CTs from *Acacia mearnsii* in lamb diets improved ADG, carcass weight, and yield [43]. Furthermore, tannin-supplemented diets have increased wool yield and improved wool fiber diameter consistency [42].

Benefits of tannins to ruminant meat and milk quality: Weight gain is typically the primary measure for animal performance, but meat and milk quality (as well as milk quantity) are also relevant metrics. Yanza et al. [33] reported that including tannins in the diet of dairy cows increased milk production by up to 15% by

increasing rumen escape protein and nitrogen utilization. Increasing the dose of HTs up to 40g (maximum tested) increased milk yield in dairy cows [84, 27, 28]. Ali et al. [84] reported increasing the HT content of dairy cow diets increased milk protein and lactose percentage, and decreased urea content and somatic cell counts in the milk. Consumers express a marked taste preference for dairy products sourced from animals consuming diets that include a diversity of phytochemicals, including tannins and other polyphenols, when compared to dairy products from animals consuming diets devoid of these compounds [57]. Tannins can enhance meat quality through various mechanisms. One of the primary benefits is their ability to increase the concentrations of conjugated linoleic acid (CLA), which is linked to improved flavor and nutritional value in meat products [73]. The fatty acid profile of lambs fed tannin-rich diets is significantly enhanced, with higher ratios of omega-3 to omega-6 fatty acids, which are beneficial for human health [42]. When ruminants consume tannins and other potentially health-promoting plant compounds, these compounds accumulate in the animals' tissues and are highly bioavailable for humans consuming meat products from those animals [79-80]. In goats, Pimente et al. [44] revealed that CTs improved, among many other attributes, flavor, aroma, softness, overall acceptance, and fatty acid composition, and beneficially reduced meat luminosity and collagen deposition. Furthermore, tannin-rich plants and extracts can improve the shelf life of animal food products by enhancing product oxidative stability and color retention and controlling pathogenic bacteria and parasites in ruminants [57]. Agrippina et al. [85] reported improved meat product shelf lives and quality during storage via this mechanism. Cattle supplemented with tannin extract at 0.3% of dietary DM produced meat products with significant improved shelf-life measures [39]. These studies suggest that dietary tannins enhance the performance, productivity, and meat quality of ruminant animals. However, further research on the impact of dietary tannins on the quality ruminant meat, milk, and wool is essential, as market acceptance and consumer perceptions are less understood.

5. BENEFITS OF TANNINS ON ENVIRONMENTAL SUSTAINABILITY

Livestock, particularly ruminants, contribute significantly to global greenhouse gas (GHG)

emissions, with the Food and Agriculture Organization (FAO) estimating that livestock accounts for about 14.5% of total emissions. Methane (CH₄), nitrous oxide (N₂O), and carbon dioxide (CO₂) are the primary gases involved, with ruminants contributing approximately 16% of global methane emissions [86, 56]. Methane is produced by methanogenic archaea in the rumen, which convert hydrogen (H₂) and carbon dioxide into methane, later eructated into the atmosphere [25]. Nitrous oxide, making up 10% of livestock emissions, is generated from nitrification and denitrification processes in soils exposed to nitrogen-rich urine [87]. CO₂ emissions arise from land-use changes and feed production related to livestock operations. Various strategies have been proposed to reduce these emissions, including rumen defaunation, which targets methane-producing protozoa but has limited long-term effects [51]; antimethanogen vaccines, which reduce methane by up to 8% but face high costs and inconsistent efficacy [18] selective breeding of low-methane animals, which is slow and resource-intensive [73] and feed additives like ionophores and nitrate salts, which show promise but pose health and cost concerns [80]. Dietary changes involving highly digestible feed and organic acids also reduce methane but require substantial feeding practice modifications. In contrast, CTs offer a cost-effective and practical solution for mitigating both CH₄ and N₂O emissions. CTs bind with nitrogen-containing compounds in the rumen, reducing their degradation and lowering hydrogen availability for methanogenesis, thereby decreasing methane production [49] CTs in tanniferous forages or tannin extracts are relatively affordable and easily integrated into both free-grazing and confined systems [26,50]. Extensive research indicates that diets rich in tannins can decrease carbon and nitrogen footprints [72, 12]. In addition to reducing GHG emissions, tannins enhance soil health by forming humic substances, improving soil structure, water retention, and nutrient availability [45-48]. Tannins are also useful in industrial applications, particularly as eco-friendly alternatives in leather tanning, replacing hazardous chemicals. Sources like banana bunches and Tara tree extracts provide high extraction efficiency, producing high-quality leather with minimal environmental impact [46]. Despite their benefits, challenges remain in optimizing tannin extraction and application processes for greater sustainability across industries.

6. STRATEGIES FOR TANNIN IMPLEMENTATION IN RUMINANT PRODUCTION SYSTEMS

Implementation in confined animals:

Incorporating dietary tannins into confined animal operations presents challenges related to the source, type, and quantity of tannins, which also impact the economic feasibility of supplementation. Both condensed tannins (CT) and hydrolysable tannins (HT) offer unique and overlapping benefits to animal nutrition, metabolism, health, and productivity, making a mixture of both types beneficial. Such combinations are commonly used in commercially available tannin-based supplements, as they may help mitigate potential negative effects from overconsumption due to their different detoxification pathways. Various plant sources, including grape seed extract, quebracho, and chestnut, have shown efficacy in providing the desired benefits. However, no single source has proven superior performance when tannin type is accounted for [41]. Therefore, cost-effectiveness becomes a key factor in selecting tannin sources, with by-products or co-products offering more affordable options. However, tannins represent a diverse group of compounds with differing molecular structures, and their functions are not yet fully understood. Determining the optimal inclusion rate for dietary tannins dosage in ruminants is complex due to their dose-dependent effects and the potential for animals to self-regulate intake based on health and physiological status [73]. Research indicates that the optimal rate of tannin consumption is likely between 1.5% and 5% of total dry matter intake, which is crucial for maximizing benefits while minimizing toxicity risks [6, 23]. Notably, animal performance declines when tannin levels exceed 5% of forage weight, highlighting a critical threshold for dietary inclusion [81]. Lavrenčič and Pirman [24] also found that 24-hour gas production and total volatile fatty acid content were optimized within a similar range of 1.5% to 6% condensed tannins. The researchers suggest that while tannins can enhance nutrient availability and improve animal performance at appropriate levels, higher tannin dosage reduces feed intake and may have adverse effects. Therefore, careful management of tannin-containing supplements is essential to ensure that ruminants receive the benefits without the drawbacks associated with higher dosage.

Implementation in free-grazing animals: Free-grazing ruminants are largely responsible for self-constructing diets based on the available forage base. Thus, it is ultimately the task of land managers to ensure the forage base contains plants that are not only nutritious but provide a diverse array of functional secondary compounds that act as “tools in the toolbelt” for animals to withstand the various nutritional and health challenges that inevitably occur on rangelands. Ruminants achieve this through post-ingestive flavor-feedback mechanisms that allow them to consume appropriate doses of both nutrients and secondary compounds, like tannins [82]. Free-grazing ruminants have been demonstrated to self-medicate with tannin-containing plants against conditions like nematode infections [68]. This phenomenon can be prophylactic or therapeutic [11, 23]. However, animals cannot utilize a plant or compound which is absent from the landscape. While this is seldom a concern on in-tact native ecosystems, rangelands are increasingly facing domination by invasive and introduced species, often exacerbated by anthropogenic disturbances like overgrazing, maladaptive fire regimes, and climate change [65, 20]. In these systems, where plant diversity is diminished, managers should consider establishing plant species that provide specific functions, such as provisioning of tannins and other beneficial compounds. In some regions, certain tannin-containing species are common, but considered weedy, toxic, or undesirable. In these cases, land managers should avoid completely eradicating plant species that provide a potentially beneficial compound, like tannins. Managers aiming to retain or promote tannin-containing plants that already occur on the landscape should learn how those plants respond to various disturbances and management practices. Then, disturbances or management practices that favor those plants can be applied.

7. CONCLUSION

Tannins are the most common secondary compounds with significant evidence supporting their benefits to ruminant animals. Tannin are polyphenolic compounds present in many plants that play a significant role in modulating rumen function and overall animal health, productivity, and environmental sustainability. Tannins impact carbohydrate digestion by binding to dietary carbohydrates and affecting enzyme activity. Low doses enhance fermentation, while high doses of tannin may inhibit digestion and reduce

efficiency. Tannins form complexes with dietary proteins, reducing rumen protein degradation and increasing the availability of bypass proteins for absorption in the small intestine. Tannins also affect rumen microflora, allowing animals to maintain a balanced microbiota, and producers to reduce antibiotic drug use, especially in confined feeding operations. Moreover, tannins can also increase milk and meat quality and quantity and decrease environmental impacts by reducing methane gas production. Tannins possess antimicrobial, anti-parasitic, antioxidant, and anti-inflammatory properties. In free-grazing systems, these properties address challenges such as parasitic infections and nutrient variability. However, further research is warranted on the use of native and introduced tannin-containing plants within the diets of ruminants on rangelands. Studies should assess the economic and environmental costs and benefits of tannin use. This comprehensive approach will facilitate the integration of tannins into ruminant diets, ultimately improving animal health, productivity, environmental sustainability while ensuring the quality of ruminant animal-derived products. Understanding consumer attitudes towards tannin-supplemented products will further support broader adoption in the market. This ongoing research underscores the dynamic nature of our understanding of tannins and their potential in animal health, production, and environmental sustainability.

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DISCLAIMER (ARTIFICIAL INTELLIGENCE)

Author(s) hereby declare that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc) and text-to-image generators have been used during writing or editing of this manuscript.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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