

Review Article

Potential benefits of tannins on ruminant health, production and environmental sustainability: A review

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, 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. Combined with other mechanisms, tannins can improve the quality, quality, shelf life, and consumer acceptance 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 [73]. These studies indicate that relatively small and controllable doses of numerous plant secondary compounds 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 research evidence for their beneficial effects in ruminants supported by their body morphology and physiological adaptations enhancing utilization of these compounds [62;20]. However, in ruminant livestock, the strategic use of dietary tannins in confined animal feeding operations is far from widespread and even less so in free-grazing systems.

Tannins are polyphenolic compounds found in plants that can be extracted from roots, bark, leaves, and seed husks of plants [1]. For instance, oak (*Quercus* spp.) and pine (*Pinus* spp.) tannins are extracted from the bark, whereas eucalyptus (*Eucalyptus* spp.) tannins come from the leaves [3]. Other common tanniferous plants 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]. Tannins are processed into various edible forms, including pellets, blocks, liquids, and powders for animals to reduce parasites, prevent bloat, or lower gaseous emissions. Generally, tannins are classified according to their chemical structures into two main types: hydrolyzable tannins (HTs) and condensed tannins (CTs) [7].

Supplementation of tannin extract in confined ruminant feeding operations has shown promising evidence supporting 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 body absorption and utilization. This mechanism has been demonstrated to decrease ammonia production and increase nitrogen efficiency, improve feed efficiency and growth performance [1], enhance gastrointestinal health, improve meat quality [4], maintain a balanced microbiota and prevent pathogens [13] thereby reducing the need for in-feed antibiotics [14]. Tannins modulate carbohydrate fermentation, potentially reducing methane emissions and improving energy efficiency. Moreover, tannins inhibit the activity of methanogenic archaea, decreasing methane emissions from ruminants [17]. The benefits of tannins in ruminant diets are not limited to confined feeding operations. Free-grazing ruminants may benefit similarly from tannin sources. 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 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 describe the mechanisms behind the many effects of tannins on ruminant nutrition, highlight the role of tannins in ruminant health, production, and environmental sustainability, and offer promising new applications in both free-grazing and confined feeding systems.

Tannins and Ruminant Health

Health benefits of tannins to ruminants in confined systems

Tannins possess antimicrobial, anti-parasitic, antioxidant, immunomodulatory, and anti-inflammatory properties for ruminants [27;74]. Their antimicrobial effects arise from disrupting bacterial cell membranes, inhibiting biofilm formation, interfering with quorum-sensing systems, and suppressing bacterial growth. Tannin extracts from plants like *Tanfloc* and *Penthorum* mitigate pathogens such as *Staphylococcus aureus* and *Escherichia coli*, proving useful in confined animal operations where antibiotic use is common. Tannins 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. Stress, novel diets, and pathogen exposure often immunocompromise animals in confined operations. 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 and enhance methionine absorption, promoting DNA methylation for epigenetic immune regulation [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].

Health benefits of tannins to ruminants in free-grazing systems

Tannins may also be important in addressing the health concerns of free-grazing ruminants. One challenge that is more pronounced in free-grazing systems is parasite load. Tannin-rich plants possess anthelmintic properties. CTs can bind to and disrupt the cuticle of nematodes, increasing rigidity and affecting 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 many rangelands. The anti-inflammatory and antioxidant properties that tannins exhibit are relevant to the health of free-grazing ruminants. Tannins' well-known antioxidant effects protect ruminants from free radicals and oxidative stress. Tannin supplementation significantly improved antioxidant status in sheep [37] and cows [32]. 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 highlighted above demonstrate that tannins offer benefits such as immunomodulatory, antimicrobial, anti-parasitic, and antioxidant effects, improving overall health, productivity, and disease resistance in ruminant animals in extensive ruminant grazing systems.

Tannins and Ruminant Production

Benefits of tannins to ruminant animal performance

While bolstering animal health will undoubtedly lead to gains in animal production, tannins may also have the ability to 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% rise in net meat percentage [83]. While [40] reported no affect 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. [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]. [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, [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]. [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.

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 account 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 pasture-based and confined systems [26]. 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.

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, but no single source has proven superior in performance when tannin type is accounted for. 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]. [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.

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.

References

1. Min B.R., Barry T.N., Attwood G.T., McNabb W.C. The effect of condensed tannins on the nutrition and health of ruminants fed fresh temperate forages: a review. *Anim Feed Sci Technol.* 2003;106(1-4):3-19.
2. Mueller-Harvey I. Unravelling the conundrum of tannins in animal nutrition and health. *J Sci Food Agric.* 2006;86:2010-2037.
3. Barry T., McNabb W. The implications of condensed tannins on the nutritive value of temperate forages fed to ruminants. *Br J Nutr.* 1999;81(4):263-272.
4. Waghorn G.C. Beneficial and detrimental effects of dietary condensed tannins for sustainable sheep and goat production—Progress and challenges. *Anim Feed Sci Technol.* 2008;147:116-139.
5. Serrano J., Puupponen-Pimiä R., Dauer A., Aura A.M., Saura-Calixto F. Tannins: current knowledge of food sources, intake, bioavailability and biological effects. *Mol Nutr Food Res.* 2009;53(S2)
6. Frutos P., Hervás G., Giráldez F.J., Mantecón A.R. An in vitro study on the ability of polyethylene glycol to inhibit the effect of quebracho tannins and tannic acid on rumen fermentation in sheep, goats, cows, and deer. *Crop Pasture Sci.* 2004;55:1125-1132.
7. Naumann H.D., Tedeschi L.O., Zeller W.E., Huntley N.F. The role of condensed tannins in ruminant animal production: advances, limitations and future directions. *Rev Bras Zootec.* 2017;46:929-949.
8. Soldado D., Bessa R.J., Jerónimo E. Condensed tannins as antioxidants in ruminants—Effectiveness and action mechanisms to improve animal antioxidant status and oxidative stability of products. *Animals.* 2021;11(11):3243.
9. Kim J.-S., Kwon C.-S., Son K.H. Inhibition of alpha-glucosidase and amylase by luteolin, a flavonoid. *Biosci Biotechnol Biochem.* 2000;64(11):2458-2461.
10. Waghorn G.C., McNabb W.C. Consequences of plant phenolic compounds for productivity and health of ruminants. *Proc Nutr Soc.* 2003;62:383-392.
11. Makkar H.P.S. Effects and fate of tannins in ruminant animals, adaptation to tannins, and strategies to overcome detrimental effects of feeding tannin-rich feeds. *Small Rumin Res.* 2003;49:241-256.
12. Patra A.K., Saxena J. Exploitation of dietary tannins to improve rumen metabolism and ruminant nutrition. *J Sci Food Agric.* 2011;91(1):24-37.
13. [13] G., Venema K., Lucini L., Rocchetti G., Delmas D., Daglia M., De Filippis A., Xiao H., Quiles J.L., Xiao J., Capanoglu E. Interaction of dietary polyphenols and gut microbiota:

Microbial metabolism of polyphenols, influence on the gut microbiota, and implications on host health. *Food Frontiers*. 2020;1(2):109-133.

14. Karnwal A., Malik T. Exploring the untapped potential of naturally occurring antimicrobial compounds: novel advancements in food preservation for enhanced safety and sustainability. *Front Sustain Food Syst*. 2024;8:1307210.

15. Pitta D.W., Kumar S., Veiccharelli B., Parmar N., Reddy B., Joshi C.G. Bacterial diversity associated with feeding dry forage at different dietary concentrations in the rumen contents of Mehshana buffalo (*Bubalus bubalis*) using 16S pyrotags. *Anaerobe*. 2014;25:31-41.

16. Daniel I.K., Njue O.M., Sanad Y.M. Antimicrobial effects of plant-based supplements on gut microbial diversity in small ruminants. *Pathogens*. 2023;13(1):31.

17. Jayanegara A., Leiber F., Kreuzer M. Meta-analysis of the relationship between dietary tannin level and methane formation in ruminants from in vivo and in vitro experiments. *J Anim Physiol Anim Nutr*. 2012;96(3):365-375.

18. Beauchemin K.A., Kreuzer M., O'mara F., McAllister T.A. Nutritional management for enteric methane abatement: a review. *Aust J Exp Agric*. 2008;48(2):21-27.

19. Hoste H., Jackson F., Athanasiadou S., Thamsborg S.M., Hoskin S.O. The effects of tannin-rich plants on parasitic nematodes in ruminants. *Trends Parasitol*. 2006;22(6):253-261.

20. Muzzo, B.I., Maleko, D.D., Thacker, E. and D PROVENZA, F.R.E.D., 2023. Rangeland management in Tanzania: Opportunities, challenges, and prospects for sustainability. *International Journal of Tropical Drylands*, 7(2).

21. Menci R., Coppa M., Torrent A., Natalello A., Valenti B., Luciano G., Priolo A., Niderkorn V. Effects of two tannin extracts at different doses in interaction with a green or dry forage substrate on in vitro rumen fermentation and biohydrogenation. *Anim Feed Sci Technol*. 2021;278:114977.

22. Makkar H.P., Blümmel M., Borowy N.K., Becker K. Gravimetric determination of tannins and their correlations with chemical and protein precipitation methods. *J Sci Food Agric*. 1993;61(2):161-165.

23. Frutos P, Mantecón ÁR, Angulo GH, García FJ. Tannins and ruminant nutrition. *Span J Agric Res*, 2004;2(2):191-202.

24. Lavrenčič A, Pirman T. In vitro gas and short-chain fatty acid production from soybean meal treated with chestnut and quebracho wood extracts by using sheep rumen fluid. *J Anim Feed Sci*, 2021;30(4).

25. Costa M, Alves SP, Cappucci A, Cook SR, Duarte A, Caldeira RM, McAllister TA, Bessa RJ. Effects of condensed and hydrolyzable tannins on rumen metabolism with emphasis on the biohydrogenation of unsaturated fatty acids. *J Agric Food Chem*, 2018;66(13):3367-3377.

26. Lagrange, S., Beauchemin, K.A., MacAdam, J. and Villalba, J.J., 2020. Grazing diverse combinations of tanniferous and non-tanniferous legumes: implications for beef cattle performance and environmental impact. *Science of The Total Environment*, 746, p.140788.
27. Besharati M, Palangi V, Moaddab M, Nemati Z, Pliego AB, Salem AZ. Influence of cinnamon essential oil and monensin on ruminal biogas kinetics of waste pomegranate seeds as a biofriendly agriculture environment. *Waste Biomass Valor*, 2021;12:2333-2342.
28. Prapaiwong T, Srakaew W, Poolthajit S, Wachirapakorn C, Jarassaeng C. Effects of chestnut hydrolysable tannin on intake, digestibility, rumen fermentation, milk production and somatic cell count in crossbred dairy cows. *Vet Sci*, 2023;10(4):269.
29. Wang X, Hao W, Huang X, Duan Z. Lower blood lipid level from the administration of plant tannins via altering the gut microbiota diversity and structure. *Food Funct*, 2023;14(10):4847-4858.
30. Acosta-Lozano N, Barros-Rodríguez M, Guishca-Cunuhay C, Andrade-Yucailla V, Contreras-Barros K, Sandoval-Castro C, Elghandour MM, Zeidan Mohamed Salem A. Potential effect of dietary supplementation of tannin-rich forage on mitigation of greenhouse gas production, defaunation and rumen function. *Vet Sci*, 2023;10(7):467
31. Greiffer L, Liebau E, Herrmann FC, Spiegler V. Condensed tannins act as anthelmintics by increasing the rigidity of the nematode cuticle. *Sci Rep*, 2022;12(1):18850.
32. Vasta V, Nudda A, Cannas A, Lanza M, Priolo A. Alternative feed resources and their effects on the quality of meat and milk from small ruminants. *Anim Feed Sci Technol*, 2008;147(1-3):223-246.
33. Yanza YR, Fitri A, Suwignyo B, Hidayatik N, Kumalasari NR, Irawan A, Jayanegara A. The utilisation of tannin extract as a dietary additive in ruminant nutrition: A meta-analysis. *Animals*, 2021;11(11):3317.
34. Magnani E, Silva TH, Sakamoto L, Manella MQ, Dias FM, Mercadante ME, Henry D, Marcatto JO, Paula EM, Branco RH. Tannin-based product in feedlot diet as a strategy to reduce enteric methane emissions of Nellore cattle finished under tropical conditions. *Transl Anim Sci*, 2023;7(1)
35. Athanasiadou S, Kyriazakis I, Jackson F, Coop RL. Direct anthelmintic effects of condensed tannins towards different gastrointestinal nematodes of sheep: in vitro and in vivo studies. *Vet Parasitol*, 2001;99(3):205-219.
36. Petrič D, Mravčáková D, Kucková K, Kišidayová S, Cieslak A, Szumacher-Strabel M, Huang H, Kolodziejcki P, Lukomska A, Slusarczyk S, Čobanová K. Impact of zinc and/or herbal mixture on ruminal fermentation, microbiota, and histopathology in lambs. *Front Vet Sci*, 2021;8:630971.
37. Soldado D, Guerreiro O, Fialho L, Cachucho L, Francisco A, Santos-Silva J, Bessa RJ, Jerónimo E. Inclusion of the *Cistus ladanifer* L. plant and its condensed tannin extract in

lamb diets—Effects on animal antioxidant status and oxidative stability of meat. *Anim Feed Sci Technol*, 2024:116070.

38. Nawab A, Tang S, Gao W, Li G, Xiao M, An L, Wu J, Liu W. Tannin supplementation in animal feeding: mitigation strategies to overcome the toxic effects of tannins on animal health: A review. *J Agric Sci*, 2020:12(4):217.

39. Ortiz-López B, Mariezcurrena-Berasain MD, Barajas-Cruz R, Velázquez-Garduño G, Barbabosa Pliego A, Adegbeye MJ, Salem AZM, Mariezcurrena-Berasain MA. Sustainable evaluation of tannin extract biomass as a feed product additive: Effects on growth performance, meat fatty acid profile, and lipid oxidation in bullocks. *Biomass Convers Biorefin*, 2024:14(4):5101-5107.

40. Carvalho PHV, Latack BC, Ferraz MVC, Nolasco LJRP, Meireles WR, Oliveira HOM, Zinn RA. Influence of low-level tannin supplementation on comparative growth performance of Holstein and Angus× Holstein cross calf-fed concentrate-based finishing diets for 328 d. *J Anim Sci*, 2024:102:skae087.

41. He T, Yi G, Li J, Wu Z, Guo Y, Sun F, Liu J, Tang C, Long S, Chen Z. Dietary supplementation of tannin acid promotes performance of beef cattle via alleviating liver lipid peroxidation and improving glucose metabolism and rumen fermentation. *Antioxidants*, 2023:12(9):1774.

42. Torres RNS, Ghedini CP, Paschoaloto JR, da Silva DAV, Coelho LM, Almeida Junior GA, Ezequiel JMB, Machado Neto OR, Almeida MTC. Effects of tannins supplementation to sheep diets on their performance, carcass parameters and meat fatty acid profile: A meta-analysis study. *Small Rumin Res*, 2022:206:106585.

43. Ribeiro SDS, Vedovatto M, Palmer EA, Franco GL. Effects of *Acacia mearnsii* De Wild. extract and monensin on intake, digestibility, and ruminal variables of lambs. *Rev Bras Zootec*, 2024:53:e20200138.

44. Pimentel PRS, Pellegrini CB, Lanna DPD, Brant LMS, Ribeiro CVDM, Silva TM, Barbosa AM, da Silva Júnior JM, Bezerra LR, Oliveira RL. Effects of *Acacia mearnsii* extract as a condensed-tannin source on animal performance, carcass yield and meat quality in goats. *Anim Feed Sci Technol*, 2021:271:114733.

45. Rashad, Mohamed, Mohamed Hafez, and Alexander I. Popov. "Humic substances composition and properties as an environmentally sustainable system: A review and way forward to soil conservation." *Journal of Plant Nutrition* 45, no. 7 (2022): 1072-1122.

46. Fragouli, P.G., Roulia, M. and Vassiliadis, A.A., 2023. Macromolecular size and architecture of humic substances used in the dyes' adsorptive removal from water and soil. *Agronomy*, 13(12), p.2926.

47. Tiwari, J., Ramanathan, A.L., Baudh, K. and Korstad, J., 2023. Humic substances: Structure, function and benefits for agroecosystems—A review. *Pedosphere*, 33(2), pp.237-249.

48. Popescu, G.C. and Popescu, M., 2018. Yield, berry quality and physiological response of grapevine to foliar humic acid application. *Bragantia*, 77, pp.273-282.

49. Maryati, T., Nugroho, T., Bachruddin, Z. and Pertiwiningrum, A., 2019. Potency of different banana bunches cultivar (*Musa* sp) as vegetable tanning agents. In *International Seminar on Tropical Animal Production (ISTAP)* (pp. 253-257).
50. Santos LD, Silva JB, Neves LS, Renato ND, Moltó J, Conesa JA, Borges AC. Life Cycle Assessment of a Vegetable Tannin-Based Agent Production for Waters Treatment. *Water*. 2024 Jan;16(7):1007.
51. Tseten, T., Sanjorjo, R.A., Kwon, M. and Kim, S.W., 2022. Strategies to mitigate enteric methane emissions from ruminant animals. *Journal of Microbiology and Biotechnology*, 32(3), p.269.
52. Amarowicz, R., 2007. Tannins: The new natural antioxidants? *European Journal of Lipid Science and Technology* 109, 549–551.
53. Asiamah, E.K., Adjei-fremah, S., Osei, B., Ekwemalor, K., Worku, M., 2016. An Extract of *Sericea Lespedeza* Modulates Production of Inflammatory Markers in Pathogen Associated Molecular Pattern (PAMP) Activated Ruminant Blood. *Journal of Agricultural Science* 8, 1–11.
54. Bendich, A., 1993. Physiological Role of Antioxidants in the Immune System. *J Dairy Sci* 76, 2789–2794.
55. Brenes, A., Viveros, A., Goñi, I., Centeno, C., Sáyago-Ayerdy, S.G., Arija, I., Saura-Calixto, F. 2008. Effect of Grape Pomace Concentrate and Vitamin E on Digestibility of Polyphenols and Antioxidant Activity in Chickens. *Poultry Science*. 87:2, 307-316. doi.org/10.3382/ps.2007-00297.
56. Butter, N.L., Dawson, J.M., Wakelin, D., Buttery, P.J., 2000. Effect of dietary tannin and protein concentration on nematode infection (*Trichostrongylus colubriformis*) in lambs. *Journal of Agricultural Science* 134, 89–99. <https://doi.org/10.1017/S0021859699007315>.
57. Carpino, S., Mallia, S., La Terra, S., Melilli, C., Licitra, G., Acree, T.E., Barbano, D.M., Van Soest, P.J., 2004. Composition and aroma compounds of Ragusano cheese: Native pasture and total mixed rations. *J Dairy Sci* 87, 816–830. [https://doi.org/10.3168/jds.S0022-0302\(04\)73226-9](https://doi.org/10.3168/jds.S0022-0302(04)73226-9).
58. Clemensen, A.K., Provenza, F.D., Hendrickson, J.R., Grusak, M.A., 2020. Ecological Implications of Plant Secondary Metabolites - Phytochemical Diversity Can Enhance Agricultural Sustainability. *Front Sustain Food Syst* 4.
59. Demarco, C.F., Paisley, S., Goodall, R., Cassal, C., Lake, S., 2021. Effects of bacterial DFM and tannins on measures of immunity and growth performance of newly weaned beef calves. *Livest Sci* 250, 1871–1413.
60. Dey, A., Dutta, N., Sharma, K., 2015. Antioxidant status, metabolic profile and immune response of lambs supplemented with tannin rich *Ficus infectoria* leaf meal. *Japanese Journal of Veterinary Research* 63, 15–24.

61. Freeland, W.J.J., Janzen, D.H., 1974. Strategies in Herbivory by Mammals: The Role of Plant Secondary Compounds. *Am Nat* 108, 269–289.
62. Gessner, D.K., Ringseis, R., Eder, K., 2017. Potential of plant polyphenols to combat oxidative stress and inflammatory processes in farm animals. *J Anim Physiol Anim Nutr (Berl)* 101.
63. Hagerman, A.E., Riedl, K.M., Jones, G.A., Sovik, K.N., Ritchard, N.T., Hartzfeld, P.W., Riechel, T.L., 1998. High Molecular Weight Plant Polyphenolics (Tannins) as Biological Antioxidants. *J Agric Food Chem* 46, 1887–1892.
64. Hartmann, T., 2007. From waste products to ecochemicals: Fifty years research of plant secondary metabolism. *Phytochemistry* 68.
65. Hobbs, R.J., Higgs, E., Harris, J.A., 2009. Novel ecosystems: implications for conservation and restoration. *Trends Ecol Evol* 24, 599–605.
66. Hoste, H., Torres-Acosta, J. F. J., Sandoval-Castro, C. A., Mueller-Harvey, I., Sotiraki, S., Louvandini, H., Thamsborg, S. M., & Terrill, T. H. (2015). Tannin containing legumes as a model for nutraceuticals against digestive parasites in livestock. *Veterinary Parasitology*, 212(1–2), 5–17. <https://doi.org/10.1016/j.vetpar.2015.06.026>
67. Huang, Q., Liu, X., Zhao, G., Hu, T., Wang, Y., 2018. Potential and challenges of tannins as an alternative to in-feed antibiotics for farm animal production. *Animal Nutrition* 4, 137–150.
68. Lisonbee, L.D., Villalba, J.J., Provenza, F.D., Hall, J.O., 2009. Tannins and self-medication : Implications for sustainable parasite control in herbivores. *Behavioural Processes* 82, 184–189.
69. Pathak, A.K., Dutta, N., Banerjee, P.S., Goswami, T.K., Sharma, K., 2016. Effect of condensed tannins supplementation through leaf meal mixture on voluntary feed intake, immune response and worm burden in *Haemonchus contortus* infected sheep. *Journal of Parasitic Diseases* 40, 100–105.
70. Peñagaricano, F., Souza, A.H., Carvalho, P.D., Driver, A.M., Gamba, R., Kropp, J., Hackbart, K.S., Luchini, D., Shaver, R.D., Wiltbank, M.C., Khatib, H., 2013. Effect of Maternal Methionine Supplementation on the Transcriptome of Bovine Preimplantation Embryos. *PLoS One* 8.
71. Provenza, F., 2023. Nourishing Earth, Nourishing Ourselves. Part 1: Linking Plant Diversity With the Health of Livestock and Humans. *Journal of the American Holistic Veterinary Medical Association* 71, 10–17.
72. Provenza, F.D., 1996. Acquired Aversions as the Basis for Varied Diets of Ruminants Foraging on Rangelands. *J Anim Sci* 74, 2010–2020.
73. Ramah, A., Yasuda, M., Ohashi, Y., Urakawa, M., Kida, T., Yanagita, T., Uemura, R., Bakry, H.H., Abdelaleem, N.M., El-Shewy, E.A., 2020. Different doses of tannin reflect a double-edged impact on broiler chicken immunity. *Vet Immunol Immunopathol* 220.

74. Rockenbach I.I., Gonzaga L.V., Rizelio V.M., Gonçalves A.E.D.S.S., Genovese M.I., Fett R. 2011. Phenolic compounds and antioxidant activity of seed and skin extracts of red grape (*Vitis vinifera* and *Vitis labrusca*) pomace from Brazilian winemaking. *Food Res. Int.* 44, 897–901. doi: 10.1016/j.foodres.2011.01.049.
75. Schreiber, S.P., Burson, R.D., Scott, C.B., 2024. Effects of Phytochemical Diversity on Immune Response in Goats and Beef Cattle. *Range Ecology and Management*. Manuscript submitted for publication.
76. Tedeschi, L.O., Muir, J.P., 2014. Developing a conceptual model of possible benefits of condensed tannins for ruminant production. *Animal* 8, 1095–1105.
77. Tedeschi, L.O., Muir, J.P., Naumann, H.D., Norris, A.B., Ramírez-Restrepo, C.A., Mertens-Talcott, S.U., 2021. Nutritional Aspects of Ecologically Relevant Phytochemicals in Ruminant Production. *Front Vet Sci* 8, 1–24.
78. Tsiplakou, E., Mavrommatis, A., Gelasakis, A.I., Kalogianni, A.I., Simitzis, P.E., 2023. Effect of Phytochemical Feed Additives on Health Status, Milk Yield, and Quality Characteristics in Ruminants. *Sustainable Use of Feed Additives in Livestock* 191, 641–663.
79. van Vliet, S., Blair, A.D., Hite, L.M., Cloward, J., Ward, R.E., Kruse, C., van Wietmarschen, H.A., van Eekeren, N., Kronberg, S.L., Provenza, F.D., 2023. Pasture-finishing of bison improves animal metabolic health and potential health-promoting compounds in meat. *J Anim Sci Biotechnol* 14.
80. Van Vliet, S., Provenza, F.D., Kronberg, S.L., 2021. Health-Promoting Phytonutrients Are Higher in Grass-Fed Meat and Milk. *Front Sustain Food Syst* 4.
81. Vermeire, L.T., Wester, D.B., 2001. Shinnery Oak Poisoning of Rangeland Cattle: Causes, Effects & Solutions. *Rangelands* 23, 19–21.
82. Villalba, J.J., Provenza, F.D., Manteca, X., 2010. Links between ruminants food preference and their welfare. *Animal* 4, 1240–1247.
83. He T, Yi G, Li J, Wu Z, Guo Y, Sun F, Liu J, Tang C, Long S, Chen Z. Dietary supplementation of tannic acid promotes performance of beef cattle via alleviating liver lipid peroxidation and improving glucose metabolism and rumen fermentation. *Antioxidants*, 2023;12(9):1774.
84. Ali, M., Mehboob, H. A., Mirza, M. A., Raza, H., & Osredkar, M. (2017). Effect of hydrolysable tannin supplementation on production performance of dairy crossbred cows. *The Journal of Animal & Plant Sciences*, 27(4), 1088-1093.
85. Agrippina FD, Ismayati M, Hidayati S, Pratama BP. Utilization of Tannins with Various Polymers for Green-Based Active Packaging: A Review. *Jurnal Sylva Lestari*. 2024 Jul 23;12(3):648-83.
86. Food and Agriculture Organization of the United Nations. *Livestock's Long Shadow: Environmental Issues and Options*; FAO: Rome, Italy, 2020; ISBN 978-92-5-105571
87. IPCC, 2019: Climate Change and Land: an IPCC special report on climate change, desertification, land degradation, sustainable land management, food security, and greenhouse gas fluxes in terrestrial ecosystems. In press

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