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REVIEW

Value Addition of Feed and Fodder by Alleviating the Antinutritional Effects of Tannins

T. K. Bhat · A. Kannan · Birbal Singh · O. P. Sharma

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Abstract Tannins are one of the important plant secondary metabolites having wide prevalence in the plant kingdom. They are a prominent constituent of various types of feed, fodder and agro-industrial wastes. The intake of tannins at a low level has recently been found to have some positive effects in ruminants. However, the use of tannin-rich biomass as animal feed, having high content of tannins, is limited by the antinutritional effects of tannins at this level in an animal system. A number of physical, chemical, biological and miscellaneous approaches have been developed for inactivation or removal of tannins for enhancement of the feeding value of tannin-rich biomass. However, none of the individual method is successful in total inactivation or removal of tannins without loss of nutritive value, and this limits the utilization of a vast amount of plant resource. A cohesive and an integrated detanninification strategy is required for alleviating the antinutritional effects of tannins in animals and upgrading the feeding value of tanniniferous biomass.

Keywords Tannins · Tanniniferous feedstuffs · Antinutritional effects · Alleviation methods · Value addition

Introduction

A shortage of quality feed and fodder resources has been identified as the major constraint in livestock production in the developing countries, and these countries, from time to time, experience shortage of animal feed of the conventional type [24]. Although forages, such as grasses, legumes and tree forages, and the agro-industrial byproducts are available, their utilization as animal feed and fodder is limited due to the presence of dietary antinutritional factors like tannins which affect the voluntary intake and the gastrointestinal function of the animals [195]. Great economic losses through general loss of condition, poor weight gain, inefficient production and death have been attributed to these dietary factors [195].

Tannins are present in a large number of feeds and forages and are one of the most common antinutritional factors [94, 100, 193]. After lignins, tannins are the second most abundant group of plant phenolics. They are considered as plant secondary metabolites as they are not involved in metabolic pathways [137]. Tannins are water-soluble compounds, with molecular weight generally ranging from 0.5 to 3 kDa, and can be classified into two major groups: hydrolysable tannins and condensed tannins, also known as proanthocyanidins [217]. A group which occupies an intermediate position in the tannin hierarchy is the family of catechin tannins combining elements of hydrolysable and condensed tannins [28]. These tannins are quite common in tropical shrub legumes [134, 140] and tea leaves [60].

During the past decade, there has been a changing perception of the antinutritional effects of tannins in animals, especially ruminants [194]. The intake of tannins, particularly condensed tannins, at low to moderate level (2–4 % of dry matter) in the feed of animals has been observed to have a beneficial effect on protein metabolism in ruminants, reduce bloat and have an anthelmintic effect on gastrointestinal parasites [141, 158, 177].

This paper reviews the current status of knowledge on tannins, their antinutritional effects at a high level of intake

T. K. Bhat (✉) · A. Kannan · B. Singh · O. P. Sharma
Regional Station, Indian Veterinary Research Institute, Palampur 176061, Himachal Pradesh, India
e-mail: tejkbhat@gmail.com

(>5 % of dry matter) and discusses the various methods available for negating their harmful effects for enhancement of feeding value of tanniniferous feed and fodder.

Tannins in Feed and Fodder

Prevalence and Nature of Tannins

Tannins are widely prevalent in plant material, in both leguminous and non-leguminous species, and most of the species of forage and browse legumes used as ruminant feed, contain tannins [138]. Makkar [93] listed the tannin-polyphenolic contents of 62 species of trees and shrubs from India. The list included important fodder species such as *Calliandra calothyrsus, Ficus* spp., *Gliricidia sepium, Leucaena leucocephala* and various species of *Acacia*, *Albizia*, *Prosopis* and *Quercus*. Tannins are not restricted to tropical feeds as lotus, sainfoin, and other temperate species have also been found to contain condensed tannins [211]. Thus, the occurrence of tannins is not restricted to particular limited class of plants or climatic zones. They are, therefore, likely to be consumed in all agricultural systems where trees and shrubs are used as livestock feed. Besides trees and shrubs, tannins are present in a number of agro-industrial by-products, including various seeds and seed cakes, which might be useful as feeds [93]. Cassava leaves, a potentially useful forage, sorghum grain and stover also contain tannins [135, 170]. Therefore, several crop residues and by-products of considerable importance as livestock feeds in developing countries contain tannins.

Hydrolysable tannins (HTs) are abundant in leaves, fruits, pods and galls of dicotyledons such as oak, chestnut and other species, whereas condensed tannins (CTs) are even more widespread [84]. Some species contain both types of tannins. In the living plant cells, molecules of both HTs and CTs are localized in vacuoles within the cell and are believed to be only released into the cytoplasm when cell damage or death occurs. The tannin content of plants is affected by plant species, genotype and stage of growth and may vary with plant part (leaf, stem, inflorescence, seed), season of growth and other specific environmental factors such as temperature, rainfall, cutting and defoliation by grazing herbivores including insects. A major characteristic is their propensity to form chemical complexes not only with proteins but also with many other compounds like polysaccharides, nucleic acids, steroids, alkaloids and saponins [86, 137]. Robbins et al. [175] suggested that the plant defensive nature of tannins as digestion inhibitors or toxins in animals is dependent on the molecular characteristics of the tannin as it interacts with the physiological capability of the animal.

The structures of HTs are based on a hexose (usually glucose) linked to a number of gallic acid or modified gallic acid units. The variability of HTs is derived from the type of sugar, the number of gallic acid units and the number and types of linkages between the gallic acid units. CTs are flavan-3-ol oligomers carrying varying degrees of oxidation on the A and C rings of each monomer and that the chirality of C-4, where linkage of monomers occurs, and C-3 open up the possibilities for considerable structural variability. CTs, as compared to HTs, are more stable and less susceptible to hydrolysis, and the type and position of the inter-flavanol linkages affect the overall shape and flexibility of tannin molecule [136]. The complexation between tannin and protein is central to the biological action of tannins. Proteins with an open structure and those rich in the amino acid proline appear to have a particularly high complexation coefficient, while glycoproteins, globular proteins and those of low molecular weight have low affinities [138]. Tannins produced by different species or by the same species in different parts or at different times vary in their capability to precipitate proteins. Different HTs do exhibit structure-related protein precipitation profiles, while in CTs, molecular weight is important [85].

The affinity of tannins for the protein has been observed to increase regularly with the increase in molecular size of tannins. Both HTs and CTs form reversible insoluble complexes with proteins. The conditions under which complexation takes place has been shown to cause considerable variation in the strength of the interaction. The solubility of the tannin in water is a prime biological consideration. The relative proportions of tannin and protein can lead to very different outcomes as in many cases an excess level of protein will solubilize a precipitate. The pH of the system and the presence of solubilizing agents such as bile acids are able to modify the interaction between tannin and protein to a considerable degree [129]. Jones and Mangan [73] first showed that reactivity between CTs and forage protein was pH-dependant, with stable complexes being formed at pH 3.5–7.5, but the complexes dissociated and released protein at pH <3.5. CTs reacted with forage proteins in a pH-reversible manner, with reactivity determined by the concentration, structure and molecular weight of the CTs. The pH is important in governing the formation of tannin–protein complexes. Binding is particularly high at the isoelectric pH of the protein and is much less strong at high pH, where the phenolic groups of the tannins are ionized [112]. Acidity may also play an important role in breaking down tannin–protein complex in the gut [137]. Ribulose bisphosphate *c*arboxylase-oxygenase (Rubisco) enzyme, earlier known as Fraction 1 (Fl) leaf protein, predominates in forages, and its digestion in the small intestine, as opposed to fermentation in the rumen, would be advantageous to ruminants since biological value of this protein exceeds that of microbial protein [117]. It has been suggested that a complex is formed between CTs and Rubisco protein through reversible hydrogen bonding which is stable at pH values between 4 and 7, but which readily dissociates on either side of this range [158]. This complex escapes fermentation in the rumen where the pH ranges from 5 to 7, but dissociates on exposure to gastric (pH 2.5–3.5) and pancreatic (pH 8–9) secretions.

Importance of Tanniniferous Feeds and Forages

Tanniniferous feeds are important to ruminants in many developing countries. However, there are few published estimates on either the quantities or proportions of such feeds in the livestock diets. Devendra [42] has noted some broad estimates of the importance of tree browses (shoots, twigs, leaves, fruits and pods of trees and shrubs), which are generally high in tannins and important in arid and semi-arid regions. In northern Africa, tannin-rich browse forms 60 to 70 % of rangeland production and 40 % of the total available feed; other estimates put such feeds as making up 40–50 % of the total available feed [50]. Tree leaves and pods are widely consumed by ruminants in sub-Saharan Africa. Gutteridge and Shelton [61] have reviewed the role of forage tree legumes, noting that at least 75 % of the shrubs and trees of Africa serve as browse plants. In India, 60–70 % of the forage requirements for goats are tanniniferous tree browses, with tree legumes being particularly significant [42]. Browses are particularly important in extensive livestock systems and become more important when the supply of alternative feeds is restricted such as during dry seasons and periods of drought. In Australia, mulga *(Acacia aneura)* is grown in stands for use as drought reserves for grazing sheep [61]. The ability of animals such as goats and camels to survive on tannin-rich browse largely explains why these animals are preferred in drought prone areas.

Tree fodder is also important in forested highland regions. The tanniniferous tree forages are particularly essential during the dry season when alternative green fodder is often not available. This broad pattern of tree leaf usage is found in the mountainous forested lands of northern India; oak tree leaves are particularly significant in the highland (approximately 1,500–4,000 m) areas during the February to April season. A study in the middle hills (900–2,000 m altitude) in eastern Nepal identified 14 major fodder tree species used principally in the winter and dry seasons (November–June) to supplement crop residues in ruminant feeds. In this region, tanniniferous tree fodder contributed over 15 % of the dry matter and over 20 % of the crude protein to the diet, but actual usage on individual farms varied depending on the ethnic and social group of the farmers, possible as a result of different livestock holdings and opportunities for planting trees [76, 205, 212, 223].

In the more humid tropical areas, legumes are often planted specifically for forage in extensive grazing systems and in association with crops. The leguminous trees are planted along field borders or fence lines by farmers with small-land holdings. Herbage is lopped in cut and carry systems and used as supplements to low-quality feeds such as tanniniferous crop residues. The tree fodder containing tannins is also widely used in South America, Australia and southern Africa in more extensive grazing areas. In the sub-humid coastal region of Kenya, 45 % of smallholder farmers used browse from fodder trees such as *Calliandra calothyrsus* [173]. Tanniniferous tree browses formed about 1–2 % of the feed of cattle in The Gambia during the dry season, but for goats such feed may constitute 10 % of the diet [173]. In humid and sub-humid lowland regions of Bolivia, beef steers at pasture with access to poor quality pasture and *L. leucocephala* would eat about 30 % of their diets as leucaena in the dry season. Wet season consumption was somewhat lower at about 20 %, presumably due to the availability of more and better quality pasture. In Jamaica, goats at pasture ate at least 30 % of their diets as legumes [138]. Sorghum and its by-products which are rich in tannins are widely produced, particularly in semi-arid regions. Sorghum stovers are used to feed cattle in many African and Asian countries, particularly in the dry season [138, 142]. Thus, tanniniferous feeds can be an important part of the diets of livestock in high cropping areas and not just in areas where high usage often reflects a lack of alternative feeds.

A number of feed and fodder containing different levels of tannins have been used in animal feeding trials, and variable beneficial effects on the nutrition and health of the animals have been observed. These were leaves—*Acacia brevispica*, *A. nilotica*, *A. tortillis*, *Salix caprea* and *S. viminalis* fed to sheep, goats and cattle [38, 44, 45, 114, 121, 131, 134, 140], *C. calothyrsus*, *Onobrychis viciifolia* fed to goats, lambs and cattle [68, 108, 151, 221] carob (*Ceratonia siliqua*), *Lespedeza cuneata*, *Prosopis cineraria*, *Quercus semecarpifolia* given to goats [30, 188], *Desmodium ovalifolium*, *Dorycnium rectum*, *Hedysarum coronarium*, *Lotus corniculatus*, *L. pedunculatus* fed to sheep [13, 122, 150, 201, 210] and *Leucaena leucocephala* given to ruminants [72, 118]. The fruits—*Acacia tortillis*, *Dichrostachys cinerea* given to goats [105, 128], honey locust (*Gleditsia triacanthos*) avidly eaten by sheep [31] and acorns of *Quercus rotundifolia*, found to be excellent for Mediterranean pigs and ruminants [34], were also used for animal feeding. The other unconventional tannin-rich feed and fodder tried were green tea (*Camellia sinensis*) extract for calves [70], chestnut (*Castanea sativa*) wood extract and tannins for cattle, pigs and lambs [56, 83, 192, 230], peanut (*Arachis hypogaea*) skins and tamarind (*Tamarindus indica*) seed husk for dairy cows [29, 218] and rapeseed (canola) meal for pigs and ruminants [65, 79].

Antinutritional Effects of Tannins

There are several possible explanations for the antinutritional effects of tannins. As outlined by Fahey and Jung [49], they include the following:

1. depression in food intake
2. complexation with: (a) dietary proteins or other dietary components, (b) digestive enzymes, (c) endogenous protein resulting in a drain on the nitrogen supply
3. toxic effects elsewhere in the body after absorption

Tannins, because of their protein-binding properties, are known to be strongly astringent. They are reported to reduce palatability due to astringency [14, 119, 167, 171]. The astringent nature of tannins has encouraged a view that some animals find high-tannin-containing plants unpalatable which then discourages grazing and favours plant survival and appears to be the major cause of reduced food intake in mammalian herbivores. This hypothesis has been challenged by Foley et al. [53], and it seems that astringency alone is not sufficient to explain palatability and selectivity by grazing animals. Provenza et al. [165] suggest that mammals may reject tannin-containing plants because they cause internal malaise. Severe growth depression can be a consequence of reduced feed intake and has been shown to occur in rats and chicks when fed tannin-containing diets [49].

An adaptation or tolerance to astringency, however, is apparent in some ruminants based on frequency of exposure to tannins as a normal dietary component. Saliva of browsing ruminants such as the deer contains high levels of a small glycoprotein containing large amounts of proline, glycine and glutamate/glutamine. This high-tannin-affinity protein is absent, however, in the saliva of grazing ruminants such as the cow and sheep [7]. One theory suggests that mammalian evolution of binding of tannins by salivary proline-rich proteins may be a result of dietary nitrogen limitations arising from a low nitrogen diet [113].

Tannins are generally considered inhibitory to microbial growth and reproduction [56, 120, 182]. They are not only reactive with extracellular enzymes, but may also complex with the cell wall of microorganisms [56], deprive microorganisms of substrates required for microbial growth [182], as well as inhibit oxidative phosphorylation and electron transport. Scalbert [182] and Bhat et al. [28] have reviewed the susceptibility of microbes (fungi, yeasts and bacteria) to the toxic effects of tannins, the capability of microbial adaptation to tannins through synthesis and secretion of tannin-complexing polymers, tannin-resistant enzymes, small iron-chelating compounds known as siderophores, as well as oxidation, and biodegradation of tannins. The adaptation to the toxic effects is evident in some microorganisms and may include metabolic modifications such as the secretion of a bacterial cell wall glycocalyx [56] or secretion of tannin metabolizing enzymes [153].

Tannins inhibit the activity of enzymes of rumen microbes [10, 101, 111, 116]. CTs are known to inhibit several digestive enzymes, including proteases, pectinases, amylases, cellulases, and lipases. CTs from *L. corniculatus* have been shown to inhibit extracellular endoglucanase activity of *Fibrobacter succinogenes* [10], and extracts of CTs from *O. viciifolia* reduced growth and proteolytic activity of *Butyrivibrio fibrisolvens, Ruminobacter amylophilus* and *Streptococcus bovis* [71]. In contrast, *Prevotella ruminicola* appears to produce extracellular material which may protect the organism from the effects of tannins [71]. Enzyme inhibition is believed to be caused mainly by non-specific binding of tannins with the enzyme protein, but may also occur when tannins bind with the substrate [49]. There are many factors which may influence the extent of digestive enzyme inhibition by tannins. Included among them are the following: (1) amount of protein in the diet, (2) relative amounts of various enzymes in the diet and the order in which they are encountered, (3) formation of tannin–protein complexes prior to and following ingestion and (4) how various enzymes are affected by pH, type of tannin and species and age of the animal [49, 63]. The in vitro experiments have shown that while only a few tannin molecules may completely inhibit a given enzyme, this enzyme can be almost completely protected by the simultaneous presence of either a different protein or tannin-binding polymers such as polyethylene glycol or polyvinyl polypyrrlidione [52].

At high concentrations (>5 % on dry matter basis), tannins reduce intake, performance of ruminants [9, 15, 17, 172] and wool yield in sheep [164]. When tannins complex with protein in an animal's gut, they are believed to be responsible not only for growth depression, but also for low protein digestibility and increased faecal nitrogen concentrations [44, 176]. Thus, once they have been consumed, their adverse effects, once again, seem to be related to their binding of dietary protein. There is evidence to suggest that enzymatic proteins, as well as other endogenous proteins, comprise a considerable portion of excreted nitrogen when animals are fed tannins [49]. When endogenous proteins are lost in this manner, the animal may incur a deficiency of one or more essential amino acids.

Several workers have reported acute toxicity and livestock intoxication due to intake of oak leaf tannins and tannic acid at high levels [43, 54, 58, 159, 160, 200, 228]. Besides oak leaves, negative effects and toxicity in animals due to ingestion of tannins (both HTs and CTs) have been reported in rats and sheep due to quebracho (*Schinopsis* *lorentzii*) wood [39, 64], in rats and chickens due to sorghum (*Sorghum bicolor*) seeds [8, 32], in cattle and sheep due to yellow-wood (*Terminalia oblongata*) leaves [51, 144], in goats due to harendong (*Clidemia hirta*) leaf [143], karoo (*Acacia karoo*) leaves [44, 75] and babool (*Acacia nilotica*) fruits [187, 204], in lambs due to carob (*Ceratonia siliqua*) pulp [162], in livestock due to sal seed feeding [148], and in sheep due to supplejack (*Ventilago viminalis*) feeding [166].

HTs toxicity is most often associated with consumption of high levels of oak, *Terminalia oblongata* and *Clidemia hirta* leaves. Oak leaf poisoning in cattle has been reported from India [58, 88, 147], USA [78, 160], Slovakia [18], South Africa [149], China [186], Israel [224] and Spain [43, 159]. The consumption of *Terminalia oblongata* and *Clidemia hirta* leaves has been reported to cause hepatotoxicity and nephrotoxicity in cattle and sheep [51, 143]. The study of the antinutritional effects of tannins is complicated by their great structural diversity. The perception is still prevalent that HTs are more toxic than CTs. However, CTs which are considered non-toxic as they are not absorbed are associated with gastrointestinal lesions of the mucosa [171]. HTs hold the potential for toxicity as a result of consumption by ruminants and their degradation by ruminal microbes to produce pyrogallol, a hepatotoxin and nephrotoxin [160, 171].

Garg et al. [58] reported anorexia, severe constipation, and brisket oedema of cattle suffering from blue jack oak (*Quercus incana*) leaf poisoning as a result of immature leaf consumption. Faeces were reported as hard and pelleted, as well as blood- and mucous-coated. Cattle had nephrotoxicity and heptatotoxicity. They also reported depressed blood haemoglobin, as well as elevated serum bilirubin, urea nitrogen and creatine, along with hypocalcaemia, and increased serum lactate dehydrogenase, aspartate aminotransferase and alkaline phosphatase activity. Mortality was reported in 75 % of affected calves. Plumlee et al. [160] reported proteinuria, haematuria, glucosuria, as well as blood urea nitrogen and creatinine increases at 3, 4, 5 and 6 days following oak leaf ingestion, respectively. The ingestion of young oak (*Quercus pyrenaica*) leaves by cattle triggered a critical reduction in fermentation activity of rumen concomitantly with an acute oak tannin toxicosis [43]. Perez et al. [159] studied the clinical and pathological changes associated with poisoning in cattle due to ingestion of young oak (*Q. pyrenaica*) leaves. The clinicopathological findings included slight proteinuria, a marked increase in serum creatinine and blood urea nitrogen and other clinical signs consistent with renal failure. At necropsy, animals showed gastrointestinal ulcers and kidney tubular necrosis. Spier et al. [200] reported successful treatment of acute oak toxicosis in one calf as a result of diuretic administration and electrolyte/fluid replacement.

The effects of tannins on nutrient digestibility are not only thought to be the result of their interactions with protein and carbohydrates, but the result of the influence of tannins on overall rumen physiology [56]. Primarily, they affect rumen physiology as a result of enzyme inhibition and their direct effects on growth and morphology of rumen microbes. Tannins have also been suggested to affect gas and volatile fatty acid production in the rumen [56]. Smart et al. [198] first identified the presence of a *Sericea lespedeza* (*Lespedeza cuneata*) leaf extract that inhibited enzymatic hydrolysis of cellulose by cellulase. This was later supported by Lyford et al. [92] who suggested the compound of interest in the *S. lespedeza* extract to be a polyphenolic leucoanthocyanin-like compound of high molecular weight. Likewise, researchers reported that cellulase inhibition was proportional to the concentration of compound of interest in the extract [92]. Makkar et al. [101] reported decreased in vivo activity of urease, carboxymethylcellulase, glutamate dehydrogenase, glutamate ammonia ligase, as well as alanine aminotransferase as a result of ruminal incubation of tannin-containing leaf extract of blue jack oak (*Quercus incana*). Makkar et al. [101] also reported increased inhibition of hydrolytic enzymes (urease, protease and carboxycellulase), ammonia-assimilating enzymes, as well as alanine aminotransferase and aspartate aminotransferase due to addition of increasing amounts of tannin-containing leaf extract of blue jack oak to rumen fluid in vitro. This effect was not seen with extracts of *Celtis australis* leaves containing very low tannin levels. However, blue jack oak leaf extract had no effect on glutamate ammonia ligase inhibition.

The antinutritional effects of tannins present in some grains, pods and legumes (forages, trees and shrubs) are listed in Table 1. These antinutritional effects are not uniform but vary due to variation in tannin chemistry and between the animal species [84].

Alleviation of Antinutritional Effects of Tannins

An array of treatments and feeding methods has been developed to overcome the negative effects of high content of tannins (>5 % of dry matter) in temperate and tropical forages in order to improve the nutritive value of these feeds. The methods are based on the knowledge that tannins are water-soluble polymers, which form complexes, essentially with proteins [138]. These complexes are broken under conditions of high acidity ($pH < 3.5$) or high alkalinity ($pH > 7.5$). The methods have mostly been developed at the laboratory level and tested in animal experimental trials. The technology developed could be scaled up for pilot and small-scale industries level. The approaches, which are aimed at inactivation or removal of

Table 1 Tanniniferous feed and forages and their antinutritional effects

Plant source	Type of Tannin	Animal	Effect	Reference
Sorghum bicolor (grain)	CT	Monogastrics	Weight loss: lower dry matter intake	Asquith and Butler [6]
(silage)	CT	Sheep	Depressed digestion of crude fibre; less microbial activity in the rumen	Ben-Ghedalia and Tagari [25]
Abizzia chinensis (leaves)	CT	Goat	Reduced in sacco nitrogen digestibility	Ahn et al. [1]
Acacia nilotica (leaves)	HT	Sheep	Precipitation of leaf proteins: inhibition of rumen fermentation	Mueller-Harvey et al. [139]
A. aneura (leaves)	HT	Sheep	Inhibition of rumen fermentation	Pritchard et al. [164]
Bauhinia variegata (leaves)	CT	Cattle	Reduced in sacco organic matter loss	Makkar et al. [103]
Caliandra calothyrsus (leaves)	CT	Goat	Reduced in sacco nitrogen	Ahn et al. [1]
Ceratonia siliqua (leaves)	CT	Goat	Reduced protein digestibility	Silanikove et al. [189, 190]
Eugenia jambolana (leaves)	HT	Goat	Reduced feed intake, loss in weight	Panda et al. [156]
Larrea tridentata (leaves)	CT	Goat	Reduction in feed intake, digestibility and nitrogen retention	Holechek et al. [66]
Quercus gambelii (leaves)	CT	Goat	Reduced digestibility of cellular constituents and increased faecal nitrogen	Nastis and Malechek [145]
Q. grises (leaves)	CT	Goat	Reduction in feed intake digestibility and nitrogen retention	Holechek et al. [66]
Q. incana (leaves)	HT	Cattle	Reduced organic matter digestibility	Makkar et al. [103]
Q. calliprinos (leaves)	HT	Cattle	Anorexia, constipation, wasting, dullness, nephrosis	Yeruham et al. [224]
Q. pyrenaica (leaves)	HT	Cattle	Reduction in rumen fermentation activity	Doce et al. [43]
	HT	Cattle	Proteinuria, elevated serum creatinine and blood urea nitrogen	Perez et al. [159]
Q. robur (leaves)	HT	Cattle	Inhibition of ruminal enzyme activity	Kumar and Vaithiyanathan, [86]
Robinia pseudoacacia (leaves)	CT	Sheep	Reduced protein digestibility, reduced feed intake and negative acid detergent fibre digestibility	Ayers et al. [9]
		Rabbit	Decreased wool production and nitrogen retention	Singh and Negi, [193]
Leucaena leucocephala (leaves)	HT, CT	Goat	Inhibits digestibility	Hove et al. [68]
Salix tetrasperma (leaves)	CT	Cattle	Reduced organic matter loss in sacco	Makkar et al. [103]
Terminalia oblongata (leaves)	HT	Sheep	Reduction in feed intake, toxicity but no effect upon digestibility	McSweeney et al. [119]
Lespedeza cuneata (leaves)	CT	Cattle	Inhibits rumen fermentation	Windham et al. [222]
Ceratonia siliqua (carob pods)	HT	Monogastrics,	Depression of growth	Tamir and Alumot [203]
		Chickens	Depression of growth	Joslyn et al. [74]
		Ruminants	Inhibition of rumen fermentation	Haddock et al. [62]
Vicia faba (faba beans)	CT	Chickens	Decreased feed intake and weight gain; decreased retention of protein and calcium	Marquardt and Ward [109]
Shorea robusta (salseed)	HT	Chickens	Depressed growth and feed conversion	Zombade et al. [229]

tannins from tanniniferous feed and fodder resources, are categorized as follows:

Physical Methods

A number of physical treatments from chopping to storage, alone or in combination, and with varying effect have been tried for detannification of tannin-rich feed and fodder. These treatments are as follows:

Chopping

It reduces the tannin content by increasing the contact of tannins with plant phenolic oxidases, which causes their oxidation [22, 104, 220].

Grinding

It increases surface area, facilitates contact between plant phenolic oxidases and tannins and may decrease tannin level [106, 209].

Drying

The drying of mature oak leaves under different conditions (90 °C for 24 h, 60 °C for 48 h, shade drying for 24, 48 and 72 h and sun drying for 24 and 48 h) had no effect on the levels of total phenols, CTs, protein precipitation capacity, degree of polymerization, specific activity of tannins and bound CTs [96]. On the other hand, drying at 90 °C for 24 h decreased tannin content in cassava and leucaena leaves [209]. One of the reasons for this difference was found to be different level of moisture in these leaves. Cassava and leucaena leaves had about 65 % moisture, whereas oak leaves had 40 %. The increase in moisture of oak leaves followed by the heat treatment decreased tannin levels [96]. Ben Salem et al. [22] reported sun drying was more efficient than shade drying in reducing levels of CTs in acacia foliage.

Similarly, removal of water from leucaena leaves by lyophilization also decreased the extent of tannin inactivation by the heat treatment [96]. The steaming or autoclaving (1.05 kg/cm^2) for 10 or 20 min of fresh oak leaves did not decrease the level of total phenols, CTs, ellagitannin and protein precipitation capacity [98]. At a 1:2 (w/v) ratio of dry ground leaves and water, steaming and autoclaving for 10 min reduced protein precipitation capacity by 25 and 53 %, respectively. The increase in treatment time did not increase the reduction in tannin. The *in sacco* dry matter digestibility increased marginally (from 24 to 27 %) on steaming or autoclaving [98].

The above drying conditions do not appear to hold promise for inactivation of tannins in oak leaves, but may be effective for feedstuffs having higher moisture content [209].

Storage

A number of workers have reported the decrease in tannins due to storage [22, 178, 209]. The rate and extent of decrease in both total phenols and CTs were highest at 37 °C, followed by 50 °C and room temperature, on storage of whole fresh leaves containing 40 % moisture [104]. The storage of chopped fresh leaves (40 % moisture) at 37 °C increased the rate of inactivation of total phenols and CTs. The change in protein precipitation capacity was also similar to that for total phenols or CTs. The inactivation of tannins during storage was due to their polymerization to higher "inert" polymers [96, 104].

The chopping of fresh leaves and then storage can be of practical use to the farmer as it requires only a minor change in normal farm practices. The leaves instead of being fed on the day they are lopped are only to be chopped and stored for about 5–10 days before feeding.

Chemical Methods

The treatment with various chemicals under alkaline conditions led to a decrease in tannin content and activity up to 90 % in agro-industrial by-products and tree leaves. However, a major disadvantage of the chemical treatments is the loss of soluble nutrients, for which methods have to be devised to minimize the loss during chemical treatment. Moreover, a method has to be standardized for each tanniniferous feed and fodder resource. The various methods of chemical treatment are as follows:

Ferrous Sulphate

It is a tannin-complexing agent, and at 0.015 M concentration reduces tannins by 85 %. Ferrous sulphate is known to form complex with tannins and the increase in the degree of polymerization in the treated material could be due to binding of phenolics through ferrous ions [41, 104].

Urea Treatment

Urea is the preferred alkali for treatment due to its low cost and ease of availability and handling [77, 179]. The extra nitrogen supplied by urea increases the crude protein concentration of crop residues [115]. The destabilization of tannin–protein complexes at various urea levels (2–8 %) with satisfactory results (72–89 % decrease in tannins) has been reported by various workers [22, 95, 178, 209]. The factor responsible for increased tannin inactivation observed on urea addition could be the higher pH caused [95] by evolution of ammonia from urea (urea-ammoniation). At 4 % urea level in fresh leaves (moisture adjusted to 55 %, 30 °C), the reduction in total phenol and CTs was 88 and 100 %, respectively, on day 10. The *in sacco* dry matter digestibility did not decrease up to day 5. Thereafter, a decrease in the dry matter digestibility was observed. The decrease in the values of total phenol, CTs and protein precipitation capacity at day 1 were 55, 77 and 65 %, respectively, and 72, 89 and 83 %, respectively, at day 5 [104]. The wide spread use of urea for tannin inactivation and improvement of tannin-rich feed and fodder has lagged due to lack of farmer's awareness, which has hindered the realization of the potential of this method [24].

Oxidizing Agents

Potassium permanganate (0.03 M) and potassium dichromate (0.02 M) decrease tannin level by about 95 % [99]. These oxidizing agents convert tannins to quinones, which are not capable of forming complexes with proteins and can be used for large scale removal of tannins from tanniniferous feeds because of their low cost [100]. These reagents are simple to use and do not require any complex equipment. Moreover, potassium permanganate is easily available in villages in the developing countries as it is generally used for water purification and hence farmers can use this chemical for removal of tannins from tannin-rich feedstuffs.

Alkaline Treatments

The alkalis like sodium hydroxide, sodium carbonate and sodium bicarbonate act by oxidation of phenolics at higher pH [96, 99]. Sodium hydroxide (0.05 M) is most effective, followed by sodium carbonate (0.05 M) and sodium bicarbonate (0.1 M). The reduction in tannins in oak leaves using these alkalis ranged between 70 and 90 % [96]. The alkaline treatment with calcium hydroxide can be very effective in preventing the toxic or antinutritional effects of tannins. The calcium hydroxide treatment reduced the concentrations of extractable tannin by as much as 92 % in *Clidemia hirta* leaves [143], *Albizia procera* [2] and *Acacia villosa* [220].

Some agro-industrial by-products (seeds of *Acacia nilotica*, *Mangifera indica* and *Tamarindus indica*) and oak leaves were also detanninified by using hydrogen peroxide (a strong oxidizing agent) in the presence of sodium hydroxide. The decrease in tannin content was as high as 99 % [95].

Wood Ash

Wood ash, a source of alkali potentially available to farmers, is effective in reducing tannin content. The pH of wood ash is alkaline, and it has tannin-precipitating activity. The inactivation of tannins is caused by high pH-mediated oxidation of tannins [97]. Wood ash at various levels (1–24 %) has been evaluated by different workers [22, 23, 87, 97, 199]. A 10 % solution of oak wood ash and pine wood ash decreased the content of total phenols, CTs and protein precipitation capacity in oak leaves by 66, 80, 75 % and 69, 85, 80 %, respectively [97]. The higher effectiveness of pine wood ash was attributed to a higher level of alkalis in the pine wood ash (pH value of 10 % ash solution of pine wood and oak wood was 11.3 and 10.5, respectively). Kyarisiima et al. [87] reported that treatment of high-tannin sorghum with 5 % wood ash extract was effective in reducing the tannin level and improved its nutritive value. Ben Salem et al. [22] observed that wood ash treatment was a cost-effective way to deactivate tannins in the foliage of *Acacia cyanophylla*, which improved digestion of this foliage in sheep. Wood ash solutions have also been used traditionally for treatment of high-tannin-containing sorghum and millet for human consumption. The use of wood ash, a cheap source of alkali, holds potential for detanninification of tannin-rich feedstuffs. However, as this treatment also removes nutrients, its overall effectiveness is unclear and the method has to be validated by more animal experimental studies [23, 104, 199].

Treatment with Tannin-Binding Polymers

Tannin-binding agents like polyethylene glycol (PEG) and polyvinyl polypyrrolidone (PVPP) have been widely used as research tools to investigate the in vivo and in vitro effects of tannins [196]. Both compounds are commercially available in a range of molecular weights. The lower molecular weight polymers of PEG and PVPP are highly water soluble, bind strongly to tannins and can reduce their antinutritional or toxic effects in vitro and in vivo in rats, rabbits and sheep [107]. PEG is more effective at binding tannins than PVPP [138]. The benefits from the use of PEG as tannin-inactivating agent are well documented. PEG is an inert and unabsorbed molecule that can form a stable complex with tannins, preventing the binding between tannins and protein [40]. Therefore, PEG releases forage proteins from tannin–protein complexes and improves their nutritional value leading to improved animal performance.

Tannins have higher affinity to PEG than proteins. The incorporation of PEG (molecular weight 4,000 or 6,000) has been shown to have beneficial effects in monogastrics [5, 67, 110, 169, 226, 227]. It has, however, both beneficial and adverse effects in ruminants. The incorporation of PEG in the diet has beneficial effects, particularly for tanniniferous feeds having of 5–10 % content of CTs [12, 19, 20, 86, 164, 188, 190, 191, 201, 225]. The PEG-inactivation of tannins increases voluntary feed intake, availability of nutrients and decreases microbial inhibition in degrading the tanniniferous feeds, which in turn increases the performance of animal. However, at low to moderate levels of CT (2–4 % of dry matter), addition of PEG to tanniniferous forages cause adverse effects. The addition of PEG to *L. corniculatus* containing 2–4 % CTs, decreased wool growth, weight gain [213, 214], reproduction [16] and milk yield [215]. This was attributed to substantially lower absorption of amino acids from the intestine due to increased protein digestibility in the rumen. The adverse effects of depressed voluntary feed intake and digestibility of nitrogen, organic matter, neutral detergent fibre and acid detergent fibre have also been reported [59, 86, 151, 154] in sheep fed on diets supplemented with PEG-treated leaves containing low to moderate levels of tannins. Krebs et al. [82] also did not observe any improvement in feed intake, nitrogen balance and rumen metabolism in sheep fed *Acacia saligna* foliage supplemented with PEG-4000 or 6000.

Thus treatment with tannin-binding agents can be highly effective in overcoming the negative effects of tannins leading to improved animal performance. However, their effects can be variable which may relate to the nature and level of the tannins and the tannin-feedstuff complexes which are formed. The use of PEG for detannification of animal feeds has been observed to be successful in most of the experiments, but field application has hardly been done due to unfavourable cost-benefit ratio [22]. The price of such chemicals in developing countries would depend very much on local circumstances for carrying out an analysis of either the costs or the benefits. A commercial tannin-binding product called "Browse Plus", which contains PEG-4000, PVPP, calcium hydroxide and an emulsifier, has been marketed so far only in Zimbabwe (Africa) by "Agricura" [180]. The product is added to drinking water mainly for the consumption of cattle at a dosage rate of 1–3 g of product per livestock unit per day [146]. The product is said to have beneficial effects on cattle particularly during a period of drought, when presumably high-tannin browses are an important component of the diet. The cattle which normally did not feed on high-tannin browses, reportedly consumed such browses when supplemented with "Browse Plus", and farmers reported increased feed intake and better animal condition [146]. There is, however, a lack of data from properly designed scientific trials on the benefits of the product [138]. It is said that low-cost grades of PEG can be used as feed supplements and that different costs of different grades may account for the diverse opinions as to the cost of treatment. It is also notable that the supplementation level with "Browse Plus" is very much less than that used experimentally when the objective is to overcome all the effects of the tannins. A less ambitious improvement with lower levels of supplementation may be more appropriate commercially. A cocktail of active ingredients, which is apparently the case in "Browse Plus", may be more effective than supplementation with PEG alone.

Charcoal has been advocated as an alternative to reagents like alkalis, oxidizing agents and PEG whose high cost limits their use in practice, and in some cases, their utilization could contribute to environmental pollution. Charcoal as a powder or as tablets has been widely used among humans for centuries to cure indigestion and, more importantly, as an antidote to detoxify poisons. It is also used as an antidote in veterinary medicine [37]. Mturi [132, 133] suggested that the habit of eating wood charcoal by the Zanzibar red colobus monkey (*Procolobus kirkii*), which consumes a diet of foliages containing high levels of phenolic material, is known to reduce or eliminate such toxicity by binding part of the phenolic compounds to the charcoal, thus preventing their gastrointestinal absorption. Charcoal has also been used in the diets for livestock to reduce antinutritional effects of secondary compounds in feeds. According to Poage et al. [161], lambs fed bitterweed (*Hymenoxys odorata*) alone, consumed considerably less than lambs that received bitterweed with activated charcoal, and higher doses of activated charcoal resulted in higher consumption of bitterweed. The effects of charcoal on elimination of harmful substances are reported to be due to the adsorption of a wide range of compounds such as phenols, alkaloids and salicylates [11, 161, 202].

Biological Methods

Solid-State Fermentation

Concerted efforts are in progress worldwide to improve tannin-rich feed and fodder by biodegradation of their tannins by microbial strains which are known to be strong tannin degraders. The attention has been mainly focused on fungal detannification, and recently, there have been endeavours to utilize the tannin-degrading activity of different fungi for detannification of tannin-rich biomass. These are detannification of oak leaves by the fungus *Sporotrichum pulverulentum* [102], biodegradation of tannins in *Sericea lespedeza* (*Lespedeza cuneata*) by the white rot fungi *Ceriporiopsis subvermispora* and *Cyathus stercoreus* [57] and reduction in tannins in canola meal by an enzyme preparation from a white rot fungus *Trametes versicolor* [89]. A fungus identified as *Aspergillus niger* van Tieghem having tannin–protein complex–degrading activity was isolated from the faeces of hill cattle by Bhat et al. [26, 27]. This fungus which is a prolific degrader of tannins has high tannase activity [184] and has been tried to upgrade feed value of a tannin-rich tree fodder, *Robinia pseudoacacia* [168]. Recently, a tannase-producing bacterial strain *Enterobacter ludwigii* has been isolated from the rumen of migratory goats exposed to tannin-rich browse and may be of use for reducing tannin toxicity in these animals [197]. The enzyme tannase, alone or in combination with other hydrolytic enzymes like phytase and β-galactosidase, has been tried for the enhancement of the feed value of various foodstuffs [46–48, 183, 208].

The solid-state fermentation approach has not become popular due to loss of cell solubles which are consumed by the fungi for their growth. The loss of cell solubles may be prevented by adding an energy source to the fermentable biomass. Further work is required for isolating fungal strains capable of preferentially degrading tannins with minimum loss of dry matter and digestible material.

Direct-Fed Microbials

The introduction of tannin-tolerant microbes into the rumen of an animal through one or more inoculations of bacterial cultures may be beneficial in developing a system to improve the productivity of ruminants consuming high-tannin forages or diets, especially in the tropics. Ruminal microbes that are resistant to high levels of tannins, either singly or in a consortium, may constitute a unique part of this response. There is little and intermittent information on the use of live microbial cultures (direct-fed microbials) for the detannification and utilization of tannin-rich feed and forages. Miller et al. [125], on the basis of their preliminary results, were the first to suggest that ruminal microorganisms from animals adapted to high-tannin diets may be potentially transferable to non-adapted ruminants to improve crude protein digestion of high-tannin diets. The potential of this approach, using an inoculum of a single bacterial species, seemed promising. However, the results of their later work indicated that a consortium of bacteria, rather than a single species, may be required to improve the digestibility of forages or diets that contain high levels of tannins [126, 127]. Moreover, a longer and more detailed study involving a larger number of animals would be necessary to confirm these results. Molina et al. [130] reported that the inoculation of a tannin-tolerant bacterial isolate did not improve dry matter or crude protein digestibility of sheep consuming a diet containing 29.5 % peanut skins. However, even with the small number of animals in their study, they did see a positive effect in the crude protein balance in animals receiving the laboratory-cultured live inoculum. No post-inoculation effects were detected in animal performance, but the presence or absence of the inoculated bacteria in the rumen of the animals was not studied.

Recently, Chaudhary et al. [36] have shown that the feeding of live culture of a tannin-degrading isolate as a direct-fed microbial to goats fed tannin-rich pakar (*Ficus infectoria*) leaves did not show any effect on the rumen fermentation pattern viz. pH, production of ammonia nitrogen, trichloroacetic acid-precipitable nitrogen, and activities of carboxymethylcellulase, xylanase, avicelase and protease. The population of rumen protozoa, total bacteria and fungi were similar in all the three groups, whereas tannin-degrading/tolerating bacteria were higher in the live isolate-fed group. The dry matter intake and digestibility of nutrients were also not influenced by feeding of the direct-fed microbial. The average live weight gain and feed conversion efficiency were also not affected due to the feeding of direct-fed microbial to the kids given *F. infectoria* leaves as the main roughage source. The feeding of the bacterial isolate did not have any effect on the nutrient utilization, rumen fermentation or growth performance in goats.

All the direct-fed microbial studies have been done using a live inoculum of a single bacterial species. This again underscores the importance of using a consortium of tannin-degrading bacteria, rather than a single species, for a synergistic and effective utilization of tanniniferous feed and forages.

Supplementation

The live weight losses associated with feeding CT-rich mulga (*Acacia aneura*) to livestock during drought periods in Australia have traditionally been overcome with mineral supplements. These may assist in the detoxification process and also provide additional nutrients to rumen microorganisms, as mulga tannins are known to reduce protein digestibility [91]. The addition of methionine and choline to chick diets alleviated the toxicity of tannic acid and also the toxicity of CTs or possibly the low molecular weight phenolics in sorghum [33], presumably because they functioned as methyl donors in the detoxification process and facilitated the excretion of compounds such as 4-*O*-methyl gallic acid [35]. However, the addition of methionine did not overcome the toxic effects of faba bean tannins in chick diets [216]. These differences between sorghum and faba bean diets have not been explained so far. Soya bean meal given as a supplement along with small amounts of *Acacia cyanophylla*, tannin-rich shrub foliage, had beneficial effects in sheep fed on oat hay [23].

Feed Mixtures

Free-ranging animals can select their diets so as to avoid the worst effects of tannins. It is said that incidence of fatalities in which tannins have been implicated occur when animals are very hungry and are unable to select alternative feeds. In the cut and carry feeding systems of farmers, there are some indications that mixtures of different tree fodder are used on occasions, possibly in part as a strategy of avoiding possible toxicity due to excessive amounts of some fodder species. Lowry [90] observed that farmers usually minimize antinutritional problems by feeding leaf mixtures, which dilute or reduce toxic effects. Studies have shown that mixtures produced less deleterious effects than tanniniferous browses fed as sole feeds [44, 123, 124, 155, 157, 185]. Using tree fodder as supplements to roughages may help in reducing the intake of tannins and may be the best strategy for herbivores to decrease the energy costs of detoxification [53], but the benefit that may be derived from such an approach for utilizing tannin-rich feeds has not been worked out.

Addition of Energy Source

A number of tannin-containing feeds have high levels of soluble sugars and/or starch and also a high nutritive value for both ruminants and non-ruminants. Some of these feeds are—fruits from *Gleditsia triacanthos* and *Piliostigma thonningii*, acorns from *Quercus* spp., *P. cineraria* and sainfoin leaves [138]. Although even low concentrations of carob tannins *(*2.5 g%*)* produced growth-depressing effects, the high concentrations of sugars *(*4.7 g%*)* in carob pulp may be responsible for the low but positive lamb growth rates of 48 g/day [163]. The addition of maize grain to browse leaves may have increased the weight gain of sheep either by balancing energy and protein requirements or by supplying energy for the detoxification process [219]. This hypothesis is also supported by observations that European roe deer (*Capreolus capreolus*) selected diets containing high concentrations of low molecular weight phenolics, tannins and soluble sugars [207]. A good source of energy is likely to assist in the detoxification of some tannins, low molecular weight phenolics or their metabolites. This could also explain why sugar-rich cactus (*Opuntia ficus-indica*) fruits, cactus pads and molasses removed the toxic effects of kermes oak (*Q. coccifera*) and increased the nutritive value of several browses [4, 19, 21, 176].

Silages

Silages prepared from tanniniferous plants tend to have reduced soluble nitrogen content, which improves their feeding value [3, 174, 181]. Only a few studies done so far have investigated the merits of conserving tannin-rich fodder in tropical countries for feeding during dry season. In one study, mixtures of grasses and tree leaves from *Leucaena leucocephala* or *Gliricidia sepium* were ensiled, resulting in high-quality silages which promoted weight gain in sheep, and apparently, a significant proportion of the "ruminal escape protein" survived the silage fermentation process [152]. It was observed that silages containing maize (*Zea mays*) stover mixed with tree leaves from species of *Calliandra, Acacia, Gliricidia* or *Leucaena* could be used to replace commercial feed supplements for dry season and lactation feeding without loss of milk yield from dairy cows [206]. When *L. corniculatus* silage was fed to dairy cows, it compared favourably with alfalfa (*Medicago sativa*) and red clover (*Trifolium pratense*) silages. The dry matter intakes were similar among these silage diets, but milk and protein yields were higher for the *L. corniculatus* silage [69]. *L. corniculatus* silage also achieved a significantly higher nitrogen balance in lambs than red clover or alfalfa silage [55]. Goats fed with silage made from green tea (*Camellia sinensis*) waste and whole-crop oat (*Avena sativa*) had increased nitrogen retention [80]. The feed proteins possibly survived the ensiling process and were digested post-ruminally, as the added nitrogen did not increase ruminal ammonia, urinary or faecal nitrogen [81].

Concluding Remarks

There is a need for more in vivo experimental and pilot-scale studies at farm level for complete validation of these methods. Tannins by virtue of their structure–activity relationship and content in a plant biomass can act as a double-edged sword, and as such present a conundrum that requires a tannin content-specific solution [138]. Although tanniniferous feed and forages containing low to moderate level (<5 % dry matter) can be safely fed to animals with the added advantage of some beneficial effects to the animal, it is the high-tannin (>5 % dry matter)-containing plant biomass which is the focus of attention. At 5–10 % tannin content, the approaches other than physical, chemical and biological methods can be tried. It is only at a tannin level of >10 % of the dry matter that one should think of physical and chemical methods as high-tannin content can only be inactivated or removed by these methods. The biological methods have not shown much success and need further refinement.

The aim of future studies would be to explore the potential of these approaches for a wide range of tanniniferous feed and fodder and then to develop simple and economically viable detanninification technologies for use by farmers for available feed and fodder resources. The feeding strategies, although lesser known but promising due to ease of use and cost-effectiveness, are supplementation, feed mixtures, addition of energy source and ensilage. Some of these techniques will have to be adapted and upgraded for use by small-scale industry to treat agro-industrial and forestry by-products which are available in large quantities at one place. These technologies will help in the value addition and utilization of various tanniniferous feed, fodder and agro-industrial byproducts and solve the problem of shortage of conventional feed and fodder in the developing countries.

Conflict of interest None

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