

EFFECT OF DIETARY TANNIN SOURCE FEEDS ON RUMINAL FERMENTATION AND PRODUCTION OF CATTLE; A REVIEW

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ABSTRACT: Generally, tannins are widely distributed throughout the plant kingdom, especially among trees, shrubs and herbaceous leguminous plants. Tannins are naturally occurring polyphenols with different molecular weights and complexity that are synthesized during the secondary metabolism of plants. Tannins might bind to macromolecules (proteins, structural carbohydrates and starch) and decrease their availability to digestion. Tannins based on their chemical structure and properties divided into two groups, hydrolyzable tannins (HT) and Condensed tannins (CT, proanthocyanidins). Tannins are polyphenols, which directly or indirectly affect intake and digestion. They are the primary source of astringency in plants, which results from binding to proteins, forming soluble or insoluble complexes. The nature of the interaction is greatly dependent on the structure of the polyphenols and the proteins involved. Relatively low concentration of tannins (0.5% of DM intake) is sufficient to destabilize the bloat proteins while high concentration (2-4% of DM intake) is needed for improvement of protein utilization. High concentration (> 5% of dry weight reduces feed intake and feed conversion efficiency. Tannins containing forages will be important for small ruminants to control of gastrointestinal parasites. Animals fed condensed tannin had lower dressing percent than controlled one; with dressing percent being intermediate for animals fed hydrolysable tannin. Neither tannin source affected the animal's consumption of the diet or the animal's growth. Additionally, the tannin sources did not affect the meat or by-product tissues, making tannin supplementation a viable option in finishing beef cattle. Therefore, tannin source feed will have its own advantages and disadvantages on animals' performance.

Keywords: Dietary Tannin, Digestion, Ruminal fermentation

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INTRODUCTION

In animal production, nutrition is one of the most important factors, being determinant to productive performance. Consequently, the understanding of ingestive behavior, and particularly dietary choices and adaptation to pastures, is of extremely importance in livestock management. The major constraints to increase ruminant productivity in developing countries are the scarcity, fluctuating quantity and quality of the year-round supply of conventional feeds and the inadequate nitrogen supply from low quality forages such as straw and stovers (Leng, 1990), which often contain as low as 20–50 g/kg of crude protein which do not meet the minimum crude protein requirement (80 g/kg DM) for optimal rumen microbial function (Annison and Bryden, 1998). Differences among free-grazing ruminant species, concerning food selection, allow an efficient pasture use at the habitat scale. Additionally, an effective and sustainable animal management, as well as ecological and environmental aspects, would benefit from a well founded knowledge on animal-plant interactions. Intake is influenced primarily by hunger, which is distressing, and by satiety, which is generally pleasant (Forbes, 1996). However, food intake is not so simple. In fact, it is a complex behavior, which involves simultaneously homeostatic and hedonic aspects.

On one hand, factors related to the biological requirements for energy and nutrients modulate the beginning and the end of an ingestion episode, also influencing the type of feed chosen. On the other hand, affective factors, linked to past experiences, will affect the likeness and the consumption of a particular food item. This complexity is further increased by the interaction of these homeostatic and hedonic aspects (Berthoud, 2006). Among the substances present in herbivores' diets, plant secondary metabolites (PSMs) have an ecological function of plant protection from the attack of pathogens and consumption by herbivores. PSMs comprise a wide range of chemicals, such as terpenes, alkaloids, oxalates, saponins and tannins. In ruminant nutrition, the levels of tannins present in food items represent a major component of food choice. Tannins are obtained upon the decomposition of vegetation. They will generally be found in surface water supplies or shallow wells. Although these compounds are not a health risk, they are aesthetically displeasing. Tannins are difficult to remove from water. Tannins can cause a yellow to brown cast in water and may also affect a taste and odour (Ashok and Upadhyaya, 2012). The inverse relation between high tannin levels in forage and palatability, voluntary intake, digestibility and nitrogen retention has long been established in several herbivores (Robbins, 1987). Reduced palatability, low evacuation

rate of the digested material out of the rumen and toxicity are factors that were considered as an explanation for the negative effects of tannins on ruminants feed intake. However, according to the report of Bhatta et al. (2009) recently, tannins have been increasingly investigated as a means to reduce the methane emission of ruminants, because they are considered to represent promising substances to reduce rumen methanogenesis. According to the report of Bunglavan and Dutta (2013), protection of proteins is essential for productive ruminants, where the protein requirement of these animals cannot be met from microbial protein synthesis. Mueller-Harvey (2006) was also summarized the beneficial and detrimental effects of tannins in ruminant nutrition. One of the main benefits is their effect on protein digestion. There has been considerable interest in reducing ruminal degradation of proteins. This was also in line with that of Gxasheka et al. (2015) Tannins rich plants have a potential to improve absorption of essential amino acid and also controlling gastro-internal parasites. Moreover, these plants can also be used to mitigate feed shortage during winter since rural farmer tend to have less potential to buy supplementary feeds. However, several ruminant species seem to tolerate (or even prefer) considerable amounts of tannins in their diets. The discrepancy in the tolerance to tannins among herbivores, in general, and ruminants, in particular, can be related to different defense mechanisms that each species present to PSMs. The oral cavity plays an important role in the process of tannin ingestion, both by being the place of detection of these plant compounds, and through the presence of salivary proteins which act as defense mechanisms. Therefore the objective of this paper is to review the effect of dietary tannin source feeds on ruminal fermentation and production of cattle.

Tannins

Tannins are polyphenolic secondary plant compounds that have been shown to affect microbial activity to impact fermentation, protein degradation, methane production, and potential to mitigate food borne pathogens. Tannins, a group of chemical compounds produced by a number of broadleaf forage plants, can bind proteins. Typically, grasses don't contain tannins, although sorghum (*Sorghum bicolor*) has a significant tannin content. Tannins are often found in higher concentrations in broadleaf plants adapted to warm climates (MacAdam et al., 2013) Plants contain various secondary compounds which protect them from attack by fungi, bacteria, herbivorous insects and vertebrates. Classes of compounds known to act in this way include saponins and tannins (Makkar et al., 1995; Pell et al., 2001), which are prevalent in many tropical fodder plants. Tannins are oligomeric compounds with multiple structure units that have free phenolic groups. Tannins are usually soluble in water (Haslam, 1989) except for some with high molecular weight structures. They are also capable of binding proteins and forming soluble and insoluble tannin-protein complexes. Tannins are usually divided into two groups, hydrolyzable tannins (HT) and CT (proanthocyanidins), based on their chemical structure and properties (Athanasiadou et al., 2001).

Hydrolyzable Tannins

Hydrolyzable tannins are molecules with a carbohydrate, generally D-glucose as a central core. The hydroxyl groups of these carbohydrates are partially or totally esterified with phenolic groups like gallic acid (gallotannins) or ellagic acid (ellagitannins). Hydrolyzable tannins are usually present in low amounts in plants (Mueller-Harvey, 2001). These tannins are found in oak (*Quercus* spp.) Acacia, Eucalypts and a variety of browse and tree leaves (Waghorn and McNabb, 2003). The browse that contain these leaves and apices can contain anywhere from 200g per kg of dry matter (DM) and in some species they can contain phenolic compounds that can exceed 500g per kg of dry matter (Reed, 1995; Lowry et al., 1996). Hydrolyzable tannins are potentially toxic to animals, but most ruminants can adjust to a diet of these tannins (Waghorn and McNabb, 2003). Ruminants are able to adjust to these toxic tannins by reducing their urinary excretion of degradation products, thus allowing them to consume these diets (Lowry et al., 1996). Although ruminants have this ability, an excessive amount of this tannin diet can lead to liver and kidney lesions, as well as death (Waghorn and McNabb, 2003). Death usually occurs five to ten days after the first excessive consumption; the toxic compound responsible is not known. Information concerning the digestion, absorption, and impact on metabolism and productivity of hydrolyzable tannins is rare.

Condensed Tannins

The presence of CT in forage species may provide a practical means of protecting dietary forage protein from ruminal degradation, thus increasing plant protein uptake in the small intestine with implications for animal performances (Piluzza et al., 2013). Of the tannins, condensed tannins are the most widely distributed. Condensed tannins are oligomers or polymers of flavonoid units linked by carbon-carbon bonds (Waghorn and McNabb, 2003) not susceptible to cleavage by hydrolysis (Reed, 1995). They are called condensed tannins because of their condensed chemical structure. CT, are also termed proanthocyanidins (PA), which is derived from the acid catalyzed oxidation reaction that produces red anthocyanidins through heating of PA in acidic alcohol solutions (Haslam, 1982). Cyanidin (procyanidin) and delphinidin (prodelphinidin) are the most common anthocyanidins produced (Reed, 1995). Condensed tannins can contain as little as two or greater than fifty flavonoid units. Due to the

variability of flavonoid units to some substituents and because of the variable sites for interflaven bonds, condensed tannin polymers have complex structures. Condensed tannins may or may not be soluble in aqueous organic solvents, depending on their chemical structure and degree of polymerization.

It is speculated that plants containing condensed tannins evolved over time to implore them as a defense mechanism, which protected them against pathogenic microorganisms and against being consumed by insects or grazing animals (Swain, 1979). Now they are being extracted from various plants to be used in improving animal health. Extraction of these condensed tannins was once performed using acetone-water, but full extraction of the CT was not obtained with this method (Barry et al., 1999). Condensed tannins found in tropical forages are thought to promote plant growth by reducing the release of leaf litter into the soil (Palm et al., 1991) and reducing the release of animal feces (Waghorn and McNabb, 2003). Condensed tannin containing forages have different benefits for ruminants, depending on the species of plant. For example, lotus has been proven beneficial in the prevention of bloat (Beddows, 1956). Other condensed tannins have been efficient at improving live-weight gain (Waghorn et al., 1999). In sheep, they have been shown to increase milk protein concentration (Wang et al., 1996), improve lambing percentages (Min et al., 1999), and reduce, gastrointestinal nematode infection (Niezen et al., 1995), incidence of fly strike (Leathwick et al., 1995), and methanogenesis in sheep (Waghorn et al., 2002).

Tannin Chemistry

Tannins are oligomeric, polyphenolic compounds, often with high molecular weight, and accumulate in many plants as natural products of secondary plant metabolism (Caygill and Mueller-Harvey, 1999). They show great structural diversity among different plant species but one feature that most tannins have in common is that they precipitate protein. Tannins can be divided chemically into two important groups: the hydrolysable tannins and the condensed tannins (CT). Hydrolysable tannins are polyesters of sugars (mostly glucose) and gallic or ellagic acids (Figure 1) and are generally considered detrimental to animal nutrition (Serrano et al., 2009). Condensed tannins are polymers of flavan-3-ols (Figure 2). They form colorful anthocyanidins upon oxidative cleavage (heating in presence of acid) and are therefore also called proanthocyanidins. Each CT polymer can consist of a variety of flavan-3-ol subunits of which the most common are catechin and epicatechin or gallic catechin and epigallocatechin which form procyanidins or prodelphinidins.

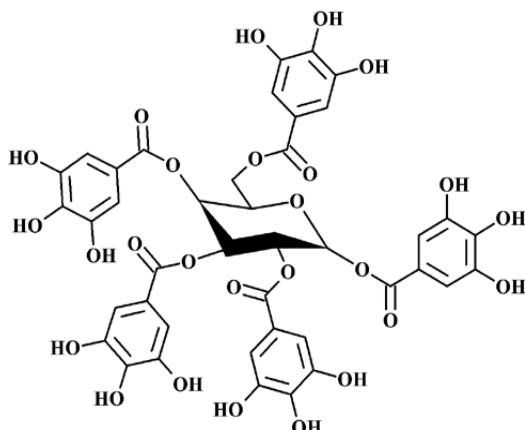


Figure 1. Structure of the hydrolysable tannin with $n+2$ flavan 3-ol subunits.

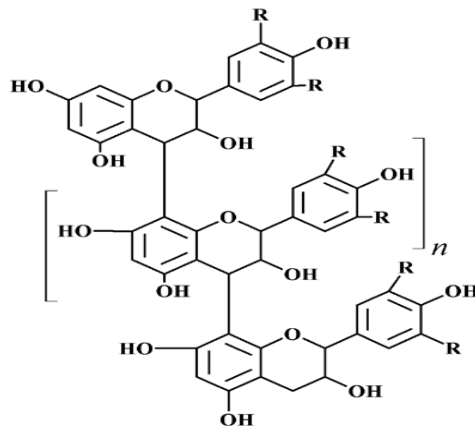


Figure 2. Possible structure of condensed Pentagalloylglucose.

Biological Features of Tannins

Tannins are functionally known by their competence to bind with proteins which forms the bases of many biological effects of tannins (Hagerman and Butler, 1991). They can have detrimental effect against many microorganisms and fungi (Bernays et al., 1989) which may be one of the major reasons of their evolution (Swain, 1979; Bernays et al., 1989; Ayres et al., 1997; Aerts et al., 1999). Intense deposits of tannin contents occur in the epidermis of leaves and stems of many leguminous forage plants, herbs and grasses with different concentrations including *Onobtychis vicifolia* (sainfoin), *Lotus (L.) corniculatus* (birdsfoot trefoil), *L. pedunculatus* (big trefoil), *Hedysarum coronarium* (sulla), and *Lespedeza cuneata* (sericea lespedeza) (Jones et al., 1976; Terrill et al., 1989, 1992). Interestingly, it has been reported that plants higher in tannins produced fewer leaves as compared to those having low tannins (Coley, 1986).

Effect of Tannin in Ruminant Fermentation

Tannins can be beneficial or detrimental to ruminants, depending on which (and how much) is consumed, the compound's structure and molecular weight, and on the physiology of the consuming species (Hagerman and Butler, 1991).

Voluntary Feed Intake

Until fairly recently, most researchers believed that the consumption of tannins reduced voluntary feed intake. It would appear that the consumption of plant species with high CT contents (generally > 50 g kg⁻¹ of dry matter, DM) significantly reduces voluntary feed intake, while medium or low consumption (< 50 g kg⁻¹ DM) seems not to affect it (Barry and Duncan, 1984; Barry and Manley, 1984; Waghorn et al., 1994a). The effect of HT has also been reported variable, mainly dependent on the quantity consumed. McSweeney et al. (1988) observed no significant reduction in voluntary feed intake in sheep whose diet included *Terminalia oblongata*, a species low in HT (34 g kg⁻¹ DM). However, a reduction did occur when the same animals were fed *Clidemia hirta*, a shrub with a high HT content (> 50 g kg⁻¹ DM). Frutos et al. (2004) found no reduction in voluntary feed intake among sheep provided a feed containing soya bean meal treated with HT (20.8 g HT kg⁻¹ DM of feed).

There are three main mechanisms have been suggested to explain the negative effects of high tannin concentrations on voluntary feed intake: a reduction in feed palatability, the slowing of digestion, and the development of conditioned aversions. A reduction in palatability could be caused through a reaction between the tannins and the salivary mucoproteins, or through a direct reaction with the taste receptors, provoking an astringent sensation (McLeod, 1974). The tannin-proline-rich protein complexes formed, unlike other protein-tannin complexes, are stable across the whole pH range of the digestive tract. This might cancel their negative effect on palatability, and therefore on feed intake, and improve the digestion of tannin-rich feeds (Robbins et al., 1987; Austin et al., 1989; McArthur et al., 1995; Narjisse et al., 1995). It would seem very likely that, throughout evolution, herbivores would have developed different adaptive mechanisms for the consumption of tannin-rich plants (Robbins et al., 1987; Leinmüller et al., 1991; Hagerman et al., 1992; Narjisse et al., 1995). Browsing animals secrete proline-rich proteins constantly, while sheep, for example, only produce them when consuming plants rich in tannins (Robbins et al., 1987; Austin et al., 1989).

In cattle, however, no increase in the production of such proteins has been observed in response to tannin ingestion, although other proteins with high affinity for these polyphenols have been found in their saliva (Makkar and Becker, 1998). With respect to the second possible mechanism, Narjisse et al. (1995) infused tannins directly into the rumen to determine whether factors independent of palatability were responsible for the reduction in voluntary feed intake. Slowing the digestion of dry matter in the rumen impairs the emptying of the digestive tract, generating signals that the animal is full and providing feedback to the nerve centres involved in intake control. In agreement with some authors, this could influence voluntary feed intake more than a reduction of palatability (Waghorn et al., 1994a).

Digestibility of the Diet

Tannins mainly exert this effect on proteins, but they also affect other feed components to different degrees (Kumar and Singh, 1984). Their main effect on proteins is based on their ability to form hydrogen bonds that are stable between pH 3.5 and 8 (approximately). These complexes-stable at rumen pH- dissociate when the pH falls below 3.5 (such as in the abomasum, pH 2.5-3) or is greater than 8 (for example in the duodenum, pH 8), which explains much about the activity of tannins in the digestive tract (McLeod, 1974; Mangan, 1988; Hagerman et al., 1992). Evidently, the modifications of the digestibility caused by tannin ingestion are mainly associated with changes in the ruminal fermentation pattern, along with changes in intestinal digestibility. The two subsections below discuss these effects, but it is worth mentioning here the repeatedly published conclusion that «one of the clearest pieces of evidence showing that tannins reduce the digestibility of feed is the increase in faecal excretion of nitrogen with increased dietary tannin content». Numerous examples of this argument exist, such as that in which sheep fed only carob (*Ceratonia siliqua*) leaves (tannin concentration = 50 g kg⁻¹ DM) lose liveweight and excrete more protein in their faeces than they consume (Silanikove et al., 1994). It is important to realise, however, that the consequences of tannin ingestion include increased secretion of endogenous proteins such as salivary glycoproteins, mucus and digestive enzymes, and increased desquamation of intestinal cells (Mehansho et al., 1987; Waghorn, 1996). This increase in faecal nitrogen could therefore be an increase in metabolic faecal nitrogen, i.e., nitrogen of endogenous origin that does not represent a fall in the amount of protein absorbed from feed.

Ruminal Fermentation

The reduction of ruminal protein degradation may be the most significant and well-known effect of tannins (e.g., McLeod, 1974; Mangan, 1988; Hagerman et al., 1992; Mueller-Harvey and McAllan, 1992). The affinity of tannins for these molecules is very great, and the pH of the ruminal medium favours the formation of tannin-protein complexes. In general, this reduction in protein degradation is associated with a lower production of ammonia nitrogen and a greater non-ammonia nitrogen flow to the duodenum (Barry and Manley, 1984; Waghorn et al., 1994b; Waghorn, 1996). The effect of tannins on protein degradation is basically a reduction in the immediately degradable fraction, and a reduction of the fractional rate of degradation (Aharoni et al., 1998; Frutos et al., 2000;

Hervás et al., 2000). Though tannins mainly exert their effects on proteins, they also have effects on carbohydrates, particularly hemicellulose, cellulose, starch and pectins (Barry and Manley, 1984; Chiquette et al., 1988; Leinmüller et al., 1991; Schofield et al., 2001). For a long time, the effect of tannins on the degradation of fibre was seen as a secondary anti-nutritional effect. However, several studies have shown that fibre degradation in the rumen can be drastically reduced in animals that consume tannin-rich feeds (e.g., Barry and McNabb, 1999; McSweeney et al., 2001; Hervás et al., 2003a).

Tannins are also chelating agents, and this could reduce the availability of certain metallic ions necessary for the metabolism of rumen microorganisms (Scalbert, 1991). With respect to enzyme inhibition, tannins can react with microbial (both bacterial and fungal) enzymes, inhibiting their activity (Makkar et al., 1988; Mueller-Harvey and McAllan, 1992; McAllister et al., 1994b; McSweeney et al., 2001). Several authors (Leinmüller et al., 1991; O'Donovan and Brooker, 2001) indicate that tannins alter the activity of bacterial proteolytic, cellulolytic and other enzymes, but it is important to point out that the binding of tannins to enzymes – whether bacterial or endogenous – does not necessarily simply their inhibition (Makkar et al., 1988). With respect to fibrolytic enzymes, CT more easily inhibits the activity of hemicellulases than cellulases (Waghorn, 1996). This is possibly due to the fact that the latter are associated with bacterial cell walls while the hemicellulases are extracellular and therefore more sensitive (Van Soest, 1994). This would explain why the majority of researchers report a greater reduction in the degradability of hemicellulose in the presence of tannins (Barry and Manley, 1984; Waghorn et al., 1994a; Hervás et al., 2003a). However, this can vary depending on the tannin in question (McAllister et al., 1994a). Finally, tannins might have a direct effect on ruminal microorganisms, e.g., by altering the permeability of their membranes (Leinmüller et al., 1991; Scalbert, 1991). Nonetheless, some rumen microorganisms can tolerate tannins (Nelson et al., 1998; O'Donovan and Brooker, 2001). The degree of tolerance is specific to the microorganism in question, explaining the different susceptibility of bacterial strains. It also depends on the tannin, and the differences between HT and CT in this respect are notorious.

Effects of Tannins on Nutritive Value of Forages

Tannins in forage have both negative and positive effects on nutritive value (Reed et al., 1990; Mueller-Harvey and McAllan, 1992). Tannins in high concentrations reduce intake, digestibility of protein and carbohydrates, and animal performance (Reed et al., 1990). Tannins in low to moderate concentrations prevent bloat and increase the flow of non-ammonia nitrogen and essential amino acids from the rumen (McNabb et al., 1993). The positive effects of tannins on protein utilization have practical importance because problems associated with extensive proteolysis and (or) deamination in the rumen limit production in modern feeding systems (Beever et al., 1989).

Negative Effects of Tannins

Normally condensed tannins and hydrolysable tannins supplementation at low levels does not have detrimental effects on animal performance or other economically important traits (Krueger et al., 2010).

Intake

Tannins may reduce intake of forage legumes by decreasing palatability or by negatively affecting digestion. Astringency is the sensation caused by the formation of complexes between tannins and salivary glycoproteins. Astringency may increase salivation and decrease palatability. Waghorn et al. (1994a) suggested that decreased ruminal turnover and rate of digestion was more important than palatability in reducing intake of sheep fed pure diets of *Lotus pedunculatus* in comparison to sheep fed *L. pedunculatus* along with polyethylene glycol (PEG) the latter binds the tannins making them relatively inactive in the rumen.

Growth

Rate of gain of young animals reflects total intake and availability of nutrients in the diet. Low growth rates because of low total feed intake were observed in animals eating fruits of *A. sieberiana* and *A. nilotica*, which contained high levels of tannins (Tanner et al., 1990). Low total intake and low growth rates were also observed in animals eating *A. sieberiana* pods and leaves of *A. cyanophylla* (Reed et al., 1990). The negative effect of tannins on growth rate was caused by a combination of reduced intake and low true digestibility of protein.

Digestion of Fiber Fractions

Tannins may reduce cell wall digestibility by binding bacterial enzymes and (or) forming indigestible complexes with cell wall carbohydrates (Reed et al., 1990). Digestibility of organic matter and fiber fractions was lowest for sheep fed *A. cyanophylla*, the supplement with the highest content of CT and soluble phenolics. At high levels (5-9 %) tannins become highly detrimental (Barry, 1983) as they reduce digestibility of the fiber in the rumen

(Reed et al., 1985) by inhibiting the activity of bacteria and anaerobic fungi (Chesson et al., 1982). High levels also leading to reduced feed intake (Akin and Rigsby, 1985), and above 9 % tannins may become lethal to an animal that has no other feed (Kumar, 1983).

Positive Effects

Rumen Escape: Tannins may complex protein at the pH of the rumen and protect protein from microbial enzymes. These complexes are unstable at the acid pH of the abomasum and the proteins become available for digestion (Barry and Manley, 1984). The evidence for the stability of tannin-protein complexes in the ruminal environment comes from highly simplified *in vitro* systems with purified proteins and tannins in the absence of ruminal microorganisms (Jones and Mangan, 1977). However, a tannin-protein complex that survives the ruminal environment may or may not be digested in the lower tract (Waghorn et al., 1994b).

Urea Recycling: Tannins may increase the efficiency of urea recycled to the rumen. Tannins lower the rate of protein degradation and deamination in the rumen and therefore lower ruminal $\text{NH}_3\text{-N}$ (Woodward, 1989). Plasma urea nitrogen, ruminal $\text{NH}_3\text{-N}$, and urinary N loss were lower when sheep and goats were fed legumes that contained tannins (Woodward, 1988). Tannins may increase the glycoprotein content and excretion of saliva, which could lead to more N recycled to the rumen (Robbins et al., 1987).

Microbial Efficiency: Tannins increase microbial yield per unit of organic matter digested. Several researchers have observed increases in non-ammonia nitrogen (NAN) flows to the duodenum that were greater than N intake for forage legumes that contain tannins. Because N is not created in the rumen, part of the increased flow of NAN must be from endogenous sources that have been incorporated into the microbial fraction. Nitrogen flows at the duodenum that are greater than N intake are common for diets low in N (< 1%), but for forage legumes with greater than 2% N, the N flows at the duodenum are normally lower than N intake (Barry and Manley, 1984).

Moreover, no effect of CT was found on voluntary feed intake, live weight change and digestibility when beef steers were supplemented with mangosteen peel (*Garcinia mangostana*) that contained tannins. However, the efficiency of rumen microbial protein synthesis and P/E ratio were slightly higher in steers fed on mangosteen peel than the control group.

Possible Explanations of Tannin Effects

Nutritional Aspect: The beneficial effects of tannins in sheep are associated with the greater outflow and absorption of amino acids especially in sheep fed with the forages containing tannin percentage ranging from 2-4% (Waghorn et al., 1987; Wang et al., 1994, 1996b; Min et al., 1999). Enhanced growth rate and increase in production performance and nutritive value of milk in sheep may be due to increased availability of essential amino acids (Waghorn et al., 1987; Wang et al., 1994). Increase outflow of sulphur containing amino acids which are key precursors of wool production may contribute to increased wool production (Wang et al., 1994; McNabb et al., 1993). Tannins make complexes with the proteins in which prevent the degradation of proteins in rumen thus increase flow of proteins to the intestines (Waghorn et al., 1987, 1994; McNabb et al., 1996). Moreover, the pH value in rumen (6.0-7.0) is very favorable for the formation of stable complexes between tannin and proteins. When the complexes come in intestines, the lower pH (2.5-3.5) separates the bond between tannin contents and proteins resulting in enhanced digestion of essential amino acids in the intestines of sheep (Waghorn et al., 1987, 1994). This greater quantity of proteins is available to be absorbed in the intestine of sheep. In contrast, high tannin concentration reduces percentage digestion of proteins thus leads to reduced growth rate, wool production and milk quality and quantity (Waghorn et al., 1994).

Control of Parasites

Although, most of the parasitic control programs are based on chemotherapeutic control (Waller, 1999; FAO, 2002) but, various problems have been evolved with this practice such as increasing problem of development of resistance by the parasites to several families of drenches (McKenna et al., 1995; Vermunt et al., 1995; Chandrathani et al., 1999; Chartier et al., 2001; Leathwick et al., 2001), hazards of chemical residues and toxicity (Kaemmerer & Buitenkotter, 1973), un-economical, non-adaptability and non-availability of drugs in remote areas. Recent reports on the small ruminants suggest that tannin containing fodder decrease the detrimental effect of gastrointestinal parasites by killing larval and adult worms (Athanasiadou et al., 2000). Similarly, various scientists observed lower fecal count and worm burden with no parasitic species difference in the sheep drenched with several concentrations of condensed tannins (Niezen et al., 1998; Paolini et al., 2003a, 2005; Molan et al., 1999, 2000, 2002; Waghorn and Molan, 2001). Tannins bind with free available proteins in the gastrointestinal tract and reduced nutrient availability of nutrients would have resulted in larval and worm starvation and death (Athanasiadou et al., 2001). Additionally, tannins would also bind with cuticle of larvae which is high in glycoproteins ensuing in death of larvae (Thompson and Geary, 1995).

Bloat Safety

Bloat is frequent muddle in small ruminants caused by the formation of stable protein broth in the rumen of animals fed with high nutritive value legumes including white clover or Lucerne. These protein foams avert the fermented gases to liberate from the rumen resulting in expansion of rumen. The course of bloat formation is very acute and leads to serious damage of vital organs such as lungs and heart (Mangan, 1959) and ultimately leading to death of animals. While, moderate concentration of tannins in the food of animals destabilizes the protein foams which refers them bloat safe (Tanner et al., 1995).

Reduced Proteolytic Enzyme Activity and Growth of Rumen Bacteria

Condensed Tannins considerably reduce the proteolytic enzyme activity and growth of bacteria in the rumen of sheep (Jones et al., 1993). CTs form complexes with the cell coat polymers of bacteria and proteolytic enzymes secreted by them which enable the protein to sidestep in the rumen. These complexes subsequently release the protein when come in the acidic condition of abomasum. These protein molecules undergo enzymatic hydrolysis in the small intestine leading to availability of enormous number of amino acids to be absorbed from the intestine (Jones and Mangan, 1977; Martin and Martin, 1983; McNabb et al., 1998).

Effect of Tannins on Animal Production

Since tannin consumption can affect voluntary feed intake and its digestive utilisation, there are likely to be consequences on the productivity of the animals that consume them. In general, high tannin intakes have a clear negative effect on productivity; nutrient availability is reduced because of the complexes formed between tannins and several types of macromolecules, voluntary feed intake and digestibility are reduced, the digestive physiology of the animal may be impaired, and there may be mucosal perturbations, etc. Barry (1985) observed a significant reduction in the gain of live weight in lambs fed *L. pedunculatus* (which has a high CT content; 76-90 g kg⁻¹ DM). In any event, the importance of the quantity consumed is receiving more and more recognition since tannins in several types of forage can have beneficial effects in moderate amounts (Aerts et al., 1999; Barry and McNabb, 1999; Min et al., 2003; Waghorn and McNabb, 2003). The intake of under 50 g CT kg⁻¹ DM (10 - 40 g kg⁻¹ DM) improves the digestive utilization of feed by ruminants, mainly because of a reduction in ruminal protein degradation and, as a consequence, a greater availability of (mainly essential) amino acids for absorption in the small intestine (Schwab, 1995; Barry and McNabb, 1999; Min et al., 2003). Barry and Manley (1984), by comparing with predicted values for non-tannin-containing diets, report positive effects on the retention of nitrogen in lambs fed *L. corniculatus* (< 50 g CT kg⁻¹ DM). Wang et al. (1994 and 1996a) observed that the grazing of *L. corniculatus* (34 g CT kg⁻¹ DM) reduced feed intake but increased the gain in live weight, carcass weight, and dressing proportion, compared with a group supplemented with polyethylene glycol (PEG), which binds to tannins and inactivates them. Montossi et al. (1996) observed a 23% improvement in liveweight gain when lambs grazed *Holcus lanatus* (4.2 g CT kg⁻¹ DM).

With respect to milk production, Wang et al. (1996b) reported an increase of 21% during mid and late lactation in sheep fed *L. corniculatus* (44.5 g CT kg⁻¹ DM) vs. sheep dosed with PEG. They also report significant increases in the efficiency of milk production, increased protein and lactose production, and a decrease in the fat content of the milk. This increased concentration of protein might be explained by the greater availability of intestinal amino acids, especially of methionine and lysine, which are thought to limit milk production. The greater concentration of lactose can be explained by greater glucose supply; most lactose synthesis in the mammary gland relies directly on blood glucose, and in ruminants gluconeogenesis mainly involves propionic acid and amino acids. Thus, a greater availability of amino acids would contribute to greater synthesis of glucose. The reduction in the concentration of fat was attributed to a simple dilution effect as the concentrations of lactose and protein increased. Montossi et al. (1996) also observed that grazing on *H. lanatus*, with its much lower CT concentration (4.2 g CT kg⁻¹ DM), increased wool production by 10%.

Treatments to Avoid the Negative Effects of Tannins

Numerous papers offer information on how to reduce or even avoid the negative effects of tannins in certain feeds. This information is especially useful in impoverished areas with few plant resources and where the majority of available species are rich in tannins. For example, wetting the feed with water or alkaline solutions can separate these phenolic compounds from the most nutritive parts, thus reducing their activity. Treatments with wood ash, as a good and cheap source of alkali, or urea have also been commonly used. «Chopping the leaves and then storage» has been found as an easy practical application by farmers. In this process, tannin inactivation seems to be due to oxidation of tannins and polymerisation to higher inert polymers (Makkar, 2001). More recent (and more studied) alternatives include treatment with polyethylene glycol (PEG), polyvinyl- polypyrrolidone, calcium hydroxide, etc. (Murdiati et al., 1990; Makkar et al., 1995; Ben Salem et al., 1999 and 2000; Makkar, 2001).

Treatments to Protect Dietary Protein from Ruminal Degradation

One of the basic goals of protein nutrition in ruminants is to optimise dietary protein use in order to maximize animal growth and milk production per unit of protein consumed (Schwab, 1995). Tannins could protect dietary proteins from ruminal degradation. With respect to HT, in 1972 Driedger and Halfield managed to reduce the *in vitro* ruminal protein degradability of soya bean meal through treatment with tannic acid. Its effect on intestinal digestibility however, was not very consistent. Pace et al. (1993) observed that the CT of quebracho provoked a greater reduction in the degradability of soya bean meal than commercial tannic acid, but in general the results obtained were very variable and depended on many factors.

Hervás et al. (2000) and Frutos et al. (2000) treated soya bean meal with different doses (0, 1, 4.7, 9, 13 and 20%) of tannic acid or commercial quebracho CT extract, and significantly reduced the extent of crude protein degradation in the rumen. The effect was significant even at the lowest dose. With respect to the intestinal digestibility of the non-degraded protein, no negative effects were seen until the 13% dose was reached with tannic acid and until the 20% dose was reached in the quebracho CT treatment. One of the drawbacks of using tannins as additives to protect protein rich feeds is the possibility of their degradation by rumen microorganisms. If this were to happen, the treated feeds would be just as vulnerable to ruminal degradation as untreated feeds. In the experiment of Frutos et al. (2000), the intraruminal administration of quebracho CT extract to sheep for 60 days did not increase the capacity of the microorganisms to degrade tannins. Although somewhat obvious, it is worth pointing out that proper management of natural tannin-containing resources (e.g., selective grazing or supplementing the diet with the right kind of shrubs) could provide the same beneficial effects with respect to protein degradation.

Bloat Prevention

It is well documented that bloat occurs when grazing ruminants consume large quantities of leguminous plants (e.g., alfalfa or clover). The gases produced in the rumen during fermentation cannot be released in the normal way since they are trapped in persistent foam caused by the rapid release of soluble proteins during chewing and ruminal degradation. However, when these animals graze on leguminous plants containing CT (for example *Onobrychis viciifolia*) this does not occur (Mangan, 1988; Aerts et al., 1999; Barry and McNabb, 1999; McMahan et al., 2000). The substitution of a small amount (approximately 10%) of ingested alfalfa DM by *Onobrychis viciifolia* provides unquestionable benefits in the prevention of bloat (McMahan et al., 1999 and 2000). The problem of this strategy is, however, the low persistence of this plant species in mixed cropping with alfalfa. However, the difficulty of the molecular techniques required has made progress slow. Very recently, the preliminary results of a study on the ruminal fermentation of transgenic alfalfa were published. The modification of the alfalfa decreased its initial rate of degradation in the rumen, but not the extent of degradation. This offers an interesting way to help to prevent bloat.

Control of Internal Parasite

The tannins of numerous plant species help to control certain internal parasites of animals, for example the nematode *Trichostrongylus colubriformis* (Butter et al., 2000). It is speculated that the positive effect on the host animal might be associated with a direct negative effect on the parasites themselves plus an indirect effect in the form of increased availability and digestive utilization of protein (Niezen et al., 1995; Min and Hart, 2003). The literature has several examples of this in sheep and goats grazing *L. corniculatus* or *Hedysarum coronarium* (Robertson et al., 1995) and after having ingested quebracho CT (Butter et al., 2000) etc.

Competing Interests

The authors declare that they have no competing interests.

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