The Potential of Tropical Tannin Rich Browses in Reduction of Enteric Methane

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Submission: September 18, 2017; Published: January 11, 2018

Abstract

This paper reviewed the effect of tannin on intake, digestibility, fermentation and methane production of various tropical browses. Under communal production system in Africa, ruminants have free access to trees and shrubs throughout the year, especially in dry season. These browse contains high nitrogen in addition to tannins that can suppress rumen methanogenesis. Hydrolysable and condensed tannins and their extracts have been shown to decrease methane (CH₄) production under both in vivo and in vitro conditions. The molecular weight is a key factor for its effect on digestive enzymes and microbes in the rumen. Low molecular weight tannins could be more effective inhibitors of microbes, including methanogens, compared with high molecular weight tannins. Consumption of low to moderate concentrations of tannins did not affect voluntary feed intake, while high tannin concentrations resulted in reduced intake. The effect of tannins on protein degradation is a reduction in the immediately degradable fraction and fractional rate of degradation. Thus a systematic evaluation is needed to determine optimum levels of supplementation in a mixed diet in order to attain a maximal depressing effect on enteric CH₄ production with a minimal detrimental effect on rumen fermentation of poor quality roughage based diet. Therefore, more in vivo studies for tannin rich plants and their extract should be conducted with hydrolysable tannins since they appear to be more promising.

Keywords: Browses; Digestibility; Intake; Methane; Reduction

Abbreviations: CH₄: Methane; GHG: Greenhouse Gasses; CO₂: Carbon Dioxide; N₂O: Nitrous Oxide; Gt: Giga Tone; CO₂-eq: Carbon Dioxide Equivalent

Introduction

The global human population is estimated to be 9.15 billion in 2050 and most of the increase is expected to be in developing countries [1]. This growth was driven by the rapidly increasing demand for livestock products, coupled with population growth, urbanization and increasing incomes. Despite this, the animal product consumption level is still lower in developing countries than in developed countries [2], indicating substantial need for expansion of livestock production. In smallholder crop-livestock, agro-pastoral, and pastoral livestock systems of tropical Africa, livestock production is one of the options that could increase income and sustain the livelihoods of farmers. Above all, ruminants are capable of converting plant fibres (structural carbohydrates), which constitute the planet's most renewable abundant resource, into useful end products (high-quality protein, fibre, etc). Despite such contributions, currently livestock production faces climate change challenges globally, in addition to feed shortages in the developing and least developing countries.

The primary problem of livestock production in Africa is low quality and quantity of feed throughout most of the year. In this region, livestock production is dominated by smallholder farmers with communal and small-sized private grazing areas [3]. Such areas are characterized by an inadequate supply of feed, which is low in quality with low nitrogen and high fibre contents. Similarly, crop residues, which are other major sources of feed, are characterized by low nitrogen concentration, high fibre and low digestibility. Thus, these materials may be not sufficient to meet the maintenance and production nutritional requirements of the animal, which may increase the environmental footprint of livestock production from the system [4]. Therefore, supplementation with nitrogen and energy is essential to improve palatability, intake, and rumen fermentation and improve animal production [5].

In current decades, the impact of global warming and continued uncontrolled release of greenhouse gases (GHG) have negatively influenced livestock production and food security [6]. Livestock production contributes a significant amount of GHG emissions worldwide, generating carbon dioxide (CO₂), methane and nitrous oxide (N₂O) throughout the production cycle. Livestock contributes to total GHG emissions through land use and land-use change (2.5Gt CO₂-eq); feed production, except C released from soil (0.4Gt CO₂-eq); enteric fermentation from ruminants (CH₄) and on-farm fossil fuel use (CO₂) (1.9Gt CO₂-eq); manure management (2.2Gt CO₂-eq);...
eq); and processing and international transport (0.03Gt CO₂-eq) [7]. The contribution of livestock by respiration accounts for only a small part of GHG emissions, but other livestock-related activities play a much greater role. It is reported that the rate of increase in GHG emission has differed over time, most noticeably with global atmospheric CH₄ concentrations appearing to stabilize between 1999 and 2007; however, CH₄ concentrations are again rising [8]. In the developed world, they are expected to decline due to increased productivity, coupled with declining number of ruminants [7]. However, in the developing world and from the African continent they are expected to rise due to increases in animal numbers [9].

One important strategy for improving fibre fermentation in ruminants is to supplement poor quality diets with browses rich in nitrogen [10]. Tropical browses contain reasonably high nitrogen and low fibre content, and can be good candidates for supplementing poor quality feeds. However, it contains tannins in a variable amount as a means of its defence mechanism against herbivores. Several studies have indicated that tannins have anti-methanogenic activity, either by direct inhibition of methanogens or indirectly through inhibition of protozoa [11-13]. Interestingly, tannins can be beneficial or detrimental to ruminants depending on its type, amount consumed, structure and molecular weight, and the physiology of the animal. It has been reported that consumption of low or moderate concentrations of tannin does not affect voluntary feed intake, but can suppress CH₄ production. Tannins vary in its structure depending on source, type and level that further vary depending on the rumen environment: The rumen, the main site of enteric CH₄ production, contains a diverse and dense microbial population living symbiotically, and plays a significant role in the feed digestive processes of ruminant animals [16]. The rumen has a stable and dynamic environment, which is well established to perform the function of bioconversion of feed into rumen fermentation products [17]. The microbial ecosystem comprises numerous populations of bacteria, anaerobic fungi, ciliate protozoa [17-19]. These microbes play a crucial role through their involvement in fibre fermentation, either through direct attachment to feed particles and secreting fibre fermenting enzymes or indirectly by enhancing the attachment of other microbes to increase fibre digestion. According to Niwinski [20], rumen microbes have highly complicated and diverse synergistic and antagonistic relationships among the classes of microbes. For example, populations of fibrolytic bacteria producing H₂ are positively correlated to methanogens due to the inter-species hydrogen-transfer relationship in the rumen [21]. During this process, carbohydrates are fermented to produce volatile fatty acids (VFAs), energy CH₄, CO₂ and heat. CO₂ and CH₄ are eliminated via the nose and mouth by belching and eructation, leading to loss of energy. The relationship between fermenting species and H-utilizing microbes normally exists as a symbiotic function, which is called ‘interspecies hydrogen transfer’ [22]. Thus, synthesis of CH₄ occurs because of the exchange of metabolites between H-producing microbes such as fibrolytic fungi and bacteria and H-consuming microbes such as methanogens [23]. This continuous production and removal of H facilitates continuous fibre fermentation in the rumen.

**Methane production and associated loss of feed energy:** Methane is produced by methanogenic archaea as a by-product of anaerobic fermentation of feed in the rumen. This production causes a significant loss of dietary energy [24]. With normal rumen functioning, methanogenesis is essential for optimal rumen performance, because it prevents H accumulation that can lead to inhibition of dehydrogens involved in the oxidation of reduced co-factors [21]. Fermentation is an oxidative process in which co-factors such as NADH, FADH, NADPH have to be reduced to NAD+, NADP+, FAD+ through dehydrogenation reactions by releasing H in the rumen [21]. As soon as reduced co-factors are produced, H is used by methanogens to reduce CO₂ by forming CH₄ according to the following equation:

\[
\text{CO}_2 + 4\text{H}_2 = \text{CH}_4 + 2\text{H}_2\text{O} \quad \text{equation (1)}
\]

Methane is a source of feed energyloss to the animal [25]. It represents on average 10% of gross energy (GE) intake, which ranges from 7% to 17% of gross energy (GE), depending on diet characteristics [26,27]. Methane contains 892.6KJ/mol energy at 25 °C and 101.3kPa [28]. This amount of gross energy is lost instead of contributing to the total supply of energy for metabolism in the ruminant. In tropical rumen production systems, this value might be higher due to poor-quality diets, which are often deficient in vital nutrients for optimal microbial growth in the rumen.

**Relationship between chemical composition, digestion and CH₄ production:** The amount of H produced during fermentation of feed is highly dependent on the quality of diet and the proportion of the different types of rumen microbes, because the pathways for VFA production differ in terms of H input/output. Other factors, such as pH, feeding strategy, animal species and environmental factors, also determine CH₄ production in the rumen [29].

Feed intake is a critical factor for improving productivity, increasing feed efficiency and decreasing CH₄ production in ruminant feeds. Dietary NDF concentration is one of the important regulators of feed intake that determine energy yield, digesta flow and the so-called fill-limitation mechanism [16]. Increased intake of poor-quality feeds has little effect on CH₄ production, while increasing the digestibility of feed results in a depression in the amount of CH₄ produced per unit of feed consumed [30]. As the
digestibility of a feed increases, the amount of energy available to the animal rises, therefore the \( \text{CH}_4 \) emitted per kg of production, for example weight gain, decreases. Thus, increased digestibility of diets often means fewer \( \text{CH}_4 \) emissions per unit of production. However, with digestibility above 72%, the increasing effect on the emissions becomes marginal. Broderick compared ryegrass silage with alfalfa silage as part of a total mixed ration of iso-nitrogenous and similar amount of NDF and reported that feed intake and milk production were much higher with the alfalfa silage diet, but with a relatively lower feed efficiency. This indicated that the major challenge with forage-based diets is improving diet quality in order to reduce \( \text{CH}_4 \), as the correlation between forage quality and \( \text{CH}_4 \) emissions is sometimes low [15,31-33].

In extensive grazing systems, where diets are of low to moderate digestibility, increased dry matter intake (DMI) is associated with increased \( \text{CH}_4 \) production [32]. In such conditions, \( \text{CH}_4 \) released per unit of additional intake is more than the \( \text{CH}_4 \) produced per unit intake of highly digestible feeds. On the contrary, \( \text{CH}_4 \) production per unit metabolizable energy (ME) intake is lowest for high-energy diets. In addition, small changes in energy intake result in corresponding minor changes in \( \text{CH}_4 \) output and large changes in animal performance. Many studies have attempted to determine the relationship between \( \text{CH}_4 \) production and GE intake using empirical prediction equations. These equations, however, do not fully describe changes in composition of the diet and have limited use in estimating the impact of varying nutritional strategies on \( \text{CH}_4 \) emissions [16]. These challenges can be addressed by expressing \( \text{CH}_4 \) energy loss on a DE basis or per unit of animal product, which better reflects forage quality and other mitigation practices, such as grain or fat inclusion in ruminant diets [16].

**Rumen modulators used to reduce \( \text{CH}_4 \) production**

Enteric \( \text{CH}_4 \) production depends primarily on quantity and quality of the diet [15,33-36], the nature of fermented carbohydrates [34,35], concentration of NDF and ADF [36], the acetate to propionate ratio of fermented feeds [37] and the type and harvest stage of forage consumed by the animal [38]. If rumen fermentation patterns shift from acetate to more propionate in the total VFA production, net hydrogen and \( \text{CH}_4 \) production will be reduced. Thus, any viable strategy has to result in one or more of these goals:

i. Reduction of hydrogen production that should be achieved without impairing feed digestion.

ii. Stimulation of hydrogen utilization towards pathways that produce other end products beneficial for the animal such as propionate production.

iii. Inhibition of the methanogenic activity and its numbers. When using this strategy, it is important to suppress \( \text{CH}_4 \) producing micro-biota activities and proliferation without limiting rumen function.

Increased concentrate proportions in ruminant rations are generally associated with a reduction in \( \text{CH}_4 \) emission per unit of feed intake and per unit of animal product [39,40]. For example, fermentation of a diet with 70% concentrate produced a 59% increase in ruminal propionate concentration and a 44 % drop in the A: Pratio in lactating dairy cows compared with a 50% concentrate diet [41]. Bannink et al. [42] also reported that the fermentation of sugars and starch would shift rumen fermentation toward the production of propionate. In a relationship proposed by Sauvant et al. [43], methane yield and A: P ratio in ruminal fluid showed a quadratic relationship in 23 experiments. These findings generally showed that higher inclusions of grain or starch content in ruminant diets lowered enteric \( \text{CH}_4 \) production.

However, in most tropical and sub-tropical livestock production systems, ruminants receive only small quantities of concentrates owing to direct competition with human and monogastric animals and high costs of concentrates. In addition, previous research suggested that increased forage quality would reduce \( \text{CH}_4 \) emissions per unit of weight gain [44,45] or per unit of animal product [46], owing to improvement in animal productivity. Many research reports have also shown potential for direct inhibition of methanogens through immunization of animals, and the use of plant polyphenols, bacteriophages and bacteriocins [14,47,48]. Currently, indirect methods of redirecting hydrogen are also receiving a lot of scientific attention. These methods include the use of ionophores such as monensin, fatty acids/lipids, organic acids [49], nitrate and sulfate supplementation. Some of these strategies are discussed below in the context of ruminants consuming high forage diets.

**Supplementation with plant tannins**

Tannins are compounds with high molecular weight that have the capacity to form reversible and irreversible complexes with proteins, polysaccharides (cellulose, hemicellulose, and pectin), alkaloids, nucleic acids and minerals [33,50]). They are synthesized naturally in nutritionally important forage trees, shrubs and legumes, fruits, cereals and grains in variable amounts. Tannins are categorized broadly into condensed or hydrolyzed tannins. Hydrolysable tannins are made up of a carbohydrate core whose hydroxyl groups are esterified with phenolic acids. Condensed tannins (pro-antho-cyanidins) are non-branched polymers of flavonoid units and usually have a higher molecular weight relative to hydrolysable tannins [51]. Hydrolysable tannins can be hydrolyzed and utilized by rumen microbes, while condensed tannins are resistant to hydrolysis.

**Effects of tannins on methanogenesis:** Hydrolysable and condensed tannins and their extracts have been shown to decrease \( \text{CH}_4 \) production under both \textit{in vivo} and \textit{in vitro} conditions [12,14,40,52,53]. The molecular weight is a key factor for its effect on digestive enzymes and microbes in the rumen. Low molecular weight tannins could be more effective inhibitors of microbes, including methanogens, compared with high molecular weight tannins [14,52,54]. This is because low molecular weight tannins form strong complexes with microbial enzymes, while high molecular weight tannins cannot penetrate to bacterial proteins, causing lower toxicity to methanogens [55]. The anti-methanogenic
effect of CT may be attributed to the direct inhibitory effect on methanogens, depending on the chemical structure of CT and methanogen species [11,56]. The anti-methanogenic activities of tannins may involve tannin action on functional proteins (enzymes) at accessible sites in or on methanogens [57].

Most studies conducted so far support the anti-methanogenic effects of tannins in the rumen. The decrease in CH₄ production due to supplementation of tannins had been reported by many researchers [11-13,53,58-61]. On the contrary, some researchers reported that tannins did not show any effect on methanogenesis or even enhanced CH₄ production in sheep [47]. Such discrepancies could be the result of doses, types and sources of tannins and types of diets. However, several studies have indicated that tannins have anti-methanogenic activity, either by direct inhibition of methanogens or indirectly through inhibition of protozoa [11-14,46]. The effects of tannins on rumen feed fermentation, digestibility, and methane production were reviewed in Table 1 & 2.

Table 1: Effect of tannins or their extracts on rumen CH₄ production and fermentation parameters in-vitro.

<table>
<thead>
<tr>
<th>Tannin Sources</th>
<th>Level of Inclusion</th>
<th>Feed Used in the Study</th>
<th>Effect on CH₄ (Decrease)</th>
<th>Effect on Digestion and Fermentation Parameters</th>
<th>Sources</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Acacia angustissima</em></td>
<td>20% of substrate</td>
<td>Brachiaria grass</td>
<td>12.30%</td>
<td>Digestibility unaffected</td>
<td>Zeleke et al. (2006)</td>
</tr>
<tr>
<td><em>Acacia mangium</em></td>
<td>20% of substrate</td>
<td>Elephant grass</td>
<td>28.90%</td>
<td>Digestibility, TVFA &amp; protozoa numbers unaffected</td>
<td>Hariadi &amp; Santoso (2010)</td>
</tr>
<tr>
<td><em>Biophytum petersianum</em></td>
<td>20% of substrate</td>
<td>Elephant grass</td>
<td>25%</td>
<td>Digestibility, TVFA &amp; protozoa numbers unaffected</td>
<td>Hariadi &amp; Santoso (2010)</td>
</tr>
<tr>
<td><em>Castanea sativa</em></td>
<td>0.5 and 2.5 gkg⁻¹ DM</td>
<td>Grass silage and hay: barley (77:23)</td>
<td>2.6-13.3%</td>
<td>Digestibility, TVFA, A: P, protozoa &amp; total bacterial numbers unaffected</td>
<td>Sliwinski et al. [47]</td>
</tr>
<tr>
<td>Chestnut tannins</td>
<td>1- 10%</td>
<td>Soybean</td>
<td>5.1- 33.3%</td>
<td>No information</td>
<td>Roth et al. [92]</td>
</tr>
<tr>
<td><em>Emblica officinalis</em></td>
<td>0.5 ml per 0.2g substrate</td>
<td>Wheat straw: concentrate (1:1)</td>
<td>20 and 27.7%</td>
<td>TVFA, A: P &amp; digestibility unaffected, protozoa numbers decreased</td>
<td>Patra et al. [14]</td>
</tr>
<tr>
<td><em>Jatropha curcas</em></td>
<td>20% of substrate</td>
<td>Elephant grass</td>
<td>22.40%</td>
<td>Digestibility, TVFA &amp; protozoa numbers unaffected</td>
<td>Hariadi &amp; Santoso (2010)</td>
</tr>
<tr>
<td><em>Lotus corniculatus</em></td>
<td>As sole diet</td>
<td>Itself</td>
<td>29.70%</td>
<td>TVFA unaffected, A: P increased</td>
<td>Tavendale et al. (2005)</td>
</tr>
<tr>
<td>Mimosatannins</td>
<td>1- 10%</td>
<td>Soybean</td>
<td>7.7-30.8%</td>
<td>No information</td>
<td>Roth et al. [92]</td>
</tr>
<tr>
<td><em>Populus deltoides</em></td>
<td>5.0.0-150gkg⁻¹ DM</td>
<td>Wheat straw: concentrate (1:1)</td>
<td>14.6-21.5%</td>
<td>TVFA, A: P &amp; protozoal numbers unaffected</td>
<td>Patra et al. [11]</td>
</tr>
<tr>
<td><em>Psidium guajava</em></td>
<td>20%</td>
<td>Elephant grass</td>
<td>18.40%</td>
<td>Digestibility &amp; protozoal numbers decreased, TVFA unaffected</td>
<td>Hariadi &amp; Santoso (2010)</td>
</tr>
<tr>
<td>Quebracho tannins</td>
<td>10-20gkg⁻¹ DM</td>
<td>Wheat grass</td>
<td>24.6-51.1%</td>
<td>Digestibility decreased</td>
<td>Min et al. [60]</td>
</tr>
<tr>
<td>Quebracho tannins</td>
<td>5-25% of substrates</td>
<td>Timothy hay: concentrate (65:35)</td>
<td>12.9-38.2%</td>
<td>Digestibility, TVFA &amp; methanogen numbers decreased; A: P unaffected</td>
<td>Bhatta et al. [12]</td>
</tr>
<tr>
<td><em>Sesbania grandiflora</em></td>
<td>20%</td>
<td>Elephant grass</td>
<td>9.20%</td>
<td>Digestibility, TVFA and protozoal numbers unaffected</td>
<td>Hariadi &amp; Santoso (2010)</td>
</tr>
<tr>
<td><em>Sesbania sesban</em></td>
<td>20% of substrate</td>
<td>Brachiaria grass</td>
<td>37.40%</td>
<td>Digestibility unaffected</td>
<td>Zeleke et al. (2006)</td>
</tr>
<tr>
<td><em>Terminalia belerica</em> seed pulp extracts</td>
<td>0.5-30ml of 0.2g substrate</td>
<td>Wheat straw: concentrate (1:1)</td>
<td>4.4 - 27.7%</td>
<td>TVFA, digestibility, A: P and protozoal numbers unaffected</td>
<td>Patra et al. [14]</td>
</tr>
<tr>
<td><em>Terminalia chebula</em> seed pulp</td>
<td>0.33 ³/gl⁻¹ or 50-150gkg⁻¹ DM</td>
<td>Wheat straw: concentrate (1:1)</td>
<td>10.6-25.5%</td>
<td>TVFA, A: P and protozoal numbers unaffected</td>
<td>Patra et al. [14]</td>
</tr>
<tr>
<td><em>Persea americana</em></td>
<td>20%</td>
<td>Elephant grass</td>
<td>11.80%</td>
<td>Digestibility, TVFA &amp; protozoal numbers unaffected</td>
<td>Hariadi &amp; Santoso (2010)</td>
</tr>
</tbody>
</table>

How to cite this article: Belete S G, Abubeker H. The Potential of Tropical Tannin Rich Browses in Reduction of Enteric Methane. Appro Poult Dairy & Vet Sci. 2(3). APDV:000538. 2018. DOI: 10.31031/APDV.2018.02.000538
Table 2: Effect of tannins or its extracts on rumen CH$_4$ production and fermentation parameters in vivo.

<table>
<thead>
<tr>
<th>Tannin Sources</th>
<th>Study Condition/Animals used</th>
<th>Level of Inclusion</th>
<th>Feed Used in the Study</th>
<th>Effect on CH$_4$ (Decrease)</th>
<th>Effects on Other Fermentation Parameters</th>
<th>Sources or References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acacia Mearnsii</td>
<td>Sheep</td>
<td>41gkg$^{-1}$ diets (extract)</td>
<td>Mixture of ryegrass and lucerne (1:1)</td>
<td>9.90%</td>
<td>Digestibility, TVFA &amp; total protozoa numbers unaffected, A: P decreased</td>
<td>CaruBa et al. [59]</td>
</tr>
<tr>
<td>Acacia Mearnsii</td>
<td>Cattle</td>
<td>8.6 and 14.6gkg$^{-1}$ DM</td>
<td>Grazing rye grass pasture with 4.5 kg grain</td>
<td>117.1 and 30%</td>
<td>Digestibility decreased</td>
<td>Grainger et al. [53]</td>
</tr>
<tr>
<td>Hedysarum coronarium</td>
<td>Dairy cows</td>
<td>As sole feed</td>
<td>Rye grass pasture</td>
<td>2.35%</td>
<td>No information</td>
<td>Woodward et al. [58]</td>
</tr>
<tr>
<td>Lespedeza cuneata</td>
<td>Goats</td>
<td>As sole feed</td>
<td>L. cuneata</td>
<td>51.40%</td>
<td>Digestibility &amp; protozoa numbers decreased TVFA &amp; A: P unaffected</td>
<td>Animut et al. [11]</td>
</tr>
<tr>
<td>Lespedeza cuneata</td>
<td>Goats</td>
<td>As sole diet</td>
<td>In pasture of crabgrass/tall fescue</td>
<td>30.20%</td>
<td>TVFA &amp; A: P unaffected</td>
<td>Puchala et al. [61]</td>
</tr>
<tr>
<td>Lespedeza striata</td>
<td>Goats</td>
<td>33-100%</td>
<td>sorghum-sudangrass</td>
<td>32.9-58.4%</td>
<td>Digestibility &amp; protozoal numbers decreased, TVFA &amp; A: P unaffected</td>
<td>Animut et al. [11]</td>
</tr>
<tr>
<td>Lotus pedunculatus</td>
<td>Sheep</td>
<td>As sole feed</td>
<td>In ryegrass &amp; lucerne pasture</td>
<td>No effect</td>
<td></td>
<td>Woodward et al. [26]</td>
</tr>
<tr>
<td>Quebracho tannins</td>
<td>Beef cattle</td>
<td>10-20gkg$^{-1}$ of DM</td>
<td>Barley silage, barley grain and rye grass mixture</td>
<td>No effect</td>
<td>No effect on digestibility; TVFA decreased; A: P decreased</td>
<td>Beauchemin et al. [77]</td>
</tr>
</tbody>
</table>

**Effects of tannins on feed intake, digestion and fermentation:** The negative effects of high tannin concentration include reduced voluntary feed intake, reduced feed palatability, decreased digestion and development of conditioned aversions. Tannins affect intake by slowing down digestion and emptying the digestive tract, and stimulating the nervous system to inhibit further intake of feed. Loss of palatability could be a result of reactions between tannins and salivary mucoproteins, or a direct reaction with taste receptors, provoking an astringent sensation [62]. Consumption of low to moderate concentrations of tannins did not affect voluntary feed intake, while high tannin concentrations resulted in reduced intake [63].

Although many reports indicated negative effects of tannins, ruminants rely on tanniferous forages, which are usually high in N content, especially in tropical regions. The saliva of these ruminants is rich in proline protein, which binds to tannins, forming tannin-proline-rich protein complexes [64,65]. The complexes are stable within a wide range of pH of the digestive tract, unlike other protein-tannin complexes [66]. In addition, ruminants have developed various adaptive mechanisms against the effects of tannins. Ruminants can benefit from dietary CT when the increases in protein flow from the rumen exceed the reduction in absorption of amino acids from the intestine. This is owing to the formation of tannin-proline-complexes, coupled with adaptive mechanisms developed by the microbes and the host animal. The ability of micro-organisms to degrade tannin-protein complexes is another important phenomenon that explains the utilization of tanniferous feeds by ruminants. There are Streptococcus species in the caecum [67] and entero-bacteria in the alimentary tracts of koalas [68] that are capable of degrading tannic-acid-protein complexes. Brooker et al. [69] have also isolated Streptococcus caprinus from feral goats that browse tannin-rich Acacia species with similar activity. In such scenarios, microbes may develop adaptive mechanisms to become resistant to adverse effects of tannins. For example, proteolytic bacteria that were initially sensitive to tannins were found to adapt after a short period of exposure by modifying their metabolism when tannin levels were not too high [37,70].

Various findings have reported the effect of tannins on digestibility feeds. McSweeney noted that CT might increase the intestinal digestibility of organic matter. However, other authors reported a negative effect of tannins on feed digestion and nutrient absorption from the small intestine [17]. The explanations for the anti-nutritive nature of tannins included poor solubility of tannin-protein complexes in the abomasum, formation of tannin-digestive-enzyme complexes or new tannin-dietary-protein complexes and changes in intestinal absorption, due to the interaction of tannins with intestinal mucosa [71]. Tannins affect degradation of proteins in the rumen owing to their high affinity with proteins, as the ruminal pH is conducive to the formation of tannin-protein complexes [62]. The reduction in protein degradation is associated with a lower production of ammonia-N and a greater non-ammonia nitrogen flow to the duodenum. The effect of tannins on protein degradation is a reduction in the immediately degradable fraction and fractional rate of degradation [72-74]. Though tannins exert their negative effects mainly on proteins, they have negative effects on carbohydrates, particularly hemicellulose, cellulose, starch and pectins [50,75].
Application of tannins in ruminant feeding

Addition of quebracho tannins up to 1.5gkg-1 BW in the diets of sheep did not affect feed intake, but decreased CH4 production [76]. Beauchemin et al. [77] also reported that inclusion of quebracho CT up to 2 % of DM had no influence on feed intake in cattle. On the other hand, inclusion of quebracho tannins at 8.93 % of DM in a diet of sheep reduced feed intake. In the study of Carulla et al. [59], feed intake in sheep was enhanced when an Acacia Mearnsii tannin extract was included in the diet, while CH4 emissions were suppressed, which is an important aspect for the practical application of tannins in animal diets. It is generally suggested that condensed tannin concentrations of more than 5% in diets may have adverse effects on nutrient utilization and productivity of animals, though the response depends on the types of tannin. In other studies, digestibility was not affected and CH4 production was reduced by inclusion of tannin extracts from Terminala bellerica [14], Acacia Mearnsii [59], Quebracho tannins [12] in the diet of ruminants. Other reported beneficial effects of tannins are a protection of protein from degradation in the rumen, thereby increasing metabolizable protein supply to the duodenum, preventing bloat and increasing conjugated linoleic acid concentrations in ruminant-derived foods. However, tannins exert an anti-microbial action on microbial growth, including cellulolytic bacteria and fungi, which may adversely affect fibre utilization. Inclusion of quebracho tannins at a dosage of 22.5gkg-1 DM to lucerne hay decreased the fibre digestibility, whereas no effect was noted at dosages of 7.5 and 15g CT kg-1 DM. It has been proposed that higher concentrations of tannins in diets, which remain free after binding with proteins, may depress fibre digestion. This occurs through complexation with ligno-cellulose, thus preventing microbial digestion or by directly inhibiting cellulolytic micro-organisms and activities of fibrolytic enzymes or both.

The responses of tannins on concentrations of TVFA are not conclusive, with some researchers reporting no effect [11,14,61], while others reported decreased concentrations [53,60,77], depending on dose and source [12]. There is some evidence that a significant decrease in methanogenesis could be possible without a considerable reduction of TVFA concentration and digestibility [12,59], and such interventions need to be tested further to refine the technology for practical application under field conditions.

Conclusion

It is possible to obtain substantial decrease in methane production with the inclusion tannin rich browse in ruminant diets but this is achieved not without compromising production especially with high tannin levels. Although there is a decrease in rumen protein degradability, there is an increase in post-rumen protein availability due to partitioning of excreted nitrogen more towards faeces and lesser towards urine. This in general can increase in efficiency of microbial protein synthesis and might make the use of tannins attractive significant in ruminant nutrition. The higher the number of hydroxyl groups in tannin structure, the higher the potential methane reduction [78-86].

Thus hydrolysable tannins appear to decrease methane production through inhibition of the growth and/or activity of methanogens- and/or hydrogen-producing microbes, and methane production per unit organic matter is digested to a greater extent than condensed tannins that decrease methane more through reduction in fibre digestion. Since the effects of tannins are a function of their nature, which varies from source to source, a systematic evaluation is needed to determine optimum levels of supplementation in a mixed diet in order to attain a maximal depressing effect on enteric CH4 production with a minimal detrimental effect on rumen fermentation of poor quality roughage based diet. Therefore, more in-vivo studies for tannin rich plants and their extract should be conducted with hydrolysable tannins since they appear to be more promising [86-94].

Acknowledgement

The authors would thank the University of Pretoria for financing the first author with bursary during the review of this work.

References


