New perspectives on the use of tropical plants to improve ruminant nutrition

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Inadequate nutrition is the main cause of low productivity by ruminants in sub-Saharan Africa. The primary feed resources in the region include natural pasture and crop residues that have tough texture, poor digestibility and are deficient in nutrients. These deficiencies can be corrected by supplementation with high-density feeds such as oilseed cakes and proteins of animal origin. However, protein sources such as oilseed cakes are beyond the economic reach of most farmers, while the incidence of bovine spongiform encephalopathy in Western intensive animal production may be thought to argue against the use of animal proteins. Local tree legumes have been investigated as potential supplements for ruminants because of their beneficial effect of increasing metabolizable energy intake, N intake and feed efficiency, and improving animal performance. However, our work has suggested that some plant materials may have a nutritional value beyond simply their nutrient content, i.e. as rumen-manipulating agents. The foliage of some tree legumes has been shown to be selectively toxic to rumen protozoa. Rumen protozoa ingest and digest bacteria and fungi, degrading their cellular protein to NH₃. Microbial protein turnover due to protozoal predation in the rumen may result in the net microbial protein outflow being less than half the total protein synthesized. Results from in vivo experiments have clearly shown that duodenal flow of both undegraded dietary and bacterial protein is generally increased by defaunation. However, no practical method has been developed to date to eliminate protozoa. Anti-protozoal plants may be promising, safe, natural defaunating agents.

Ruminants: Defaunation: Rumen: Tree legumes

Ruminants play an important role in the livelihood of farmers in the developing world, providing sustenance as milk and meat, animal traction, manure for crop production, cash income from sales of their products and a safety net of capital assets to face risks and misfortune in harsh environments (Øsrskov, 1993). Projected increases in the human population throughout the developing world and the limited availability of land for increased food and forage production suggest that agricultural production needs to be intensified considerably to satisfy the escalating demand for food. The intensification of ruminant production systems demands the introduction of high-producing breeds and a better quality of feeds. Lack of adequate nutrition all year round is one of the major causes of the low productivity of ruminants in sub-Saharan Africa (Osuji *et al.* 1995).

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Abbreviations: CT, condensed tannin; NDF, neutral-detergent fibre. **Corresponding author:** Belete Teferedegne, fax +44(0)1224 716687, email bt@rri.sari.ac.uk

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Maximizing ruminant productivity involves meeting the nutrient requirements for both rumen microbial metabolism and mammalian metabolism in the tissues. In ruminants nutrient inputs are subjected first to fermentative digestion by rumen micro-organisms. The microbial fermentation products eventually become available as energy (volatile fatty acids) and protein (microbial cells) for animal tissue metabolism. Hence, with low-quality feeds the maximum amounts of nutrients should be extracted, by microbial digestion, from the basal diet (crop residues and natural pasture), and the growth efficiency of the rumen microbes must be optimized by providing sufficient rumendegradable substrates. This maximization can be achieved by supplementation. Tree forages are potential sources of supplements that could provide an array of minerals and soluble N for rumen micro-organisms (Osuji et al. 1995).

Recently, interest has increased in the use of tropical plants that may have a nutritional value beyond simply their nutrient content, i.e. as rumen-manipulating agents. The application of sub-therapeutic amounts of antibiotics as rumen-manipulating agents to enhance the growth rate and efficiency of ruminants has been widely used in Western animal husbandry. However, increasing awareness over antibiotic residues in animal products and the threat of bacterial antibiotic resistance in the wider environment has led to a call for the banning of antibiotics as growth promoters (House of Lords, 1998). This factor will obviously increase the opportunities for alternative rumenmanipulating agents. The present paper attempts to summarize nutritive values of tree legumes and possible novel uses of these trees as modifiers of digestive function.

Nutritive value of tree legumes

DM intake and the ability of a feedstuff to provide the nutrients that are required by the animal for maintenance, growth and reproduction determine its nutritive value. Feed intake in ruminants consuming fibrous forage is primarily determined by the level of rumen fill, which in turn is directly related to the rate of digestion and passage of fibrous particles from the rumen (Van Soest, 1994). There is no simple predictor of the quality of tree legume foliage. Chemical composition alone is inadequate for several reasons, but primarily because the availability of nutrients from the forage is variable. Digestible DM intake may also be a poor predictor of potential productivity, since the composition of nutrients is not described. Feeds are rated on their productive energy and protein content (Van Soest, 1994). Analyses based on detergent extraction are more useful, since plant DM is separated into a completely digestible fraction (neutral-detergent soluble) representing the cell contents, and a partially digestible fraction (neutraldetergent fibre; NDF) representing plant cell walls (Van Soest, 1994). The digestibility of plant material in the rumen is related to the proportion and lignification of cell walls (NDF; Van Soest, 1994). Tree forages with a low NDF content (200-350 g/kg) are usually of high digestibility (Norton, 1994). It may therefore be predicted, from NDF content (Table 1), that hay and crop residues such as teff straw will have a low digestibility and most tree legumes will have a high digestibility. The protein content of forage

Table 1. The crude protein (nitrogen \times 6-25; CP) and neutral-detergent fibre (NDF) and tannin contents of some forages and leaves of tree legumes (g/kg DM)

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	СР	NDF	Tannins	Reference
Sesbania sesban 15019	209	162	31	Kiatho (1997)
Enterolobium cyclocarpum	250	361	ND	Ahn <i>et al.</i> (1989)
Samanea saman	219	446		Kiatho (1997)
Acacia angustissima	225		66	Ahn <i>et al.</i> (1989)
Acacia cyanophylla	141	879	38	Salem et al. (1999)
Teff straw	38	648	ND	Kiatho (1997)
Slulta hay	59	738		Osuji <i>et al.</i> (1995)

ND, not detected.

tree legume leaves (150–300 g/kg) is usually high compared with that of hay and crop residues (30–100 g/kg) (Table 1).

The effective nutrition of the ruminant is not what it eats, but rather the combination of the products of rumen microbial fermentation and unfermented feed that escapes from the rumen. Maximum fermentation rates are attained when all factors required by the rumen micro-organisms are available (mainly energy and N). Low-quality diets (hay and crop residues) are characterized by low animal productivity, resulting from the shortage of one or more essential nutrients required for rumen microbial activity, typically N. Supplements are required to correct these deficiencies. Most forage tree legumes have a N content higher than 13 g/kg (Norton, 1994). Supplementation of roughages with adequate quantities of rumen-degradable browses invariably alleviated N deficiency (Bonsi et al. 1994). The amount of foliage needed to provide effective supplementation varied with the quality of basal diets, the rate of fermentation of the foliages (Osuji et al. 1995; Umunna et al. 1995; Kiatho, 1997) and the level of animal production expected (Norton, 1994). Although the N content might be a dominating factor providing bypass dietary protein as well as rumendegradable N, it should be recognized that legumes with a high N content are likely to contain less NDF (Table 1), and the total organic matter may be more easily fermented. Thus it is conceivable that the energy available to the rumen micro-organisms is a factor equal in significance to the supply of digestible N.

The potential uses of tree leaves as supplements to ruminants is often limited by the presence of anti-nutritional factors that might affect the availability of nutrients, palatability and feed intake (Reed *et al.* 1990; Reed, 1995; Bonsi *et al.* 1994; Norton, 1994; Kiatho, 1997, Salem *et al.* 1999). However, the effect of anti-nutritional factors depends on the digestive process of the animal (Kumar, 1992). Common anti-nutritional factors which have been implicated in limiting the utilization of shrub and tree forages include non-protein amino acids (mimosine and indospecine), glycosides (cyanogens and saponins) and polyphenolic compounds (tannins and lignins; Kumar, 1992).

Among the polyphenolic compounds, tannins have received most attention in ruminant nutrition. Tannins are divided into hydrolysable tannins and proanthocyanidins

(condensed tannins; CT). Hydrolysable tannins are more susceptible to enzymic and non-enzymic hydrolysis than CT. Hagerman & Robbins (1993) found that hydrolysed tannins did not affect the nutrient digestibility in ruminants. However, the microbial and acid-hydrolysis of hydrolysed tannis in the gut produced metabolites that had antimicrobial activity and toxicity in the liver (Cheeke, 1998).

Much of the nutritional and toxicological effects of tannins depends on the ability of CT to complex proteins (Hagerman & Butler, 1981) and carbohydrate (Reed, 1995). The tannin-protein complexes are stable over the pH range 3.5-7 and dissociate at pH < 3 and > 8.5 (Mangan, 1988). The tannin-protein complex decreases the fermentation (degradability) of forage proteins (Robbins et al. 1987; Bonsi et al. 1994) in the rumen, thereby decreasing rumen NH₃ concentration and increasing the amount of plant bypass protein available for abomasal and intestinal digestion. This phenomenon can sometimes lead to inefficient mammalian enzyme digestion of the protein in the small intestine when the complex fails to dissociate (Reed, 1995). Tannins may therefore have either a beneficial or detrimental effect. The protein in the leaves of and Sesbania Enterolobium cyclocarpum (undetectable and low tannins respectively; Table 1) will be rapidly degraded in the rumen. Whereas Acacia angustissima is very high in tannins (Table 1), sometimes depressing DM intake in sheep to such an extent that many of the animals die (Osuji et al. 1995). Some browsing ruminant animals such as deer have evolved to produce CT-binding proline-rich salivary proteins, while grazing ruminants (sheep and cows) have not (Austin et al. 1989). This means that tree legumes containing CT can potentially be used to manipulate N digestion in sheep and cattle in the tropics (Barry & McNabb, 1999).

Beneficial effects of forage mixing would be expected if the CT content is high and the protein content relatively low in the CT-containing plant, thus releasing some free CT to bind with proteins in the non-CT-containing plant (Barry & McNabb, 1999). The negative effect of A. angustissima (high tannins) might be reversed if it is mixed with Sesbania spp. that have low tannin, low NDF and high crude protein $(N \times 6.25; Table 1)$. This combination would decrease the binding of free tannins from A. angustissima to rumen enzymes, and would increase the efficiency of protein utilization of Sesbania spp. by reducing its rate of fermentation. In this context a new opportunity exists to use the high-tannin-containing plants as supplements along with the appropriate combination of plants which could not be used alone, in order to improve ruminant production in sub-Saharan Africa. However, information on the proportions of hydrolysed tannins and CT, and the existence of other toxic compounds should not be overlooked in the prediction of the nutritional value of protein in tree forages.

Anti-protozoal properties of tropical plants

As noted earlier, N metabolism in the rumen affects both the efficiency of ruminant production and the environmental impact of excreta from ruminant livestock production. Inefficient N retention by rumen micro-organisms is compensated in production terms by feeding excessive

amounts of dietary protein to the animal to meet required output levels. This process leads directly to the excretion of N-rich wastes. Microbial protein turnover in the rumen may result in the net microbial protein outflow being less than half the total protein synthesized (Nolan & Stachiw, 1979). *In vitro* studies suggest that engulfment and digestion of bacteria by protozoa is by far the most important cause of microbial protein turnover in the rumen (Wallace & McPherson, 1987). Thus, it is apparent that removing ciliate protozoa from the rumen (defaunating) should prevent the recycling of N between bacteria and protozoa, and thereby increase the efficiency of N metabolism in the rumen and stimulate the flow of microbial protein from the rumen (Williams & Coleman, 1992).

Defaunation has not been practicable in routine animal production systems due to the absence of a suitable defaunating agent. However, several methods are available for experimental purposes, mostly based on the use of surface-active agents that are toxic to protozoa (Bird et al. 1979; Bird & Leng, 1984; Newbold & Chamberlain, 1988). Unfortunately, none of the methods has been without a negative effect either on the rest of the rumen microbes or on the host itself (Williams & Coleman, 1997). Alternatively, young animals can be isolated within a few hours of birth before protozoa become established (Williams & Dinusson, 1973; Bird & Seccombe, 1998). Defaunation can also be achieved by emptying the rumen, carefully washing the rumen mucosa and treating the digesta by freezing before re-introducing it into the rumen (Jouany & Senaud, 1979), but obviously this is not a practical on-farm approach. A successful defaunation treatment for use in feeding practice would be one that could be applied continuously throughout the desired period and be safe to the rest of rumen microbes and host.

Recently, there has been increased interest in saponincontaining plants as a possible means of suppressing or eliminating protozoa in the rumen. Saponins are glycosides that are generally considered as anti-nutritional factors. Since dietary saponins are poorly absorbed, their biological effects occur in the digestive tract (Cheeke, 1996). The anti-nutritional effects differ depending on the digestive process of the ingesting animal. In ruminants saponins are differentially toxic to rumen protozoa. The differential toxicity may be explained by the presence of cholesterol in eukaryotic membranes but not in prokaryotic cells (Kilta et al. 1996). Saponins are degraded in batch cultures of rumen fluid in vitro (Makkar & Becker, 1997), although apparently the resultant sapogenins are more resistant to degradation (Wang et al. 1998). Sapogenins do not have the anti-protozoal property of the parent saponin (Teferdegne et al. 1998). Metabolites produced by rumen microbial metabolism of steroidal saponins were implicated as a cause of secondary photosensitization in sheep (Miles et al. 1991). However, experimental induction of photosensitization by administration of isolated saponins required larger quantities than could have been obtained from consumption of the plants (Kellerman et al. 1991). Moreover, the sporadic incidence of the condition in a flock grazing on saponin-containing plants suggested that saponins and mycotoxins might have synergistic effects (Miles et al. 1992). Saponin-containing yucca extract appeared to have

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NH₃-binding properties (Headon, 1991). However, the reduction in rumen NH₃ concentrations when *Yucca schidigera* was fed is most probably due to suppression of ciliate protozoa (Wallace *et al.* 1994; Wang *et al.* 1998).

A decrease in protozoal numbers was reported in the rumen of sheep infused with pure saponin (Lu & Jorgensen, 1987) or fed on saponin-containing plants (Navas et al. 1993; Daiz et al. 1994; Thalib et al. 1995; Newbold et al. 1997; Odenyo et al. 1997; Teferedegne et al. 1999). Inclusion of E. cyclocarpum increased the rate of body weight gain by 24 % (Leng et al. 1992) and 44 % (Navas et al. 1993), and wool growth by 27 % (Leng et al. 1992), which was attributed to a decrease in protozoal numbers. Foliage from S. sesban, a multipurpose leguminous tree from sub-Saharan Africa, inhibited protozoal activity in vitro and transiently depressed the number of protozoa in the rumen of sheep in the UK (Newbold et al. 1997; Teferedegne et al. 1999). A feeding trial carried out in Ethiopia failed to find any effect on protozoal numbers in the rumen of sheep fed on S. sesban (Odenyo et al. 1997; Teferedegne et al. 1999). However, when S. sesban was placed directly into the rumen via a rumen cannula, protozoal numbers decreased significantly (Odenyo et al. 1997). This finding suggests that deactivation of the saponins may have occurred before reaching the rumen, probably in the mouth by saliva. Saponins bind with tannins in the gut (Freeland et al. 1985). The nullification of the toxic effects of tannins was dependent on the relative proportions of tannin and saponin (Freeland et al. 1985). Most saponin-containing plants also contained some tannin (Tables 1 and 2). As mentioned earlier, some browsing ruminant animals (deer) have evolved to produce tanninbinding proline-rich proteins in the saliva, although it is believed that grazing ruminants (sheep and cows) have not (Austin et al. 1989). Preliminary experimental results suggested that saponin may be degraded in the saliva of sheep after prolonged feeding of saponin-containing plants (Table 3). It is not known if the loss of anti-protozoal activity in the saliva of sheep fed on S. sesban for a prolonged time is due to the binding of saponin to proteins similar to those that bind tannins, or if cleaving of saponin to sapogenin occurs in saliva. Nevertheless, it might be possible that grazers in Africa may have evolved to produce salivary tannin-binding protein, since they are constantly exposed to tannin-rich feed. If tannins bind with saponins, it is possible that tannin-binding protein could react with saponins as well. This hypothesis remains to be verified. Feeding a combination of saponin-rich feeds could reduce the toxic effect of high-tannin-containing plants. Conversely, the anti-protozoal activity of saponincontaining plants might depend on their tannin content. This factor warrants further investigation. The anti-protozoal action of multipurpose plants should also be viewed in a wider context. Phytolacca dodecandra was toxic to ciliate protozoa; however, locally in Ethiopia it is used as a traditional medicine to remove leeches in cattle. Moreover, the berries of *P. dodecandra*, locally called 'endod' have a long history of use in Ethiopia as a soap substitute. Lemma (1970) showed that a preparation of P. dodecandra possessed molluscicidal properties, killing the intermediate host (snails) for schistosomiasis in human subjects. In a

Table 2. Apparent anti-protozoal properties of some saponincontaining tropical plants measured by their ability to inhibit the breakdown of [14C]leucine-labelled *Selenomonas ruminantium* (10 g/l) in strained rumen fluid *in vitro*

	Percentage inhibition of bacteriolytic activity of rumen	
Species	protozoa	Reference
Yucca schidigera	98	Wallace et al. (1994)
Enterolobium cyclocarpum	91	*
Sesbania sesban	98	Teferedegne et al. (1999)
Samanea saman	85	*
Acacia angustissima	95	*
Phytolacca dodecandra	85	*

^{*} B Teferedegne (unpublished results).

Table 3. The effect of incubating *Sesbania sesban* in saliva from sheep fed on diets with or without *S. sesban* on the subsequent anti-protozoal effect of *S. sesban* as measured by its ability to inhibit the breakdown of [14C]leucine-labelled *Selenomonas ruminantium* (0.25 g/l) in strained rumen fluid *in vitro*

	Rate of bacteriolytic activity of rumen protozoa in strained rumen fluid (% /h)		
Pre-incubation for 24 h of:	Saliva from sheep fed on <i>S. sesban</i>	Saliva from sheep not fed on <i>S. sesban</i>	
Buffer: Without S. sesban	7.5	7.0	
With S. sesban	2.9	2.8	
Saliva: Without S. sesban	7.7	7.6	
With S. sesban	6.8	2.2	

subsequent snail-control investigation with 'endod' Schistosoma mansoni infection rates were significantly reduced in human subjects, which was found to be due to molluscicidal saponins contained in P. dodecandra (Goll et al. 1983). This finding suggests that the anti-microbial action of the plant may be of use outside the rumen. Similarly, the developing interest in spices and plant extracts as manipulators of microbial activity in single-stomached animals (Newman, 1997) suggests that tropical multipurpose plants may have wider effects, and that their effects on other aspects of the inefficient fermentation process in the rumen such as methanogenesis and proteolysis should be investigated.

In conclusion, some tree legumes (Tables 1 and 2) identified as potential nutritive supplements to ruminants also have the potential to be promising, safe, natural defaunating agents. Their use may be particularly beneficial where governments are banning the use of antibiotics or other growth promoters in animal feed for fear of the transmission of organisms with antibiotic resistance to human subjects. Thus, as well as being used locally, tropical plants could have a global market, and would be an additional source of cash income to boost the livelihood of African farmers.

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