CONDENSED TANNINS AND HERBIVORE NUTRITION

G.C. Waghorn[1], J.D. Reed[2] and L.R. Ndlovu[3]

[1]AgResearch Grasslands, Private Bag 11008, Palmerston North, New Zealand
[2]Department of Animal Science, University of Wisconsin, Madison, WI 53706, USA
[3]Department of Agriculture, University of Zimbabwe, P.O. Box 167 Mount Pleasant, Harare, Zimbabwe

ABSTRACT

Condensed tannins (CT) are polyphenolic compounds expressed in a wide range of herbages, especially legumes and browse which affect animal performance in many environments. CT undergo pH dependent associations with protein and fibre fractions of digesta and can reduce protein losses to degradation from the rumen and increase the supply of protein to the intestine. However, they usually have a negative impact upon intestinal function and the overall effect of CT upon animal performance is a balance of rumen and intestinal effects. Several temperate plant species contain CT which are beneficial for ruminants and have resulted in improved milk yield, wool growth and liveweight gain and have prevented pasture bloat and alleviated effects of intestinal nematodes. However, most often the CT reduce intakes and digestibilities, especially in tropical regions where feed choices are limited and quality is often poor. At present there are few opportunities for reducing the detrimental effects of CT in these regions and future progress for improving productivity is dependent on improving our understanding of the chemical structure of CT from various sources and understanding how CT affect rumen and intestinal function. Current strategies for sharing information and facilities between laboratories in temperate regions with centers in less developed countries will benefit herbivore nutrition everywhere.

KEYWORDS

Condensed tannin, proanthocyanidin, herbivore digestion, ruminant.

INTRODUCTION

Herbivores consume a wide range of plant materials—grasses, legumes, browse shrubs, tree leaves and bark, concentrates, seeds and food processing wastes. The diet may comprise one or two predominant plant species (e.g., temperate grazing situations) or be a diverse mix of constituents dependent upon either the formulation offered under intensive production systems (total mixed rations) or availability under opportunistic food gathering (e.g., uncultivated range land). Many dietary components contain substances able to affect digestion and nutritive value of the diet, with condensed tannins (CT) being a common and often detrimental constituent (Mangan, 1988).

The recent resurgence of interest in CT for ruminant diets is due to potential benefits for both nutritive value and animal health. Incorporation of CT-containing forages into temperate pastures will reduce losses of plant protein to rumen microbial proteolysis and may increase amino acid absorption by sheep and cattle grazing protein rich diets. Potential benefits of higher production and improved efficiency of feed utilization have resulted in a number of research programmes designed to understand the ways in which CT affect both rumen function and intestinal absorption. Some studies have shown that the CT from different plant species can have quite different effects on ruminant performance, so that the chemical structures are being defined (Foo et al., 1996) in order to relate structure and dietary concentration of CT with digestive physiology. This knowledge gained from temperate forages will provide much of the basic information needed to minimise anti-nutritional effects of CT in other environments.

Condensed tannins occur primarily in dicotyledonous species; herbaceous plants often have CT in seed coats or hulls (e.g., alfalfa, faba beans, cotton seed) and sometimes in flower petals (white clover; *Trifolium repens*) although none of the above express CT in the foliage. Some temperate herbaceous forages do express CT in their foliage (e.g., *Lotus* species; Jones et al., 1976; Douglas et al., 1993) but CT are more common in forage plants originating from warmer regions (e.g, Sainfoin (*Onobrychus viciifolia* Scop.); Sulla (*Hedysarum coronarium*)) and are widespread in tropical trees, shrubs and herbaceous plants (Kumar & Vaithiyanathan, 1990; Rittner & Reed, 1992; Jackson et al., 1996). Herbivores in tropical and subtropical regions are often unable to avoid plants with CT because of feed shortages and because the forages containing CT are often more palatable than the alternative dry grasses with only 3-5% crude protein (CP) in the dry matter (DM). The CT bind with plant proteins, reducing their availability for microbial growth so that the rate and extent of fibre digestion is also reduced with consequent reductions in voluntary intake, metabolizable energy availability and amino acid (AA) absorption. In contrast, temperate forages contain 15-30% CP in the DM so that CT reduce the degradation of plant protein with minimal effects on microbial growth and the animal may benefit from an improved supply of AA to the intestine.

The CT are usually sequestered in membrane bound vesicles in the plant cell vacuole (Stafford, 1988); they are heterogeneous in nature, comprising oligomers of 3-30 flavan-3-ol (catechin) units and can account for up to about 20% of plant DM. It is important to distinguish between CT and hydrolysable tannin (HT) which rarely occur in forage legumes but are often present in leaves of trees and browse shrubs. Unlike CT, HT are rapidly hydrolyzed in the rumen by “tannases” to form lower molecular weight phenolic compounds such as gallic acid which are further metabolized to compounds such as pyrogallol (Murdiati et al., 1990; 1992) which are potentially toxic to ruminants (Dollahite et al., 1962; Holliman, 1985; Shi, 1988). The chemistry and nutritional effects of CT and HT are quite different but it has been common to use HT (tannic acid) as a model compound in nutritional and analytical studies of naturally occurring CT in herbivore diets. This practice leads to false conclusions and should be discouraged.

The occurrence of CT in forage species appears to have an inverse relationship to agricultural prosperity. Highly productive temperate agriculture does not incorporate a significant number of CT containing species into pasture (despite potential benefits to these systems), whereas subtropical and tropical regions with their predominance of poor quality forages are often further disadvantaged by excessive quantities of CT in many of the plants available to food and draught animals. This situation has necessitated a somewhat separate consideration of CT and animal agriculture for temperate and tropical regions, and although most efforts to elucidate the mechanisms of action are being undertaken in the temperate situation, the results will be of most benefit to those dependent on poor quality forages.

Associated with these challenges is a need to define how much and what type of CT will most benefit the digestive processes; once defined, plant breeders and molecular biologists should accept the challenge to develop alfalfa and white clover cultivars that express the appropriate amount of CT.

ANIMAL SPECIES AFFECTED BY CT

Dietary CT appear to nearly always have a negative impact upon small intestinal function and monogastric species will inevitably be disadvantaged (Waghorn, 1996). Sensitivity to dietary CT varies with species; young chickens appear particularly susceptible (50% mortality from a diet with 1.6% CT in the DM; Ortiz et al. (1994) whereas piglets are less affected (Jansman et al., 1993; Van Leeuwen et al., 1995) and rats are often affected to a very minor degree, in part due to their ability to secrete a proline rich saliva able to bind with and reduce the impact of CT upon digestion (Mole et al., 1990).

Ruminants often consume diets having concentrations of CT that would be injurious to most monogastric species. Their tolerance may be due in part to the microbial ecosystem responsible for fibre degradation and which appears to modify the CT polymer before it reaches the intestine. This hypothesis is not proven, but poor recoveries of CT from or added to abomasal and intestinal digesta (Terrill et al., 1994; Neuman et al., 1996) despite an absence of absorption of carbon from the molecule (Jiminez-Ramsay et al., 1993; Terrill et al., 1994) does suggest some structural changes. Ruminants may benefit from some forms of CT when concentrations are below about 10% of the DM because of reduced microbial proteolysis and a subsequent increase in amino acid supply to the intestine. However, CT nearly always reduce the fractional absorption of AA.

The anatomical arrangement of the gastro-intestinal tract in herbivores may have an important bearing on the effects of CT upon digestive function. For example, hind gut fermenters (e.g., equine) may be adversely affected because the CT will not be modified (other than by salivary protein binding) prior to the small intestine (Lowry, 1990). Unfortunately, we are not aware of any studies comparing effects of CT upon the digestive physiology of forestomach and hindgut fermenters.

The most detailed investigations of CT effects upon digestive physiology have been undertaken with sheep, initially with sainfoin diets (Harrison et al., 1973; Egan and Ulyatt, 1980; Beever and Siddons, 1985) and more recently with *Lotus pedunculatus* (Barry and Duncan, 1984; Barry and Manley, 1984; Barry et al., 1986; Waghorn et al., 1994 a, b; Waghorn and Shelton, 1995) and *Lotus corniculatus* (Waghorn et al., 1987a,b; McNabb et al., 1993; Wang et al., 1994, 1996 a, b, c). These studies have emphasised the importance of the type of CT (Waghorn and Shelton, 1995) as well as effect of concentration *per se* (Barry et al., 1986), and have led to investigations of potentially important anthelmintic effects attributable to CT from some forage species (e.g., sulla; Niezen et al., 1995; Robertson et al., 1995). A small amount of work has been undertaken with goats, but usually in relation to food preferences (Clausen et al., 1990; Holechek et al., 1990; Provenza et al., 1994) and more recently to microbial adaptation when diets containing CT have been consumed by goats (Brooker et al., 1994; Miller et al., 1995). Work with cattle has been minimal, involving either feeding trials to evaluate nutritive value of *Lotus corniculatus* (Marten et al., 1987) or examination of salivary proteins in relation to bloat when diets with CT are fed (Mangan et al., 1976).

Herbivores living in hot, often arid, environments have been used in trials for determining forage species having good or acceptable feeding value and to identify tree crops suitable for fodder in times of scarcity (e.g., Ademosun et al., 1988; Devendra, 1990). Much of this work has involved sheep and goats although cattle have been used to evaluate a commercial PEG based product (Browse Plus®) available in Zimbabwe. Feral herbivores in Africa and Latin America consume diets with varying and sometimes high concentrations of CT, often from necessity. Although browsers have larger salivary glands relative to grazing herbivores (Hofmann, 1973) which may provide some protection against dietary CT, Cooper and Owen-Smith (1985) have reported a general aversion of browsers to plants containing high concentrations of CT, and Van Hoven (1984) reported mortality in kudu due to the high tannin content of leaves that they were forced to eat during a period of feed scarcity. However, CT may not be solely responsible for these problems as many browse species contain a range of toxic substances, e.g. high concentrations of phenolic compounds (including hydrolysable tannins) in *Acacia* spp. and the toxic nature of mimosine in *Leucaena* spp. is better documented than its CT content (Lowry, 1990; Reed, 1997).

IMPACT OF DIETARY CT ON LIVESTOCK PERFORMANCE AND HEALTH

The data in Table 1 emphasises the dichotomy in production responses to dietary CT. Responses range from significant improvements in performance due to CT in *Lotus corniculatus* through the variable responses with *Lotus pedunculatus* and sulla and substantial reductions in performance with weight losses that could result in death without intervention when some *Acacia* species are fed as a sole diet. Intervention might involve administration of polyethylene glycol (PEG), usually as a drench or in the drinking water, which preferentially binds with and removes the effects of CT (Jones & Mangan, 1977). PEG can be used in experimental situations (e.g., Waghorn, 1987 b) or in production systems (Pritchard et al., 1992) but cost usually prevents widespread effective usage. In an experimental situation PEG can be given to one treatment group to bind with and remove the effects of CT, whilst other dietary components are unaffected.

The data in Table 1 show that dietary CT concentration can be a major determinant of production responses but the relationship is not linear; some forages with moderate concentrations of CT (e.g., sainfoin with about 7% CT in the DM (McNabb et al., 1997)) can be beneficial to sheep, whereas other species with lower dietary concentrations (e.g., *Lotus pedunculatus* or *Gliricidia* with pasture) may have only small benefits for production (Waghorn & Shelton, 1995; Weigand et al., 1995). Relationships between CT concentration and production are complicated by variations attributable to analytical technique and the poor productive performance by herbivores given tropical forages and browse may be due in part to other components having anti-nutritional properties (Reed, 1997). The low voluntary intakes evident with several temperate forages containing CT (e.g., Barry & Duncan, 1984, Waghorn et al., 1994 b) are due to effects upon rumen and possibly intestinal function (Tables 2 and 3) rather than palatability. The CT appears to reduce the rate of rumen fermentation with consequent increases in rumen fill (Waghorn et al., 1994 b) and in more severe situations the extent of fibre and nitrogen digestion is reduced (Barry & Manley, 1984, Wiegand et al., 1995). These effects are reversed by addition of adequate PEG to the diet. Sheep and cattle often select leaves in preference to stems despite a 3-4 fold higher concentration of CT in leaves, and they will select temperate herbages containing CT in preference to that without CT (Waghorn & Jones, 1989; Waghorn et al., 1994 a). Aversion to some tropical forages and browse shrubs containing CT is more common (e.g., Van Hoven, 1984) but this may be due to both the CT and other anti-nutritional components (Reed, 1997).

Examples of animal health problems prevented or alleviated by CT include the prevention of bloat (Jones et al., 1973), and reductions in the impact of both intestinal nematodes and the incidence of flystrike in sheep. Bloat can be a major herd health problem when high quality forages are fed to cattle because ruminal gasses become entrapped in a protein stabilised foam preventing eructation and leading ultimately to death by hypoxia. CT reduce the concentration of soluble protein in the rumen (Jones & Lyttleton, 1971; Waghorn & Jones, 1989) which prevents the formation of stable foam.

Reductions in the impact of gastro-intestinal nematodes with forages containing CT has been demonstrated by Niezen et al. (1995) who fed parasitised lambs either alfalfa (*Medicago sativa* L.) or sulla and reported daily live weight gains of -29 g and 120 g respectively. At slaughter parasite numbers in sheep fed sulla were half those in the sheep fed alfalfa. Possible mechanisms for reducing nematode numbers include an improved protein nutrition because less forage protein is degraded in the rumen, direct effects of CT upon resident worms or an increased mucous production reducing the ability of the nematodes to persist in the abomasum and intestine, or a combination of the above. However, some sources of CT do not affect nematodes (Robertson et al., 1995) so current work is focusing on both the type of CT affecting nematodes as well as mechanisms of action.

When sheep are fed lush forages, especially in the presence of a larval challenge the faeces become loose and adhere to the wool (dags), which in turn attracts flies leading to flystrike. Recent work has shown that *Lotus corniculatus* diets are able to substantially reduce the extent of dag formation and incidence of flystrike (Leathwick and Atkinson, 1995).

We are not aware of other studies relating effects of CT to faeces composition and flystrike, but benefits in prevention of bloat and reductions in both the impact of worms and flies offer considerable incentive for further study. This is especially important because resistance to anthelmintic drenches is affecting livestock industries in some regions and consumer intolerance of chemical residues (used in fly prevention) in both edible products and in wool products requires alternative methods of control.

An added environmental benefit of dietary CT is that dietary N is partitioned towards faeces and away from urine (due to a lesser proteolysis in the rumen, with consequent reductions in ammonia production). Faecal N is incorporated into the soil structure which can benefit regions with poor fertility, and reductions in urinary N will reduce both losses to aerosols and the contamination of ground water in temperate agricultural regions.

PLANT TANNIN CHEMISTRY

Condensed tannins are synonymous with proanthocyanadins. They are polymeric flavonoids (Porter, 1994) based on repeating flavan-3-ol and related flavan units linked by interflavan carbon bonds. No enzymes are known to cleave the interflavan bond but CT do undergo an autoxidation reaction under heat and strong acid to yield monomeric anthocyanidins, flavan-3-ol end groups and more complex products (phlobaphenes). This autoxidation reaction is the basis for the proanthocyanidin nomenclature for CT and has led to the development of several analytical methods (Bate-Smith, 1975; Porter, 1994).

A review of analytical methods for CT is beyond the scope of this paper. However, researchers should be aware that there are many problems associated with all of the commonly used methods. These include: poor extraction, lack of appropriate standards, differences in reactivity among standards and the CT from different plant species, and lack of correspondence between the chemistry of the analytical method and the biochemistry of their nutritional effects. CT also exist in complex mixtures with monomeric flavonoids and other phenolic compounds in plants. These compounds may not affect protein digestion but they can have profound effects on animal metabolism (such as the isoflavonoids in subterranium clover). Therefore, the relationship of CT to other phenolic compounds and secondary plant compounds is important when attempting to relate a nutritional effect of CT to herbivore ecology (Reed, 1997).

The extraction and solubility of CT have a large effect on analytical results. In most plants CT are sequestered in the vacuole in membrane bound vesicles which are destroyed during sampling and extraction, allowing the CT to form insoluble complexes with proteins and cell wall carbohydrates. Both bound CT and CT with high molecular weights are insoluble (Stafford & Cheng, 1980) so that they contribute towards elevated analytical determinations of neutral detergent fiber, lignin and the detergent insoluble nitrogen fractions of diets and faeces of herbivores even though they were not part of the original plant cell wall structure (Reed, 1995). Additional problems can arise when the forage selected by the animal differs from the material sampled for analytical determinations of CT content; this affects analyses of both temperate forages where leaves are often eaten and stems avoided, as well as material consumed by browsers.

Different analytical techniques used to determine concentrations of CT make comparisons between data sets difficult, but a crude generalization with temperate forages is that the acidified vanillin assay gives values about 60% of that for the butanol-HCl extraction of CT (Terrill et al., 1992).

CONDENSED TANNINS AND RUMEN FUNCTION

Chewing ruptures plant cells and releases the CT, enabling an association with proteins and fibre. The reaction is rapid, with much of the plant protein precipitated by the time it enters the rumen (Mangan et al., 1976); however, the association between plant proteins and CT can be reversed by addition of PEG, at least in the short term; (30-60 minutes; W.T. Jones *pers. comm.*). The net effects of dietary CT upon rumen function are well defined for sheep eating *Lotus* spp., sainfoin and to a lesser extent sulla. Table 2 summarises these effects, most notably the reduction in plant protein degradation with 30-70% lower concentrations of ammonia in rumen liquor, and less rumen digestion of N, which results in an increased flow of dietary N to the intestines. The CT in *Lotus corniculatus* and *Lotus pedunculatus* usually have minor effects on digestion of other dietary constituents. Molar ratios of the principal volatile fatty acids (VFA) are not changed appreciably, but their concentrations in rumen liquor are often reduced. This is probably a consequence of a larger rumen pool size and a slower rate of VFA production due to a lower rate of fibre digestion (Waghorn et al., 1994 a). When dietary CT is less than about 8% of dietary DM, structural fibre digestibility is similar to that of a CT-free forage (albeit slower). Reductions in microbial N outflow from the rumen have not been significant (Beever and Siddons, 1985; Waghorn et al., 1987 a; 1994 b) so that the CT does increase total protein supply to the intestine.

Forages with high concentrations of CT (over 10% of DM) are often associated with both low palatability, low intakes and poor performance (Tables 1 and 2). Low intakes can be a consequence of palatability (e.g., Holechek et al., 1990; Cooper and Owen-Smith, 1985) but they can also be a consequence of CT impaired rumen function (sometimes resulting in high rumen fills) or inappetance due to inadequate nitrogen nutrition. For example, supplementing sheep fed mulga (*Accacia aneurea*) with PEG increased voluntary intakes by 75% (Pritchard et al., 1992), suggesting impaired rumen function rather than palatability caused the low voluntary intakes. However tropical browse often contain several phenolic compounds as well as toxic substances (Reed, 1995) so it is difficult to ascribe low intakes (e.g., Reed et al., 1990; Wiegand et al., 1995) specifically to the CT content. Unfortunately the limited information from trials where tropical forages have been fed as a supplement, or occasionally as a sole diet, is confined largely to performance, intake, digestibility and sometimes indications of endogenous N losses (Reed et al., 1990; Woodward and Reed, 1995) and information concerning rumen function is not available.

The mechanisms by which CT affect rumen function are poorly understood. For example, it is well known that CT can precipitate proteins, but we do not know if precipitation has any effect on *in vivo* proteolysis. Recent work has shown that CT can have direct effects on some rumen bacteria (Jones et al., 1994), and McAllister et al. (1994) have shown that CT from *Lotus corniculatus* can cause a significant detachment of *Fibrobacter succinogenes* from fibrous substrates. This work does represent an important first step towards resolving the mechanisms by which CT affect rumen function, but it is also important to relate *in vitro* findings to the *in vivo* situation. For example, when sheep are fed *Lotus corniculatus* the CT does not reduce digestibility of structural fibre (Waghorn et al., 1987 b; Wang et al., 1994).

CONDENSED TANNINS AND INTESTINAL FUNCTION

Effects of CT upon intestinal function have been determined in several monogastric species and in sheep, but we are unaware of studies in other herbivorous animals. Most measurements in sheep have been directed towards N disappearance from the small intestine (Barry et al., 1986), AA absorption (Waghorn et al., 1987, 1994 b, McNabb et al., 1993) and recent work has determined effects of CT on the site of sulfur amino acid (SAA) absorption (Wang et al., 1996 c). Some measurements have compared absorption in sheep fed sainfoin with CT-free legumes (Harrison et al., 1973, Egan and Ulyatt, 1980, Beever and Siddons, 1985) but we are unaware of similar work involving CT from other forages. Very little effort has been directed towards understanding the physiology of the interaction between CT and intestinal function in herbivorous animals, but considerable efforts have been directed toward understanding anti-nutritional effects in monogastric species. This includes effects of CT in sorghum (*Sorghum vulgare*) grain for chickens (Mitaru et al., 1985) and pigs (Mitaru et al., 1984) and faba beans (*Vicia faba*) for chickens (Longstaff and McNab, 1991 a, b; Yuste et al., 1992) and pigs (Jansman et al., 1993). Studies with rats have provided additional insight into both enzymic (Blytt et al., 1988; Horigome et al., 1988) and histological (Ortiz et al., 1994; Vallet et al., 1994) effects of CT on small intestine function.

In vitro binding studies with sainfoin CT and fraction 1 plant protein (Jones and Mangan, 1977) have formed the basis of a supposed release of plant proteins in the acidic abomasum enabling a subsequent enzymic hydrolysis and absorption of AA and peptides in the small intestine. However data in Table 4 show that the fractional absorption of some AA are significantly reduced by some sources of CT in sheep, and the effects can be more pronounced in chickens and pigs. Inhibition of absorption is probably a consequence of two main factors: 1) lack of separation between CT and digesta proteins; 2) Effects of CT upon the intestinal mucosa resulting in impaired or delayed absorption (Table 3; Waghorn, 1996).

Evidence for a lack of separation by CT from digesta proteins is indirect, but includes the poor recoveries of CT added to abomasal (51%), duodenal (74%) and ileal (43%) digesta of sheep (Terrill et al., 1994) and reduced rates of proteolysis when CT is bound to substrate proteins (Oh and Hoff, 1986). Furthermore, the pH rises rapidly in the intestine (to 5.5 within 1.5 m of the pylorus in forage fed sheep; (Terrill et al., 1994; Wang et al., 1996 a)) so that CT will either remain bound to digesta constituents or will re-bind to digesta and endogenous proteins for nearly the entire length of the intestine. Evidence for binding between CT and digesta proteins is further supported by a shift in the site of methionine and cysteine absorption to more distal regions of the small intestine in sheep fed *Lotus corniculatus* (Wang et al., 1996 c).

Condensed tannins stimulate mucous secretions in monogastric animals (Ortiz et al., 1994; Vallet et al., 1994) probably as a means to protect the intestinal brush border (microvilli) which contains enzymes responsible for nutrient absorption. Of particular importance to herbivores are the aminopeptidases which cleave oligopeptides and facilitate transport of the peptides and AA to the enterocyte for absorption. Diets containing CT have reduced aminopeptidase activity in piglets (Van Leeuwen et al., 1995), probably because excess mucous will reduce the accessibility of oligopeptides to the enzyme. The increased secretions will also contribute to an increased endogenous loss of protein (Vallet et al., 1994) and reduce apparent digestibility of AA (Tables 3 and 4).

Hence we hypothesise that low concentrations of CT in herbivore diets will stimulate mucous production and reduce the capacity for AA absorption because of reduced accessibility to aminopeptidases. Higher concentrations of CT will lead to an erosion of the protective mucous layer and the resultant lesions will severely inhibit capacity for absorption (Table 3). Although we do not have proof of this scenario in herbivores, the shift in the site of S-AA absorption in response to the low (and usually beneficial) CT in sheep fed *Lotus corniculatus* (Wang et al., 1996 c) supports the hypothesis. This shift occurred when CT comprised only 4% of dietary DM, so it is easy to envisage substantial damage to the intestine of herbivores consuming feeds with 10 - 20 % CT in the DM, with consequent reductions in nutrient absorption and death as an inevitable outcome.

It is sometimes suggested that detrimental effects of CT upon AA absorption are a result of inhibited pancreatic enzyme activity. However a recent comparison of trypsin, chymotrypsin and pepsin activity in the digesta of sheep grazing either forages with CT (*Lotus* spp. and sulla) and those without CT revealed similar activities with all diets (Waghorn et al. unpublished data). We suggest that the activity of these enzymes exceeds requirements for normal digestion and that compensatory secretion is a possible route for overcoming any inhibition of activity. It is interesting to note that African browsers had substantially more glandular tissue in the small intestine and a greater abomasal secretion of acid than grazing herbivores (Hoffman, 1984). These differences may be a response to dietary composition or may have evolved as a mechanism for overcoming effects of CT and other phenolic compounds in the diet of browsing herbivores.

If herbivores are to benefit from CT, then the improvement in protein supply to the intestine (as a consequence of reduced ruminal losses) must exceed the increased endogenous losses from the intestine and the reduced fractional absorption of AA. Further, the largely indigestible CT represent a loss of potentially available metabolisable energy in the diet, and these losses must be overcome by increased intakes or improved nutritive value (perhaps an optimal mix of nutrients). It is surprising that any forages containing CT are able to benefit the herbivore nutrition.

STRATEGIES FOR MANIPULATING DIETARY CT

Strategies for incorporating or reducing the impact of excess CT in herbivore diets must be cost effective. Regions having profitable agriculture, yielding financial surpluses have more options available than regions where agricultural revenues are affected by political instability or poorly regulated transport and merchant industries. Extensive agriculture is often unable to support significant financial input and weather can have a dominant role in defining feeding strategies in many environments.

One strategy which is applicable to arable farming involves plant selection and sowing improved species. In southeastern United States a successful selection was carried out with *Lespedeza Cuneata* (Serecia lespedezia) to obtain a cultivar having lower CT concentrations (Donnelly & Anthony, 1970) and this has benefited ruminant performance (Windham, 1990). In temperate regions extensive screening programmes have been undertaken to identify white clover and alfalfa plants expressing CT in their foliage, but without success, so that current programmes are based on forages which do express beneficial CT in the foliage; one objective is to identify *Lotus corniculatus* plants able to persist in improved high fertility pastures (W. Rumball, *personal communication*).

Much of the research to define mechanisms of action of CT from temperate forages has resulted from field trials which have defined production responses attributable to CT. Some trials have fed CT-forages as a sole diet (Douglas et al., 1995; Terrill et al., 1992) or in combination with CT-free forages (Cosgrove et al., 1996; Wang et al., 1996 b; Waghorn and Shelton, 1995, 1997). These trials, in combination with indoor metabolic studies have identified the importance of both the concentration and chemical structure of CT in relation to rumen and intestinal function and will enable genetic engineers to make informed decisions when attempting to express CT in alfalfa using molecular biology techniques (Larkin, 1997). Levels of expression could be lower in forages fed as a sole diet compared to forages comprising only 15-20% of material eaten (for example, white clover in pasture).

Strategies for reducing CT concentrations in sub-tropical and tropical situations are more complicated because grazing systems are often extensive and costs must be kept low. Detrimental effects of CT on palatability can be reduced by cutting and wilting prior to feeding (Devendra, 1990; Lowry, 1990) and drying can reduce the negative effects of CT upon digestion (Terrill et al., 1989). In regions where cultivation is difficult or impossible, forages and tree fodders containing CT (e.g., Panda et al., 1989; Reed et al., 1990; Gupta & Balaraman, 1992; Woodward & Reed, 1995; Jackson et al., 1996) are often fed as protein supplements with poor quality grasses and crop residues (Weigand et al., 1995; Table 1) and thus enable the CT to be diluted in the diet (Sidahmed et al., 1981; Reynolds & Adediran, 1988; Devendra, 1990). Feeding trials have defined some performance responses to various types and amounts of fodder supplements given to sheep and goats (Ademosum et al., 1988; Reynolds & Adediran, 1988; Devendra, 1990; Woodward & Reed, 1995) and buffalo (Gupta et al., 1988) fed poor quality diets (Table 1). However the supplements often contain anti-nutritional compounds additional to CT (e.g., mimosine in *Leucaena leucocephala*); Lowry, 1990; Reed, 1997) so the level of supplementation and appropriate accession must be defined with care (Reed et al., 1990; Wiegand et al., 1995) and responses cannot be attributed to CT *per se*. An appropriate accession (e.g., 15019 of *Sesbania sesban*; Wiegand et al., 1995) can have benefits by reducing N loss from the rumen when poor quality diets are fed, but the proanthocyanadins in other accessions (and in some temperate forages (e.g., *Lotus pedunculatus*; Waghorn and Shelton, 1995)) can reduce N availability to the rumen microflora and to the animal.

One strategy applied to diets having a high CT content under extensive grazing has been the addition of PEG. This can be added to water supplies, and Pritchard et al. (1992) showed that supplementation with 12 and 24 g PEG/day increased intakes of mulga by sheep (about 14% CT in the DM) by 56 and 78% respectively. This level of supplementation is unlikely to be economically viable, but an alternative PEG based commercial product available in Zimbabwe (Browse Plus®), and given in doses of 1-3 g/day to cattle eating both browse and grass forage give variable and usually non significant responses in terms of liveweight gain (Table 5). Observations by Dube et al. (1993) and Smith et al. (1995) suggest that treated steers spent more time browsing than controls, without significant effects on LWG. A positive response in LWG was reported in Bos taurus steers by Duncan, 1994 (Table 5) but it is difficult to see how a small amount of PEG and polyvinyl pyrrolidane (PVP) in 3 g Browse Plus® could affect digestion. If steers consume 5 kg DM/day with only 2% CT in the DM, then 3 g PEG and PVP would be required to bind with and precipitate up to 100 g CT. Ratios of PEG:CT necessary for precipitation and removing effects of dietary CT are about 1:1, but dose-response trials to determine effects of increments of PEG on performance under grazing have not been undertaken.

A more speculative opportunity to reduce the impact of CT includes ruminal inoculation with CT resistant (or tolerant) micro-organisms. Miller et al. (1995) reported significant improvements in intake and digestibility in sheep given mulga after inoculation with rumen liquor from goats accustomed to this diet. This strategy may reduce the impact of dietary CT but benefits akin to the mimosine degrading bacteria used to inoculate Australian ruminants fed lucaena (*Leucaena leucocephala*; Jones and Megarrity, 1986) are unlikely because the interflavan bond linking catechin units of CT cannot be cleaved enzymatically.

We have speculated on methods for reducing the impact of high dietary CT concentrations on herbivore production, but our strategies for manipulating CT concentrations in forages might be improved if we understood how CT benefited the plant. There is no easy answer, but the often quoted “defence against herbivory” does not appear appropriate given the large number of insects and animals which consume these plants. Other possibilities include protection from disease, healing after physical damage, regulation of seed consumption and effects upon N and carbon cycles linking the plant and the soil (Reed, 1997).

RESEARCH FOCUS - PRESENT AND FUTURE

We have emphasized differences between temperate and tropical regions with regard to CT and herbivore nutrition because of the different focus in each environment. However funding for research and hi-tech laboratory facilities are located primarily in the temperate countries of Europe, North America, Australasia and in the Republic of South Africa. Fortunately several programs have evolved to facilitate the transfer of skills and personnel between Europe and North America with Africa, Central and South America. The criteria for funding differs between countries; however proposals which link disciplines, institutes, or form a comprehensive “molecule to product” package tend to be successful. Our program at AgResearch in New Zealand involves an integration of organic chemistry (defining CT structure in plants and changes during digestion), metabolic studies of rumen and intestinal physiology and field trials to demonstrate real effects of CT upon animal performance. This work is shared between two institutes and a university and is becoming increasingly international in scope. At the University of Wisconsin-Madison a McKnight Foundation Collaborative Crops Research Program grant has enabled collaborative research with the University of Zimbabwe and the Zimbabwean Department of Research and Specialist Services on a project entitled "The ecological biochemistry of proanthocyanidins and related flavonoids in Zimbabwean small scale farming systems." The objectives of this project are to determine the role of CT in the use of sorghum, groundnuts and multipurpose trees in mixed crop livestock farming systems and to learn how to manipulate the types and content of CT in these plants to maximize their beneficial effects and minimize their detrimental effects.

These programs enable the knowledge and techniques gained in CT chemistry, ruminant physiology and animal management to be applied to subtropical and tropical forages and farming systems. This interchange benefits both regions; tropical forages are obtained and the chemical and biological activities of the CT are evaluated, often by students who return to their home countries with new skills and knowledge. This knowledge can be used to minimise detrimental effects of CT upon nutrition and identify some sources of CT which may benefit temperate agriculture if they protect against rumen proteolysis with minimal impact on intestinal function. Some may have improved anthelmintic capacity.

Future research objectives relating dietary CT to herbivore nutrition are difficult to predict, because current work is posing more questions than answers. The scope of the problem is indicated by some current research topics which include: defining the chemical structure of CT, reactivity with proteins and enzymes *in vitro,* evaluation of optimal concentrations and types of CT for ruminants, nutrition surveys of grasses, herbaceous plants, trees, browse shrubs and seed coats to determine CT concentration and reactivity. Work is proceeding which will define some of the ways in which CT affect protein degradation *in vivo*, effects upon bacterial activity and colonization of substrates and upon the physiology of intestinal function during digestion. Field trials are used to evaluate supposedly beneficial as well as detrimental sources of CT in terms of animal performance and some work is being carried out with a view to using CT as a bloat preventative and to reduce the impact of intestinal nematodes and flies. We believe additional efforts are required to define effects of CT upon AA absorption from the intestine, to define structural changes in CT during digestion and to further investigate the tolerance of CT by some strains of bacteria reported by Miller et al. (1995).

Undoubtedly CT of some sort will be expressed in alfalfa and perhaps white clover foliage in future but no single type or concentration will meet the diverse needs of ruminants in temperate agriculture. However success in genetic engineering seems always to be just around the corner; and there is little communication between molecular biologists and ruminant nutritionists. In contrast, selection for variations in CT content and other agronomic characteristics using more conventional plant breeding techniques are producing new and useful cultivars within a 3-5 year time frame. Irrespective of the route taken, our goal should be to identify and express optimal concentrations of CT in diets for herbivores, whether by diet formulation, expression in high quality diets by genetic manipulation, or selection through conventional plant breeding. Deleterious effects may be reduced through appropriate microbial inoculations, but dietary supplements intended to reduce the impact of excessive CT are unlikely to be cost effective. Success in all environments will be dependent upon a substantial research effort needed to understand the mechanisms by which CT affect all aspects of digestion.

REFERENCES

Ademosun, A.A., H.G. Bosman and H.J. Jansen. 1988. Nutritional studies with West african dwarf goats in the humid tropics. Pages 83-91 *in* O.B. Smith and H.G. Bosman, eds. Goat production in the humid tropics. Purdoc. Wageningen.

Ash, A.J. 1990. The effect of supplementation with leaves from the leguminous trees *Sesbania grandiflora, Albizia chinensis* and *Gliricidia sepium* on the intake and digestibility of guinea grass hay by goats. Anim. Feed Sci. Tech. **28**:225-232.

Barry, T.N. and S.J. Duncan. 1984. The role of condensed tannins in the nutritional value of *Lotus pedunculatus* for sheep. 1. Voluntary intake. Br. J. Nutr. **51**:484-491.

Barry, T.N. and T.R. Manley. 1984. The role of condensed tannins in the nutritional value of *Lotus pedunculatus* for sheep. 2. Quantitative digestion of carbohydrates and proteins. Br. J. Nutr. **51**:493-504.

Barry, T.N., T.R. Manley and S.J. Duncan. 1986. The role of condensed tannins in the nutritional value of *Lotus pedunculatus* for sheep. 4. Sites of carbohydrate and protein digestion as influenced by dietary reactive tannin concentration. Br. J. Nutr. **55**:123-127.

Bate-Smith, E.C. 1975. Phytochemistry of proanthocyanidins. Phytochem. **14**:1107-1113.

Beever, D.E. and R.C. Siddons. 1985. Pages 479-497 *in* L.P. Milligan, W.L. Grovum and A. Dobson, eds. Control of Digestion and Metabolism in Ruminants. Prentice-Hall. Engelwood Cliffs, NJ.

Blytt, H.J., T.K. Guscar and L.G. Butler. 1988. Antinutritional effects and ecological significance of dietary condensed tannins may not be due to binding and inhibiting digestive enzymes. J. Chem. Ecol. **14**:1455-1465.

Brooker, J.D., L.A. O'Donovan, L. Skene, K. Clarke, L. Blackall and P. Muslera. 1994. *Streptococcus caprinus* sp. Nov, a tannin-resistant ruminal bacterium from feral goats. Letters in Applied Microbiology **18**:313-318.

Clausen, T.P., F.D. Provenza, E.A. Burritt, P.B. Reichardt and J.P. Bryant. 1990. Ecological implications of condensed tannin structure: a case study. J. Chem. Ecol. **16**:2381-2392.

Cooper, S.M. and N. Owen-Smith. 1985. Condensed tannins deter feeding by browsing ruminants in South African savanna. Oecologia **67**:142-146.

Cosgrove, G.P., P.D. Muir and M.G. Lambert. 1996. Nutritional options and implications for maximum growth rate of steers. Proc. NZ Grassland Assoc. **57**:217-222.

Degen, A.A., K. Becker, H.P.S. Makkar and N. Borowy. 1995. *Acacia saligna* as a fodder tree for desert livestock and the interaction of its tannins with fibre fractions. J. Sci. Food Agric. **68**:65-71.

Devendra, C. 1990. The use of shrubs and tree fodders by ruminants. Pages 42-60 *in* C. Devendra, ed. Shrubs and tree fodders for farm animals. International Development Research Centre, Ottawa.

Dollahite, J.W., R.F. Pigeon and B.J. Camp. 1962. The toxicity of gallic acid, pyrogallol, tannic acid and Quercus havardi in the rabbit. Am. J. Vet. Res. **23**: 1264-1267.

Donnelly, E.D. and W.B. Anthony. 1970. Effect of genotype and tannin on dry matter digestibility in *Sericea lespedeza*. Crop Sci. **10**:200-202.

Douglas, G.B., P. Donkers, A.G. Foote and T.N. Barry. 1993. Determination of extractable and bound condensed tannins in forage species. Proc. 17th Int. Grass Cong. Palmerston North, New Zealand. Pp. 204-206.

Douglas, G.B., Y. Wang, G.C. Waghorn, T.N. Barry, R.W. Purchas, A.G. Foote and G.F. Wilson. 1995. Liveweight gain and wool production of sheep grazing *Lotus corniculatus* and lucerne (*Medicago sativa*). NZ J. Agric. Res. **38**:95-104.

Dube, J.S., L. Hove, S. Ncube and T. Smith. 1993. Use of polyethylene glycol (PEG) or "Browse Plus" as stimulants to browsing by ruminants in the dry season. Journal of the Zimbabwe Society for Animal Production **5**:43-47.

Duncan, I.M. 1994. A review of the development and use of polyethylene glycol and "Browse Plus" as digestive modifiers in domestic livestock and their application during the Zimbabwe dry season. Journal of the Zimbabwe Society for Animal Production **6**: 31-36.

Egan, A.R. and M.J. Ulyatt. 1980. Quantitative digestion of fresh herbage by sheep. VI. Utilization of nitrogen in five herbages. J. Agric. Sci. Camb. **94**:47-56.

Foo, L.Y., R. Newman, G. Waghorn, W.C. McNabb and M.J. Ulyatt. 1996. Proanthocyanidins from *Lotus corniculatus*. Phytochem. **41**:617-624.

Gupta, B.K. and N. Balaraman. 1992. Tannins in relation to nutrient status of top feeds of eastern himalayan region. Indian J. Anim. Nutr. **9**:55-58.

Gupta, B.K. and A. Singh. 1989. Effect of feeding dried subabul as a replacement of concentrate mixture in buffalo calves. Indisn J. Anim. Sci. **59**: 590-596.

Gupta, B.K., R.P. Gupta and N.S. Malik. 1988. Effect of replacement of green lucerne with subabal (*Leucaena leucocephala*) leaf meal in the diet on nutrient utilization and growth in buffalo calves. Indian J. Anim. Nutr. **5**:202-206.

Harrison, D.G., D.E. Beever, D.J. Thomson and D.F. Osbourn. 1973. The influence of diet upon the quantity and types of amino acids entering and leaving the small intestine of sheep. J.Agric. Sci. Camb. **81**:391-401.

Hofmann, R.R. 1973. The ruminant stomach. East African Literature Bureau. Nairobi, Kenya.

Hofmann, R.R. 1984. Comparative anatomical studies imply adaptive variations of ruminant digestive physiology. Can. J. Anim. Sci. **64**(Suppl.):203-205.

Holechek, J.L., A.V. Munshikpu, L. Saiwana, G. Nunez-Hernandez, R. Valdez, J.D. Wallace and M. Cardenas. 1990. Influence of six shrub diets varying in phenol content on intake and nitrogen retention by goats. Tropic. Grasslands **24**:93-98.

Holliman, A. 1985. Acorn poisoning in ruminants. Vet. Rec. **116**: 546.

Horigome, T., R. Kumar and K. Okamoto. 1988. Effects of condensed tannins prepared from leaves of fodder plants on digestive enzymes *in vitro* and in the intestine of rats. Br. J. Nutr. **60**:275-285.

Ingalls, J.R., J.W. Thomas, E.J. Benne and M. Tesar. 1965. Comparative response of wether lambs to several cuttings of alfalfa, birdsfoot trefoil, brome grass and reed canary grass. J. Anim. Sci. **24**: 1159-1164.

Jackson, F.S., T.N. Barry, C. Lascano and B. Palmer. 1996. The extractable and bound condensed tannin content of leaves from tropical tree, shrub and forage legumes. J. Sci. Food Agric. **71**:103-110.

Jansman, A.J.M., M.W.A. Verstegen and J. Huisman. 1993. Effects of dietary inclusion of hulls of faba beans (*Vicia faba* L.) with a low and high content of condensed tannins on digestion and some physiological parameters in piglets. Anim. Feed Sci. Tech. **43**:239-257.

Jiminez-Ramsey, L.M., J.C. Rogler, T.L. Housleg, L.G. Butler and R.G. Elkin. 1994. Absorption and distribution of ^{14}C-labeled condensed tannins and related sorghum phenolics in chickens. J. Agric. Food Chem. **42**:963-967.

John, A. and J.A. Lancashire. 1981. Aspects of the feeding and nutritive value of *lotus* species. Proc. NZ Grasslands Assoc. **42**: 152-159.

Jones, R.A. and R.A. Bray. 1983. Agronomic research in the development of leucaena as a pasture legume in Australia. Pages 41-48 *in* Leucaena research in the asian-pacific region. International Development Research Centre, Ottawa.

Jones, W.T. and J.W. Lyttleton. 1971. Bloat in cattle (XXXIV). A survey of legume forages that do and do not produce bloat. NZ J. Agric. Res. **14**:101-107.

Jones, R.J. and R.G. Megarrity. 1986. Successful transfer of DHP-degrading bacteria from Hawaiian goats to Australian ruminants to overcome the toxicity of *Leucaena*. Aust. Vet. J. **63**:259-262.

Jones, W.T. and J.L. Mangan. 1977. Complexes of the condensed tannins of Sainfoin (*Onobrychis viciifolia* Scop.) with fraction 1 leaf protein and with submaxillary mucoprotein, and their reversal by polyethylene glycol and pH. J. Sci. Food Agric. **28**:126-136.

Jones, W.T., L.B. Anderson and M.D. Ross. 1973. Bloat in cattle XXXIX. Detection of protein precipitants (flavolans) in legumes. NZ J. Agric. Res. **16**:441-446.

Jones, W.T., R.B. Broadhurst and J.W. Lyttleton. 1976. The condensed tannins of pasture legume species. Phytochem. **15**:1407-1409.

Jones, G.A., T.A. McAllister, A.D. Muir and K-J. Cheng. 1994. Effects of sainfoin (*Onobrychis viciifolia* Scop.) condensed tannins on growth and proteolysis by four strains of ruminal bacteria. Appl. Environ. Microbiol. **60**:1374-1378.

Kumar, R. and S. Vaithiyanathan. 1990. Occurrence, nutritional significance and effect on animal productivity of tannins in tree leaves. Anim. Feed Sci. Tech. **30**:126-136.

Larkin, P. et al. 1997. Proc. 18th Int. Grasslands Cong. Winnipeg, Canada. pp. 167-178.

Larsen, H.J., G.H. Tenpas and E.L. Jensen. 1974. Birdsfoot trefoil-grass and alfalfa-grass haylage in diet for dairy cows. J. Dairy Sci. **57**: 169.

Leathwick, D.M. and D.S. Atkinson. 1995. Dagginess and flystrike in lambs grazed on *Lotus corniculatus* or ryegrass. Proc. NZ Soc. Anim. Prod. **55**:196-198.

Longstaff, M.A. and J.M. McNab. 1991a. The effect of concentration of tannin-rich bean hulls (*Vicia faba* L.) on activities of lipase (EC 3.1.1.3) and (-amylase (EC 3.2.1.1)in digesta and pancreas and on the digestion of lipid and starch by young chicks. Br. J. Nutr. **66**:139-147.

Longstaff, M.A. and J.M. McNab. 1991b. The inhibitory effects of hull polysaccharides and tannins of field beans (*Vicia faba* L.) on the digestion of amino acids, starch and lipid and on digestive enzyme activities in young chicks. Br. J. Nutr. **65**:199-216.

Loosli, J.K., V.N. Krukovsky, G.P. Lofgreen and R.B. Musgrave. 1950. The comparative value of ladino clover, birdsfoot trefoil, timothy and alfalfa hays for yield and quality of milk. J. Dairy Sci. **33**: 228-236.

Lowry, J.B. 1990. Toxic factors and problems: methods of alleviating them in animals. Pages 76-88 *in* C. Devendra, ed. Shrubs and tree fodders for farm animals. International Development Research Centre, Ottawa.

Mangan, J.L. 1988. Nutritional effects of tannins in animal feeds. Nutr. Res. Rev. **1**:209-232.

Mangan, J.L., R.L. Vetter, D.J. Jordan and P.C. Wright. 1976. The effect of the condensed tannins of sainfoin (*Onobrychis viciifolia*) on the release of soluble leaf protein into the food bolus of cattle. Proc. Nutr. Soc. **35**:95A.

Marten, G.C., F.R. Ehle and E.A. Ristau. 1987. Performance and photosensitisation of cattle related to forage quality of four legumes. Crop Sci. **27**:138-145.

McAllister, T.A., H.D. Bae, G.A. Jones and K-J. Cheng. 1994. Microbial attachment and feed digestion in the rumen. J. Anim. Sci. **72**:3004-3018.

McNabb, W.C., G.C. Waghorn, T.N. Barry and I.D. Shelton. 1993. The effect of condensed tannins on *Lotus pedunculatus* on the digestion and metabolism of methionine, cystine and inorganic sulphur in sheep. Br. J. Nutr. **70**:647-661.

McNabb, W.C., J.S. Peters, Y.L. Foo, G.C. Waghorn and F.S.

Jackson. 1997. Effect of condensed tannins prepared from several forages on the *in vitro* precipitation of Ribulose-1,5-*bis*phosphate carboxylase (Rubisco) protein and its digestion by trypsin and chymotrypsin. J. Sci. Food Agric. (in press).

Miller, S.M., J.D. Brooker and L.L. Blackall. 1995. A feral goat rumen fluid inoculum improves nitrogen retention in sheep consuming mulga (*Acacia aneura*) diet. Aust. J. Agric. Res. **46**:1545-1553.

Mitaru, B.N., R.D. Reichert and R. Blair. 1984. The binding of dietary protein by sorghum tannins in the digestive tract of pigs. J. Nutr. **114**:1787-1796.

Mitaru, B.N., R.D. Reichert and R. Blair. 1985. Protein and amino acid digestibilities for chickens of reconstituted and boiled sorghum grains varying in tannin contents. Poult. Sci. **64**:101-106.

Mole, S., L.G. Butler and G. Iason. 1990. Defense against dietary tannin in herbivores: a survey for proline rich salivary proteins in mammals. Biochem. System Ecol. **18**:287-293.

Murdiatii, T.B., C.S. McSweeney, R.S.F. Campbell and D.S. Stoltz. 1990. Prevention of hydrolysable tannin toxicity in goats fed Clidemia hirta by calcium hydroxide supplementation. J. Appl. Toxic. **10**:325-331.

Murdiatii, T.B., C.S. McSweeney and J.B. Lowry. 1992. Metabolism in sheep of gallic acid, tannic acid and hydrolysable tannin from Terminalia oblongata. Aust. J. Agric. Res. **43**:1307-1319.

Newman, R.H., L.Y. Foo, G.C. Waghorn and W.C. McNabb. 1998. Solid-state NMR spectroscopic study of condensed tannin and related degradation products in feeds and sheep faeces. *J. Sci. Food Agric* (in press).

Niezen, J.H., T.S. Waghorn, W.A.G. Charleston and G.C. Waghorn. 1995. Growth and gastrointestinal nematode parasitism in lambs grazing either lucerne (*Medicago sativa*) or sulla (*Hedysarum coronarium*) which contains condensed tannins. J. Agric. Sci. Camb. **125**:281-289.

Oh, H.I. and J.E. Hoff. 1986. Effect of condensed grape tannins on the *in vitro* activity of digestive proteases and activation of their zymogens. J. Food Sci. **51**:577-580.

Ortiz, L.T., C. Alzueta, J. Trevino and M. Castano. 1994. Effects of faba bean tannins on the growth and histological structure of the intestinal tract and liver of chicks and rats. Br. Poult. Sci. **35**:743-754.

Panda, S.K., B.K. Sahu and N.C. Panda. 1988. Nutritive value of *Agasti* (*Sesbania grandiflora*) leaves in goats. Indian J. Anim. Nutr. **5**:68-69.

Panda, S.K., B.K. Sahu, N.C. Panda and S.K. Das. 1989. Proximate composition and tannin content of some forest tree leaves of orissa. Indian J. Anim. Nutr. **6**:177-180.

Porter, L.J. 1994. Flavans and proanthocyanidins. Pages 23-55 in J.B. Harborne, ed. The flavanoids. Advances in research since 1986. Chapman and Hall, London.

Pritchard, D.A., P.R. Martin and P.K. O'Rourke. 1992. The role of condensed tannins in the nutritional value of mulga (*Acacia aneura*) for sheep. Aust. J. Agric. Res. **43**:1739-1746.

Provenza, F.D., J.J. Lynch, E.A. Burritt and C.B. Scott. 1994. How goats learn to distinguish between novel foods that differ in postingestive consequences. J. Chem. Ecol. **20**:609-624.

Purchas, R.W. and R.G. Keogh. 1984. Fatness of lambs grazed on 'Grasslands Maku' lotus and 'Grasslands Huia' white clover. Proc. NZ Soc. Anim. Prod. **44**: 219-221.

Reed, J.D. 1995. Nutritional toxicology of tannins and related polyphenols in forage legumes. J. Anim. Sci. **73**:1516-1528.

Reed, J.D. 1997. Ecological biochemistry of secondary plant compounds in herbivores. 18th International Grasslands Congress. Canada.

Reed, J.D., H. Soller and A. Woodward. 1990. Fodder tree and straw diets for sheep: intake, growth, digestibility and the effects of phenolics on nitrogen utilisation. Anim. Feed Sci. Tech. **30**:39-50.

Reid, C.S.W., M.J. Ulyatt and J.M. Wilson. 1974. Plant tannins, bloat and nutritive value. Proc. NZ Soc. Anim. Prod. **34**:82-93.

Reynolds, L. and S.O. Adediran. 1988. The effects of browse supplementation on the productivity of west African dwarf sheep over two reproductive cycles. Pages 83-91 *in* O.B. Smith and H.G. Bosman, eds. Goat production in the humid tropics. Purdoc. Wageningen.

Rittner, U. and J.D. Reed. 1992. Phenolics and in vitro degradability of protein and fibre in west African browse. J. Sci. Food Agric. **58**:21-28.

Robertson, H.A., J.H. Niezen, G.C. Waghorn, W.A.G. Charleston and M. Jinlong. 1995. The effect of six herbages on liveweight gain, wool growth and faecal egg count of parasitised ewe lambs. Proc. NZ Soc. Anim. Prod. **55**:199-201.

Shi, Z.C. 1988. Identification of the phenolic substances in bovine urine associated with oak leaf poisoning. Res. Vet. Sci. **45**:152-155.

Sidahmed, A.E., J.G. Morris, L.J. Koong and S.R. Radosevich. 1981. Contribution of mixtures of three chaparral shrubs to the protein and energy requirements of Spanish goats. J. Anim. Sci. **53**:1391-1400.

Silanikove, N., Z. Nitsan and A. Perevolotsky. 1994. Effect of a daily supplementation of polyethylene glycol on intake and digestion of tannin-containing leaves (*Ceratonia siliqua*) by sheep. J. Agric. Food Chem. **42**: 2844-2847.

Singh, C., P. Kumar and A. Rekib. 1980. Note on some aspects of the feeding value of *Sesbania aegyptiaca* fodder in goats. Indian J. Anim. Sci. **50**:1017-1020.

Smith, T., S. Ncube and J.S. Dube. 1995. Dry season supplementation with polyethylene glycol (PEG) or a digestive modifier ("Browse Plus"). Journal of the Zimbabwe Society for Animal Production. **7**:181-186.

Stafford, H.A. 1988. Proanthocyanidins and the lignin connection. Phytochem. **27**:1-6.

Stafford, H.A. and T.Y. Cheng. 1980. The procyanidins of Douglas fir seedlings, callus and cell suspension cultures derived from cotyledons. Phytochem. **19**:131-135.

Stockdale, C.R. and D.W. Dellow. 1995. The productivity of lactating dairy cows grazing white clover and supplemented with maize silage. Aust. J. Agric. Res. **46**:1205-1217.

Terrill, T.H., W.R. Windham, C.S. Hoveland and H.E. Amos. 1989. Forage preservation method influences on tannin concentration, intake and digestibility of *Sericea Lespedeza* by sheep. Agron. J. **81**:435-439.

Terrill, T.H., G.B. Douglas, A.G. Foote, R.W. Purchas, G.F. Wilson and T.N. Barry. 1992. The effect of condensed tannins upon body growth, wool growth and rumen metabolsim in sheep grazing sulla (*Hedysarum coronarium*) and perennial pasture. J. Agric. Sci. Camb. **119**:265-273.

Terrill, T.H., G.C. Waghorn, D.J. Woolley, W.C. McNabb and T.N. Barry. 1994. Assay and digestion of ^{14}C-labeled condensed tannins in the gastrointestinal tract of sheep. Br. J. Nutr. **72**:467-477.

Vallet, J., J. Rouand and P. Besançon. 1994. Dietary grape seed tannins: Effects on nutritional balance and on some enzymic activities along the crypt-villus axis of rat small intestine. Ann. Nutr. Metab. **38**:75-84.

Van Eys, J.E., I.W. Mathius, P. Pongsapan and W.L. Johnson. 1986. Foliage of the tree legumes gliricidia, leucaena and sesbania as supplement to napier grass diets for growing goats. J. agric. sci., camb. **107**: 227-233.

Van Hoven, W. 1984. Tannins and digestibility in greater kudu. Can. J. Anim. Sci. **64**(Suppl.):177-178.

Van Leeuwen, P., A.J.M. Jansman, J. Wiebenga, J.F.F.G.

Kowinky and J.M.V.M. Mouwen. 1995. Dietary effects of faba-bean (*Vicia faba* L.) tannins on the morphology and function of the small intestinal mucosa of weaned pigs. Br. J. Nutr. **73**:31-39.

Waghorn, G.C. 1996. Condensed tannins and nutrient absorption from the small intestine. Pages 175-194 *in* L.M. Rode, ed. Animal Science Research and Development. Proc. Can. Soc. Anim. Sci. Ann. Mtg. Lethbridge, Canada.

Waghorn, G.C. and W.T. Jones. 1989. Bloat in cattle, 46. Potential of dock (*Rumex obtusifolius*) as an antibloat agent for cattle. NZ J. Agric. Res. **32**:227-235.

Waghorn, G.C. and I.D. Shelton. 1995. Effect of condensed tannins in *Lotus pedunculatus* on the nutritive value of ryegrass (*Lolium perenne*) fed to sheep. J. Agric. Sci. Camb. **125**:291-297.

Waghorn, G.C. and I.D. Shelton. 1997. Effect of condensed tannins in *Lotus corniculatus* on the nutritive value of pasture for sheep. J. Agric. Sci. Camb. **128**: 365-372.

Waghorn, G.C., I.D. Shelton and W.C. McNabb. 1994a. Effects of condensed tannins in *Lotus pedunculatus* on its nutritive value for sheep. 1. Non-nitrogenous aspects. J. Agric. Sci. Camb. **123**:99-107.

Waghorn, G.C., A. John, W.T. Jones and I.D. Shelton. 1987a. Nutritive value of *Lotus corniculatus* L. containing low and medium concentrations for sheep. Proc. NZ Soc. Anim. Prod. **47**:25-30.

Waghorn, G.C., I.D. Shelton, W.C. McNabb and S.N. McCutcheon. 1994b. Effects of condensed tannins in *Lotus pedunculatus* on its nutritive value for sheep. 2. Nitrogen aspects. J. Agric. Sci. Camb. **123**:109-119.

Waghorn, G.C., M.J. Ulyatt, J. John and M.T. Fisher. 1987b. The effect of condensed tannins on the site of digestion of amino acids and other nutrients in sheep fed on lotus. Br. J. Nutr. **57**:115-126.

Wang, Y., G.C. Waghorn, T.N. Barry and I.D. Shelton. 1994. Effect of condensed tannin in *Lotus corniculatus* upon sulphur amino acid metabolism in sheep blood plasma. Br. J. Nutr. **72**:923-935.

Wang, Y., G.B. Douglas, G.C. Waghorn, T.N. Barry and A.G. Foote. 1996a. The effect of condensed tannins in *Lotus corniculatus* upon lactation performance in ewes. J. Agric. Sci. Camb. **126**:353-362.

Wang, Y., G.B. Douglas, G.C. Waghorn, T.N. Barry, A.G. Foote and R.W. Purchas. 1996b. The effect of condensed tannins upon the performance of lambs grazing *Lotus corniculatus* and lucerne (*Medicago sativa*). J. Agric. Sci. Camb. **126**:87-98.

Wang, Y., G.C. Waghorn, W.C. McNabb, T.N. Barry, M.J. Hedley and I.D. Shelton. 1996c. Effect of condensed tannins in *Lotus corniculatus* upon the digestion of methionine and cysteine in the small intestine of sheep. J. Agric. Sci. Camb. **127**: 412-413.

Wiegand, R.O., J.D. Reed, A.N. Said and V.N. Ummuna. 1995. Proanthocyanidins (condensed tannins) and the use of leaves from *Sesbania sesban* and *Sesbania goetzei* as protein supplements. Anim. Feed Sci. Tech. **54**:175-192.

Windham, W.R., J.C. Petersen and T.H. Terrill. 1990. Tannins as anti-quality factors in forages. Pages 127-135 *in* D.E. Akin, L.G. Ljungdahl, J.R. Wilson and P.J. Harris, eds. Microbial and plant opportunities to improve lignocellulose utilization by ruminants. Elsevier, New York.

Woodward, A. and J.D. Reed. 1995. Intake and digestibility for sheep and goats consuming supplementary *Acacia brevispica* and *sesbania sesban*. Anim. Feed Sci. Tech. **56**:207-216.

Yuste, P., M. Longstaff and C. McCorquodale, C. 1992. The effect of proanthocyanidin-rich hulls and proanthocyanidin extracts from bean (*Vicia faba* L.) hulls on nutrient digestibility and digestive enzyme activities in young chicks. Br. J. Nutr. **67**:57-65.

Table 1
Production responses associated with condensed tannins (CT) in diets given to herbivores.

Diet/feeding regimen[a]	Control treatment	CT in diet[b] (% DM)	Animal species	Production response	Data source
Lotus corniculatus (birdsfoot trefoil)					
grazing	PEG[c] drench	4.0	lactating sheep	15%[d] more milk from ewes	Wang *et al.* 1996a
grazing	PEG drench	4.0	young sheep	11% more wool	Wang *et al.* 1996b
grazing	graze lucerne	4.0	young sheep	11% more wool, 8% more LWG	
grazing	graze lucerne	3-6	lactating sheep	LWG 250 *vs* 65 g/day	Douglas *et al.* 1995
grazing	graze lucerne		young sheep	24% more wool; 25% more LWG	
grazing	graze ryegrass	-	young sheep	40% less flystrike; 30% less dags	Leathwick & Atkinson 1995
hay	lucerne hay	-	young sheep	12% more LWG	Ingalls *et al.* 1965
grazing	graze lucerne	-	heifers	20% more LWG	Marten *et al.* 1987
graze and conc.	lucerne, grass, conc.	-	lactating cows	6% more FC milk	Larsen *et al.* 1974
hay and conc.	lucerne hay, conc.		lactating cows	-3% to 1.5% change in FC milk	Loosli *et al*. 1950
Lotus pedunculatus (lotus major; big trefoil)					
grazing	graze white clover	-	young sheep	13% less LWG	John & Lancashire 1981
grazing	graze white clover	-	young sheep	12% less LWG; leaner carcass	Purchas & Keogh 1984
grazing	PEG drench	10	sheep	25% less LWG	Barry & Duncan 1984
stall fed	PEG drench	8	sheep	7% less wool	Waghorn *et al.* 1994a
stall with ryegrass (1:2)	PEG drench	3	young sheep	5% more wool 9% more LWG	Waghorn & Shelton 1995
Onobrychus viciifolia (sainfoin)					
grazing	graze white clover	(7)[e]	young sheep	3% less LWG	John & Lancashire 1981
grazing	graze lucerne	(7)	heifers	19% more LWG	Marten *et al.* 1987
graze and stall fed	red clover	(7)	cows	0 *vs* 33% incidence of bloat	Reid *et al.* 1974
Hedysarum coronarium (sulla)					
grazing	PEG drench	4-5	sheep	10% less LWG	Terrill *et al.* 1992
grazing	PEG drench	-	young sheep	No effect on LWG	Douglas (unpublished)
grazing	graze lucerne	-	sheep	50% less intestinal nematodes LWG 125 *vs* -29 g/day	Niezen *et al.* 1995
grazing	graze lucerne	8	sheep	28% less intestinal nematodes LWG 175 *vs* 21 g/day	Robertson *et al.* 1995
Rumex obtusifolius (dock)					
10% of lucerne diet	lucerne	0.4	cows	prevention of bloat	Waghorn & Jones 1989
Trifolium repens (white clover)					
grazing with flowers	no flowers	0.7	lactate cows	2 *vs* 60 incidences of bloat	Stockdale & Dellow 1995
Ceratonia siliqua (carob)					
frozen leaves	PEG drench	-	sheep	-150 *vs* + 120 g/day LWG	Silanikove *et al.* 1994
Acacia aneurea (mulga)					
stall feeding	24 g PEG/day	12-14	sheep	-64 *vs* + 35 g/day LWG; 46% less wool	Pritchard *et al.* 1992
Acacia saligna					
stall feeding	-	8-12	sheep and goats	LW loss of 190-230 g/day	Degan *et al*. 1995
Acacia cyanophylla					
30% DMI with straw	-	9.3	sheep	LW loss of 11 g/day	Reed *et al.* 1990
Acacia sieberiana					
42% of DMI with straw	-	8.0	sheep	LWG of 20 g/day	Reed *et al*. 1990

Diet/feeding regimen[a]	Control treatment	CT in diet[b] (% DM)	Animal species	Production response	Data source
Acacia segal					
40% of DMI with straw	-	8.0	sheep	LWG of 21 g/day	Reed *et al*. 1990
Sesbania grandiflora					
sole diet	-	1.9	goats	LWG 43 g/day	Panda *et al*. 1988
20% with *P. maximum*	*P. maximum* hay	-	goats	N retained 1.3 *vs* - 0.6 g/day	Ash 1990
15% with *P. purpureum*	*P. purpureum*	-	young goats	LWG 22 *vs* -1 g/day	van Eys *et al* 1986
Sesbania aegyptiaca					
Sole diet	with 20% barley	-	goats	LWG 17 *vs* 31 g/day; similar DMI	Singh *et al* 1980
Sesbania sesban accessions fed with maize stover and protein supplement					
Acc 10865; 29% DMI	-	0.2	sheep	LWG 51 g/day	Weigand *et al*. 1995
Acc 15019; 32% DMI	-	1.5	sheep	LWG 62 g/day	Weigand *et al*. 1995
Acc 15036; 34% DMI	-	4.3	sheep	LWG 47 g/day	Weigand *et al*. 1995
Sesbania goetzia (as for *S. sesban*)					
Acc 15007; 37% DMI	-	4.8	sheep	LWG 43 g/day	Weigand *et al*. 1995
Gliricidia sepium					
45% with *P. maxim* hay	*P. maximum* hay	-	goats	LWG 38 *vs* 20 g/day	Ademosun *et al*. 1988
20% with *P. maxim* hay	*P. maximum* hay	1.0	goats	N retained 0 *vs* loss of 0.6 g/day	Ash 1990
Gliricidia maculata					
15% with *P. purpureum*	*P. purpureum*	-	young goats	LWG 20 *vs* -1 g/day	van Eys *et al*. 1986
Lucaena leucoephala					
1:1:2 lucaena; Gliricidia *P. maximum*	P maximum	1	sheep	LWG 46 *vs* 27 g/day; 50% more lamb survival	Reynolds & Adediran 1988
45% with *P. maxim* hay	*P. maximum*	2	goats	LWG 33 *vs* 20 g/day	Ademosun 1988
lucaena-setaria	sirato-setaria	-	cattle	50-100% increase in LWG	Jones & Bray 1983
1:1:3 lucaena:concent wheat straw	1:1:3 lucerne:conc-entrate:wheat straw	1	young buffalo	0.64 *vs* 0.67 kg/day LWG; similar DMI	Supta *et al* 1988
40% as hay with wheat straw	concentrate and wheat straw	2	young buffalo	0.16 *vs* 0.17 kg/day LWG; 29% decrease in DMI	Gupta & Singh 1989

a Diets are fresh and fed as a sole diet unless indicated; similar feeding regimen for control animals.

b Concentrations based on Butanol/HCl extraction of total CT.

c PEG (polyethylene glycol) is usually given in similar quantities to the CT intake.

d responses are given as CT *vs* control diet either as a percentage for simplicity of comparison or actual values when appropriate.

e From McNabb *et al*. 1997.

Abbreviations: DMI, Dry matter intake; LWG, liveweight gain; LW, Liveweight; FC Milk, fat corrected milk; N, nitrogen; conc., concentrate.
Latin and common names of species used but not defined in the table: *Medicago sativa* (lucerne; alfalfa); Trifolium rubens (red clover); *Panicum maximum* (guinea grass); *Pennisetum purpureum* (napier grass).

Table 2
Effect of condensed tannins on rumen function. These are generalised responses which will vary with diet quality.

Low dietary concentrations[a] of CT (to 5% of DM) with temperate forages
- Reduced (20-40%) ammonia concentration
- Reduced proteolysis of plant protein and apparent N digestion in the rumen
- Possible minor reductions in rate of fermentation
- Minimal effect on pool size, turnover rate or voluntary intake
- No effect on digestibility of structural fibre
- Minimal effect on microbial outflow to the SI
- Increased availability of AA for absorption from the SI

Medium dietary concentrations of CT (5-12% of DM) with temperate forages
- Substantial reduction (30-70%) in ammonia concentration
- Reduced proteolysis of plant protein and apparent N digestion in the rumen
- Depressed microbial growth
- Reduced rate of fermentation, slower turnover rate and large rumen pool size; 20-40% reduction in VFA concentration
- Reduced voluntary food intake (10-30%)
- Minor reductions in structural fibre digestibility
- Reduced microbial flow to SI; reduced total AA flow to SI because of intake depression

Low dietary CT concentration (to 4% of DM) with tropical forages
- CT containing forages are used to supplement poor quality forage (e.g., to 30% of intake)
- Improved voluntary intakes
- Improved performance due to protection of forage protein

Medium dietary concentration of CT (4-10% of DM) with tropical forages
- Effect of low dietary N is exacerbated by CT by reducing N availability for bacterial growth
- Very low ammonia concentrations
- Depressed voluntary intakes
- Reduced fibre and nitrogen digestibility
- Weight loss

High dietary concentration of CT (over 10% of DM) with tropical forages
- Severely depressed voluntary intakes
- Inappetance and pronounced weight loss
- Death
- These effects may be exacerbated by other anti-nutritional compounds

Abbreviations: AA, amino acids; DM, dry matter; N, nitrogen; SI, small intestine; VFA, volatile fatty acids.
[a]Concentrations based on the butanol/HCl method extraction (see text for details)

Table 3
Effects of condensed tannins on intestinal function in ruminants. These are hypothetical responses derived from monogastric species.

Low-medium dietary concentrations[a] of CT (to 8% of DM)
- Mucous production increased to protect intestine
- Excess mucous slows movement of metabolites to enterocytes for absorption
- Some CT will remain associated with digesta constituents throughout intestine and inhibit enzymic hydrolysis
- Possible compensatory increase in enzyme secretion
- Delayed absorption so more metabolites absorbed in mid and distal intestine
- Small increase in endogenous protein losses
- Small (up to 20%) reductions in apparent digestibility of amino acids

Medium-high dietary concentrations of CT (over 8% of DM)
- High rate of mucous production which may be insufficient to protect the intestine
- Physical damage to the brush border region of intestine; lesions and leakage of endogenous protein
- Altered architecture of microvilli; malfunction
- Some CT will remain bound to digesta constituents and remainder will bind to endogenous mucous, enzymes and intestinal tissues
- Depressed absorption of nutrients
- High rate of endogenous protein loss
- Significant reductions in amino acid digestibility
- Death after prolonged feeding

[a]Concentration based on the butanol/HCl method of extraction.

Table 4
Effect of condensed tannins (CT) on intestinal function, indicated by fractional absorption of amino acids (AA) and percentage change due to CT relative to low CT or PEG treatments**.**

	Essential AA	Non-essential AA	BCAA	S-AA
Sheep[a]				
Lotus corniculatus				
PEG	0.636	0.671	0.620	-
2.2% CT[b]	+8.7	-14.7	+7.0	-
Lotus pedunculatus				
PEG	0.760	0.743	0.783	0.660
5.5% CT	-15.9	-16.8	-17.7	-11.6
Sainfoin (hay)				
Lucerne hay	0.631	0.608	0.615	0.692[c]
CT	+7.0	+0.4	+4.8	+17.8
Pigs				
Sorghum				
0.09% CT	0.743	0.714	0.738	0.772
4.02% CT	-9.4	-9.2	-8.4	-10.0
Faba beans				
0.02% CT	0.866	0.858	0.865	0.850[c]
0.66% CT	-8.0	-10.5	-8.2	-6.2
Chickens				
Sorghum				
0.08% CT	0.906	0.909	0.921	-
1.91% CT	-27.0	-27.2	-27.2	-
Faba beans				
0.0% CT	0.737	-	0.775	0.736
0.8% CT	-94.7	-	-75.6	-118.6

Abbreviations: BCAA, branched chain amino acids; S-AA, sulphur containing amino acids
[a]Differences in values for apparent absorption of AA for different diets or animal species may bedue in part to experimental technique rather than diet or species *per se*.
[b]Condensed tannin concentrations are based on acidified vanillin or approximately equivalent analytical techniques.
[c]Methionine only.

Sources of data:
Sheep: *Lotus corniculatus*, Waghorn et al. 1987 b; *Lotus pedunculatus*, Waghorn et al. 1994 b, McNabb *et al.* 1993; Sainfoin, Harrison *et al.* 1973.
Pigs: Sorghum, Mitaru et al. 1984; Faba beans, Jansman et al. 1993.
Chickens: Sorghum, Mitaru et al. 1985; Faba beans, Longstaff & McNab 1991 b.

Table 5
Effect of Browse plus® (BP) on liveweight gain (LWG) and on browsing and grazing activity of steers in on-farm trials in Zimbabwe.

Dose (g/day)	Duration (days)	Steers per treatment	LWG (kg)		Browse time (%)		Graze time (%)		Source
			+ BP	- BP	+ BP	- BP	+ BP	- BP	
Bos taurus x Bos indicus steers on a site dominated by *Acacia* spp.									
1	80	60	+1	0	24	17	24	32	Dube *et al.* 1993
1 PEG[a]	70	15	-1	-10	14	11	46	48	Dube *et al.* 1993
Nkone (Bos indicus) steers grazing site dominated by *Acacia*, *Terminalia sericea* and *Compretum* trees									
3	180	10	+38	+35	8	4	17	22	Smith *et al.* 1995
Nkone steers grazing site dominated by *Colophospermum mopane* trees									
3	180	10	+20	+15	10	4	13	24	Smith *et al.* 1995
Bos taurus steers grazing ranges dominated by *Brachystegia spiciformis* spp.									
1	45	20	+9	0	-	-	-	-	Duncan 1994
Bos taurus steers grazing *Acacia*, *Terminalia*, *B. spiciformis* and combretum spp.									
2.7	56	100	+26	0	-	-	-	-	Duncan 1994
Bos taurus steers grazing *Grevia*, *Combretum* and *Acacia* spp.									
1	160	20	+12	+13	-	-	-	-	Duncan 1994

[a] PEG substituted for Browse plus®