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Beneficial and detrimental effects of dietary condensed tannins for sustainable sheep and goat production—Progress and challenges☆

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Abstract

Condensed tannins (CT) have improved liveweight gain, wool production and reproductive efficiency in sheep fed temperate forages and reduced the impact of gastro-intestinal parasitism. However, their value is also linked to environmental issues, such as reducing nitrogen pollution from animals grazing lush pastures with a high nitrogen content and lessening methane emissions from rumen fermentation. When forages are fed as a sole diet, the CT in birdsfoot trefoil (*Lotus corniculatus*) have been beneficial for ruminant production, but the CT in sainfoin, (*Onobrychis*), sulla (*Hedysarum coronarium*) and lotus major (*L. pedunculatus*) do not appear to benefit productivity other than by mitigating the impact of parasites. The sainfoin, sulla and lotus major have a high feeding value, but the CT *per se* offer no benefits for nutrition. In contrast to temperate farming, the CT in browse, typical of warm and hot climates, are nearly always detrimental to ruminants, except for reducing internal parasite numbers. Grasses fed in these regions contain less protein (and usually more fibre) than temperate forages and inclusion of CT from browse further reduces protein availability for absorption by limiting ruminal microbial growth and lowering the fractional absorption of amino acids from the intestine. Intakes of CT from browse, in combination with a medium–poor quality diet, are detrimental to performance. However recent studies have shown inclusion of polyethylene glycol (PEG) in diets for sheep and goats grazing scrub and woodland can markedly improve performance, with as little as 10 g/day. The success of research to improve the performance of animals consuming diets

Abbreviations: AA, amino acid; BW, body weight; CP, crude protein; CT, condensed tannin(s); DM, dry matter; FEC, faecal egg count; GHG, greenhouse gas(es); ME, metabolisable energy; MJ, mega joule; N, nitrogen; na, not applicable; PEG, polyethylene glycol; VFA, volatile fatty acids.

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containing CT in both temperate and hot climates will depend on communication between animal scientists and chemists. Researchers must measure the astringency and chemical characteristics of CT (and other secondary metabolites), to better understand the impact of tanniniferous feeds on nutritive value. These measurements will enable findings from unrelated trials to be evaluated and provide opportunities for optimising and mitigating the CT in contrasting ruminant production systems.

Keywords: Condensed tannin; Sheep and goat nutrition; Gastro-intestinal parasites

1. Introduction

The term "tannin" refers to "tanning" or preservation of skins to create leather, and tannins also contribute to the astringency of many popular drinks, for example tea and wine. Condensed tannins (CT), also known as proanthocyanidins, are secondary plant metabolites. Their role in plant metabolism is not known, although several hypotheses have been advanced, but effects on ruminant digestion are becoming increasingly clear. Condensed tannins bind to proteins in the rumen, reduce protein degradation and when dietary crude protein (CP) concentrations exceed animal requirements for CP, these effects can improve performance. However when dietary CP concentrations are low and fibre concentrations are high, CT are nearly always detrimental.

Condensed tannins are heterogeneous compounds (*e.g*. Mueller-Harvey, 1999) and both size and structure affects their reactivity and impact on digestion. Their structure and propensity for binding to protein and fibre makes accurate measurements of concentration difficult. Determination of CT concentration requires both unbound and bound CT to be measured, using purified CT from the same forage species as a standard. Alternative standards will lessen the accuracy of CT measurements. However astringency (protein binding capacity) is equally important, and the variation between tannins has frustrated attempts to relate concentration with animal performance. The structure of the CT affects their binding capacity, the impact upon digestion, nutritive value and anthelmintic properties.

Other secondary metabolites present in browse may have a greater impact than CT upon animal performance (Acamovic and Brooker, 2005; Reed et al., 2000). Examples include hydrolysable tannins, which are potentially toxic but also degradable in the rumen. The presence of other secondary metabolites must be recognised in evaluations of CT containing forages.

Condensed tannins are widespread in dicotyledonous species and occur infrequently in graminacae. In temperate species they are often restricted to seed coats (*e.g*. faber bean, *Vicia faber*; lucerne, *Medicago sativa*) or flowers (white clover, *Trifolium repens*) (Jansman, 1993; Burggraaf et al., 2003), but they must be expressed in foliage to have real benefits for ruminant nutrition. The condensed tannins in the foliage of birdsfoot trefoil (*Lotus corniculatus*), Lotus major (*L. pedunculatus*), sainfoin, (*Onobrychis viciifolia*) and sulla, (*Hedysarum coronarium*) have provided significant benefits for ruminant performance, health and environmental sustainability. These benefits have prompted an intensive research effort to define the chemical composition of CT, identify synthetic pathways and especially to understand the regulation of CT expression in foliage. The challenges in engineering plant expression of secondary metabolites have been illustrated by Dixon (2005), and some recent progress in expression of CT in Lucerne has been demonstrated by Xie et al. (2006). Progress has been slow, but the objective is clear—breeding lucerne (Larkin et al., 1999; Xie et al., 2006) or white clover (Woodfield and Easton, 2004) that express foliar CT.

This overview describes effects of CT on digestion and highlights their importance for temperate and warm climate agriculture. A brief overview of CT structure will be included because of its importance in analysis, interpretation and comparison of findings by animal researchers. Consideration will be given to "optimal" CT content and managing CT for animal production in temperate and warm climates.

2. Condensed tannins

2.1. Synthesis

In tropical forages, condensed tannins are often one of several polyphenolic compounds, which may include hydrolysable tannins, other secondary metabolites and can exceed 300 g/kg of the dry matter (DM) (Lowry et al., 1996; Rittner and Reed, 1992; Mueller-Harvey, 1999; Reed et al., 2000). Very high CT concentrations limit the amount of DM available for digestion, but hydrolysable tannins may provide nutrients for absorption, especially following a period of adaptation (Lowry et al., 1996). Measurement of total phenolics as well as CT concentrations in browse provides a more informative overview of forage quality, than CT alone.

Condensed tannin synthesis originates in the cell cytoplasm from phenylalanine and acetate precursors (Mueller-Harvey and McAllan, 1992) to form catechin units in the cell vacuole. Lees et al. (1995) showed that CT formed in very young sainfoin leaves and concentrations increased as leaves matured. There was a progressive depletion with senescence until very little CT remained in yellow leaflets. Condensed and hydrolysable tannins were also mobilised from oak (*Quercus*) leaves prior to senescence (Grundhofer et al., 2001). The reduction in CT content of senescent leaves would facilitate degradation and nutrient recycling in soils.

The reason for CT synthesis and mobilisation are speculative. Suggestions include protection against herbivory, plant defense against pathogens, energy conservation (for mobilisation in times of need) and nitrogen conservation. If CT are intended to protect against herbivory they are remarkably ineffective, with sheep and goats inevitably selecting leaf in preference to stem, despite much higher concentrations of CT in leaf. The possibility that CT conserve nitrogen (N) in an ecosystem has credibility in low fertility environments because CT always increase the N content of faeces and decrease urinary N output (Waghorn and McNabb, 2003). Faecal N is more likely to be retained in the soil than urinary N, which is subject to volatilisation in warm climates and leaching in wet conditions. These attributes will benefit forage trees in arid conditions.

2.2. Structure

The CT are termed "proanthocyanidins" because HCl/butanol treatment releases bright red anthocyanadin chloride. Condensed tannins are polymers of flavanol (flavan-3-ol) units, linked by carbon–carbon bonds that are not susceptible to anaerobic enzyme degradation (Lowry et al., 1996; McSweeney et al., 2001).

Condensed tannin polymers in temperate forages may range in chain length from dimers to over 20 flavanol units, and there are usually several flavan-3-ol structures within each polymer (Table 2). Mueller-Harvey (1999) presents diagrams of both CT and hydrolysable tannin structures. Principle structural variations within CT include: the number of hydroxyl groups on the "A" and "B" rings of the flavanol units; positions of the hydroxyl groups, stereochemistry at carbons 2, 3 and 4 of the "C" ring; position and type of linkages between flavanol units and number of flavanol units.

Animal researchers evaluating forages containing CT will need to be familiar with terms describing structure and stereochemistry. Procyanidin is a generic term referring to polymers of catechin and epicatechin stereoisomers, both of which have two hydroxyl groups attached to the "B" ring of the flavanol (monomer). Prodelphinidin is the generic term for polymers of gallocatechin and epigallocatechin stereoisomers, each with three hydroxyl groups on the B ring. The need for detailed information about the structure of CT is driven in part by a need to understand biosynthetic pathways to express CT in foliage of high quality temperate forages, such as lucerne or white clover, but structure will also affect differences in reactivity.

The distribution of flavanol monomers that comprise CT, are not consistent within a genus (Table 2). For example CT in *L. corniculatus* is based primarily on epicatechins whilst CT in *L. pedunculatus* is dominated by epigallocatechins (Foo et al., 1997). The flowers of red clover (*Trifolium pratense*) are dominated by epicatechins, where as white clover flowers comprise a mixture of gallocatechins and epigallocatechins (Sivakumaran et al., 2004). The level of detail (Table 2) may seem excessive to animal researchers, but it is not, because structure will affect reactivity (Molan et al., 2002; Waghorn and Shelton, 1997).

2.3. Astringency

Astringency is a measure of protein binding (and precipitating) capacity, or capacity to affect changes to enzymatic activity. Comparisons between lotus species in their CT chemistry and impact on microbial or ruminal activity have shown the CT in birdsfoot trefoil to be less astringent than that from lotus major. The CT in birdsfoot trefoil comprises mainly catechin and epicatechin monomers (procyanidins) whereas lotus major has a predominance of epigallocatechin extender units (prodelphinidins) and mixed terminal units (Table 2). The dominance of procyanidins in birdsfoot trefoil may be associated with beneficial effects on animal performance and amino acid absorption (Tables 1 and 3) when fed as a sole diet, compared to the mild anti-nutritional effects of CT from lotus major (Waghorn and Shelton, 1997). However, comparison between accessions of *Calliandra calothyrsus* showed dominance of prodelphinidins in the extractable tannin fraction was associated with higher intakes and digestibility than that when procyanadins were dominant (Lascano et al., 2003). Attempts to relate CT chemistry to physiological effects and animal production are made difficult by contrasting extraction and assay protocols for the CT. Although some generalizations can be made about the proportions of flavanol monomers between species (*e.g*. of Lotus; Table 2), there can be a significant variation within a species, *e.g. L. cornicu-*

Table 1
Ruminant livestock responses to temperate legumes containing condensed tannin[a]

Forage *vs*. control parameter	Number of trials	Control value	Response (%)	Reference
Birdsfoot trefoil *vs*. pasture				
Ovulation rate	4	1.55	+6 to +30	2, 6, 7, 8
Lambs born/ewe	4	1.44	+20	2, 6, 7
Lamb daily gain (g)	2	183	+38	3, 12
Parasitised lamb daily gain (g)	4	156	+31	1, 3, 12
Lamb wood growth	2	na	+30	1
Dag score	3	na	−25	1, 13
Cow daily milk yield (kg)	1	18.5	+32	14
Birdsfoot trefoil *vs*. lucerne				
Lamb daily gain (g)	3	219	+10	5, 10, 12
Lamb wool growth	7		+11	
Birdsfoot trefoil; CT effect				
Ovulation rate	1	1.41	+10	6
Lamb daily gain (g)	2	250	+8	9
Wood production	1	na	+10	6, 7, 9
Ewe milk production	1	na	+21	4
Cow milk production (kg/day)	1	22.1	+10	14
Lotus major *vs*. white clover				
Lambs daily gain (g)	7	262	−13	15, 16
Lotus major *vs*. Lucerne				
Lamb daily gain (g)	2	219	+10	12, 15
Parasitised lamb daily gain (g)	1	121	+32	12
Lotus major; CT effect				
Lamb daily gain (g)	1	166	−25	17
Wool production		na	−12	17
Sainfoin *vs*. white clover				
Lamb daily gain (g)	2	212	−3	15
Sainfoin *vs*. lucerne				
Lamb daily gain (g)	2	165	+24	
Cow daily gain	1	na	+19	18
Sulla *vs*. lucerne				
Lamb daily gain (g)	3	224	+8	11, 12
Parasitised lamb daily gain (g)	3	62	+145	11, 12
Sulla; CT effects				
Lamb daily gain (g)	5	240	−7	9, 19
Lamb wool growth	4	na	−3	9, 19

na, not applicable—usually because data were expressed in a form that was not amenable to comparison. References: 1, Ramírez-Restrepo et al. (2004); 2, Ramírez-Restrepo et al. (2005a); 3, Ramírez-Restrepo et al. (2005b); 4, Wang et al. (1996a); 5, Wang et al. (1996b); 6, Min et al. (1999); 7, Min et al. (2001); 8, Luque et al. (2000); 9, Douglas et al. (1999); 10, Douglas et al. (1995); 11, Niezen et al. (1995); 12, Niezen et al. (1998b); 13, Leathwick and Atkinson (1995); 14, Woodward et al. (2004); 15, John and Lancashire (1981); 16, Purchas and Keogh (1984); 17, Barry (1985); 18, Marten et al. (1987); 19, Terrill et al. (1992).

[a] Comparisons are made with control forages, either pasture, legumes without CT or with the same forage where effects of CT are removed by polyethylene glycol (PEG). The control value refers to production from the forage without effective condensed tannin (*e.g*. pasture, lucerne or the forage with PEG).

Table 2
Structure[a] of condensed tannins in the foliage of birdsfoot trefoil (*Lotus corniculatus*), lotus major (*L. pedunculatus*) and the flowers of white clover (*Trifolium repens*) and red clover (*Trifolium pratense*)

	Monomers	Extender units				Terminal units			
		C	EC	GC	EGC	C	EC	GC	EGC
Birdsfoot trefoil	6.5		0.67		0.30	0.82	0.16		
Lotus major	8		0.19	0.13	0.64	0.50	0.20	0.20	0.10
White clover flower	10.3			0.39	0.56			0.48	0.52
Red clover flower	9.3	0.06	0.81	0.06	0.07	0.95	0.05		

From Foo et al. (1997); Sivakumaran et al. (2004).

[a] Data indicate the mean number of monomers, and composition (mol/mol) for principal extender and terminal units, of catechin (C), epicatechin (EC), gallocatechin (GC) epigallocatechin (EGC).

latus (Hedqvist et al., 2000), sainfoin (Marais et al., 2000) and most probably other species as well.

Other examples of differences in astringency include the CT in dock (*Rumex obtusifolius*), where only 3 g/kg CT in the dietary DM prevented bloat in dairy cows (Waghorn and Jones, 1989). Diets containing only 26 g/kg of carob (*Ceratonia siliqua*) CT in the DM reduced lamb growth from 140 to less than 50 g/day (Priolo et al., 2000) whereas the CT in sulla (72 g/kg DM) did not reduce daily gain of lambs (279 g/day) over a 17 weeks grazing trial (Douglas et al., 1999).

Comparisons between sources of CT must be made using similar concentrations and this usually requires purified material. Molan et al. (2002) illustrated differences between sources of CT by incubating *Trichostrongylus colubriformis* gastro-intestinal parasite larvae in media with a range of CT concentrations to determine the LD_{50}. Values were 92 μg CT/ml with birdsfoot trefoil but only 59 μg/ml for lotus major. Only CT from dock (*R. obtusifolius*) was more potent in that study. Other comparisons have yielded less repeatable results and McAllister et al. (2005) recommend biological assays using rumen bacteria be used in conjunction with chemical assays. They measured binding capacity of CT extracted from nine forage species and showed CT were more effective precipitating bovine serum albumin than fraction 1 plant protein (Rubisco). There was a two-fold range in astringency, but rankings differed for inhibition of cellulose digestion, demonstrating the importance of biological assays to identify the most appropriate CT for affecting specific nutritional outcomes.

Researchers persist in evaluating and comparing animal trials on the basis of CT concentration, often measured using a vanillin/HCl or butanol/HCl assay. This is probably a consequence of the relative simplicity of these assays but the first priority for animal researchers should be discussion and collaboration with chemists. If a colourimetric assay is to be used for quantifying CT, the butanol/HCl method will provide a more sensitive assay than vanillin (Kraus et al., 2003) but the "standards" used in the assay must be extracted and purified from the same plant species, preferably the same accession. The colour obtained from tannins depends on the type of inter-flavanol linkages between A and B rings (4–6 or 4–8), and the number and position of phenolic groups (Mueller-Harvey, 1999; Kraus et al., 2003). If hydrolysable tannins are present in the sample, they will also need to be analysed, and although they appear to be less astringent (Kraus et al., 2003) and have less impact upon digestion than CT (Lowry et al., 1996) they are often toxic to animals when there has been insufficient time for adaptation.

Use of inappropriate standards or assays will lead to confusion when researchers attempt to interrelate results from independent animal trials. The emphasis on CT concentration without appropriate chemical definition should be addressed by measuring the proportions of procyanidins and prodelphinidins as well as concentrations of hydrolysable tannins, other phenolics and secondary metabolites. Chemical analyses may be complimented by *in vitro* incubations with plant protein substrates.

3. Hydrolysable tannins

Hydrolysable tannins have a very different structure to CT, comprising a central sugar attached to several gallic acid groups. Their structure is also highly variable with different types and numbers of sugars and a range of crosslinkages between gallic acids and other phenolics (Mueller-Harvey, 2001). Hydrolysable tannins are widely distributed, for example in oak, some acacia species and a range of browse, with up to 200 g/kg of hydrolysable tannin in the DM of some species (Reed, 1995). Hydrolysable tannins can be toxic, especially when large quantities are given to ruminants with insufficient time for microbial adaptation. However animals can adapt to diets containing hydrolysable tannin so that acceptable levels of production can be achieved with appropriate feed management. Unfortunately, information concerning the degradation of hydrolysable tannins and products of degradation either *in vitro* or *in vivo* is very limited, with most focus on toxic effects rather than provision of nutrients (Waghorn and McNabb, 2003) to meet animal requirements. Addition of polyethylene glycol (PEG) to diets containing hydrolysable tannins (without CT) will not benefit digestion or performance. Researchers investigating browse spp. must be aware that a large variety of secondary plant metabolites, in addition to CT, may contribute to anti-nutritional effects (Cheeke, 1998; Reed et al., 2000).

4. Condensed tannins and digestion

4.1. Salivation

Chewing during eating ruptures about 60% of plant cells and the CT are able to bind with salivary and plant proteins. The CT reduces the proportion of soluble protein in ingesta, which will slow the rate of protein degradation. The saliva produced during chewing (eating and rumination) has two major roles. It assists bolus formation and the lubrication from muco-proteins facilitates swallowing, whilst salivary bicarbonate and phosphates are essential to buffer and maintain rumen pH in a range of about 5.8–6.8 during digestion. Copious saliva is produced during eating and is sometimes equivalent (in weight) to the fresh forage consumed. Salivary proteins, especially in browsers, will also affect digestion by binding dietary tannins.

The parotid glands produce the most saliva. Browsers, including goats, have larger parotid glands in relation to liveweight (Hofmann, 1973; Vaithiyanathan et al., 2001) and the saliva of some browsers contains high (sometimes inducible) concentrations of proline rich proteins (PRP), relative to grazing herbivores (Mole et al., 1990; Fickel et al., 1998). The PRP have a high CT binding capability and complex with CT, so there is less CT available for binding to forage proteins in the rumen. Dietary CT bind with forage proteins during chewing, and there was very little soluble plant protein in swallowed boli from cattle fed sainfoin (Mangan et al., 1976).

The high salivation rate and presence of PRP should enable browsers to be more tolerant of dietary CT, compared to sheep or cows. Exposure to CT can induce increased secretion of PRP in deer and rats (Robbins et al., 1991), but data do not appear to be available to indicate whether PRP induction occurs in goats. Researchers should also consider the possibility that breeding, domestication or animal selection could affect changes in the ability of individuals to tolerate diets containing high concentrations of CT and other polyphenolic compounds.

4.2. Rumen fermentation

Binding between CT and proteins occurs very rapidly following cell rupture, but CT can be displaced from proteins in neutral (rumen) pH within the first 30 min of binding, for example by addition of PEG (W.T. Jones, personal communication). The impact of CT in the rumen is well defined in terms of overall effects upon digestion (Table 3) and the extent to which CT interfere with digestion is a function of astringency, concentration and potential sites for binding. Condensed tannins bind preferentially with PEG, but have a strong affinity for protein relative to other substrates, such as fibre. Relative affinities for binding enable PEG to reduce or remove effects of CT, if sufficient is given. Typical ratios used in research trials are about 1–1.8 PEG (molecular weight 3500):1 CT (weight bases) to remove most CT effects *in vivo* and *in vitro*, but substantially lower ratios of PEG:CT (*e.g.* 1:3) appear to provide very good benefits for sheep and goat production (Gilboa et al., 2000; Priolo et al., 2002).

Under farming conditions it is not necessary to remove all of the CT effects by adding PEG and the amount required will depend on the dietary protein content as well as the CT content. The objective for all animal production systems should be to meet energy and protein requirements and optimise animal performance for maximum economic benefit. Protein requirements have been clearly defined, so when diets have excess protein relative to animal needs, CT may reduce degradation without limiting amino acid availability for absorption, however when dietary protein concentrations are close to or below animal requirements any CT will be detrimental to performance.

In vitro and *in vivo* trials have consistently demonstrated a reduction in proteolysis as a consequence of dietary CT. Net microbial flow to the intestine is not necessarily reduced (Waghorn et al., 1994b; Wang et al., 1996b) but high concentrations of CT will lower VFA concentrations in the rumen because rumen pool sizes tend to increase as a consequence of a slower rate of digestion (Waghorn and McNabb, 2003). A reduced rate of digestion, especially of fibre, will slow the clearance of feed residues from the rumen, may necessitate more rumination and will reduce voluntary feed intake (Table 3). This has serious consequences for productivity, especially if the CT does limit microbial growth or amino acid absorption from the intestine.

Table 3
Effects of dietary condensed tannins on digestion in ruminants

Condensed tannins usually
Reduce ruminal digestion of plant protein
Reduce rumen ammonia concentrations
Reduce protein solubility
Increase the proportion of plant protein reaching the intestine
Inhibit some rumen bacteria
Reduce nitrogen digestibility; increase faecal nitrogen concentration
Reduce urinary nitrogen output
Slow or reduce the rate of amino absorption from the intestine
Reduce dietary DM able to be digested
Lower the proportion of dietary energy loss to methane
Condensed tannins may also
Alter diet selection
Reduce voluntary feed intake
Reduce the rate of digestion
Increase rumen volume
Reduce rumen VFA production rate and concentration
Occasionally increase but usually reduce amino acid absorption
Improve tolerance of gastro-intestinal parasites
Reduce numbers of gastro-intestinal parasites
Reduce faeces adhering to wool or fibre (dags)
Damage abomasum or intestine
Outcomes of diets containing condensed tannins
Improved or impaired animal performance
Depends on type and concentration of dietary tannin as well as
Diet composition
Animal requirements
Other secondary metabolites

Although the net effects of CT on rumen digestion are understood (Table 3), our understanding of the mechanisms that reduce feed protein degradation, ammonia production, microbial growth, digestion rate and intake, are less well defined. Condensed tannins will bind with feed proteins, the microflora themselves or microbial enzymes and CT–protein complexes are poorly degraded under anaerobic conditions (McSweeney et al., 1999). Min et al. (2005) reported a greater affinity between CT and bacterial cells than with plant proteins, and cellulolytic bacteria were affected more than cellulolytic fungi (McSweeney et al., 2001).

Condensed tannins from a range of forages (birdsfoot trefoil, sainfoin and *C. calothyrsus*) reduce microbial numbers and cause a substantial inhibition of proteolytic activity for many bacteria, although some are relatively unaffected (Jones et al., 1994; McSweeney et al., 2001; Min et al., 2005). Jones et al. (1994) reported morphological changes in *Butyrivibrio fibrisolvens* and *Streptococcus bovis*, implicating the cell wall as a prime CT binding site. Other rumen bacteria secrete an extracellular polysaccharide to protect the cell wall from CT, which parallels the increased intestinal mucous secretion reported in chicks given a diet containing CT (Ortiz et al., 1994).

4.3. Microbial resistance to tannins

If CT reduce microbial flow from the rumen, animal performance is likely to be compromised. Any reduction in fibre degradation will limit voluntary intake and energy absorption. Suggestions that ruminants develop tolerance to tannin, or that rumen isolates from animals grazing browse enable a superior performance to non-adapted animals (*e.g*. Odenyo et al., 2001) are associated with hydrolysable tannins, which can be degraded by rumen microflora. There is good evidence for both adaptation (Lowry et al., 1993) and digestion of hydrolysable tannins (McSweeney et al., 2001).

Gallic and ellagic acids, from hydrolysable tannins can be decarboxylated to pyrogallol, phloroglucinol and ultimately to acetate and butyrate. Lowry et al. (1993) showed phenolic compounds such as *p*-coumaric and ferulic acids were excreted as hippuric acid and this can result in significant nitrogen losses for ruminants fed diets deficient in nitrogen. In contrast to CT, *p*-coumaric and ferulic acids did not reduce microbial activity, although a period of adaptation will be required to avoid toxic effects from absorbed metabolites.

There is no evidence for anaerobic cleavage of the flavan-3-ol ring systems of CT (Lowry et al., 1996; McSweeney et al., 2001), and CT will not be digested by rumen microorganisms. The suggestion that some ruminants are better able to tolerate CT, has been evaluated by Jones et al. (2001). They collected rumen contents from wild browsers including giraffe, greater kudu, eland, duiker, impala, nyala, gnu and goat for comparison with digesta from sheep using *in vitro* digestion. Substrates included several *Leucaena* spp., *C. calothyrsus*, *Gliricidia sepium* and *Acacia boliviana*, all of which contain CT. Incubations were carried out in the presence or absence of PEG. There were no interactions between source of digesta and forage type for *in vitro* nitrogen digestibility. Digestibility was related to concentration of CT in the feed. These authors concluded that it would be unlikely for rumen bacteria to be capable of digesting CT and tolerance by some species will relate to salivary PRP rather than specific bacteria or other aspects of metabolism. It should be reiterated that reports of CT disappearance during digestion can be a consequence of minor changes in structure and the inability of assays to quantify the remaining polyphenol (Terrill et al., 1994).

5. Intestinal absorption

Condensed tannins will always increase plant protein flow to the intestine and reduce net absorption of ammonia from the rumen. Although CT may dissociate from protein as the pH declines below 3.5 *in vitro*, this does not necessarily mean that the protein will be digested and absorbed distal to the acidic abomasum. Intestinal pH rises above pH 5.0 within 1 m of the pylorus (Terrill et al., 1994) which will ensure the CT and protein re-associate, if there was a true disassociation in the first place. Further, any CT that are not bound to plant protein may bind to endogenous enzymes or to the intestinal lumen, further disrupting absorption. These processes have been demonstrated in monogastric animals (rats, pigs and especially chickens (see Waghorn, 1996)) with significant damage to the intestinal mucosa and poor absorption of amino acids, especially with chickens.

A single study of the site of sulphur-AA absorption in sheep given birdsfoot trefoil with and without PEG (Wang et al., 1996b) showed the CT delayed amino acid absorption, which took place over the whole length of the intestine. When PEG was given, most AA absorption was completed in the proximal intestine. Birdsfoot trefoil CT appears to be unusual because it did not reduce the fractional absorption of AA and the increased protein flow to the intestine resulted in an increased AA absorption. Waghorn et al. (1987) showed that CT in this forage increased absorption of essential AA by 60%, but the more astringent CT in lotus major did not benefit the amino acid supply for sheep despite marked reductions in rumen protein degradation and increased flow to the abomasum (Waghorn et al., 1994b).

The impact of CT on intestinal function is not well understood in ruminants, but data suggest CT inhibit the capability of endogenous enzymes to cleave proteins into peptides and amino acids and also inhibit their absorption. Endogenous enzymatic activity exceeds requirements for proteolysis, but tannins bound to either bacterial surfaces or to forage proteins may reduce enzyme access and activity. In pigs and more especially chickens, low concentrations of dietary CT (10–20 g/kg DM) cause villous shortening, distortion and atrophy with a proliferation of mucous secreting goblet cells (Ortiz et al., 1994) and a severe inhibition of amino acid absorption (see Waghorn, 1996).

Sheep appear less sensitive of effects of CT than monogastric species. Walton et al. (2001) did not detect significant changes in intestinal villus structure in sheep given lotus major as a sole diet for 4 weeks. However, when Robins and Brooker (2005) fed sheep mulga (*Acacia aneura*), which contains higher concentrations of astringent tannins, for a similar period, the CT reduced enzyme activity by 50–70%. It also resulted in abomasal damage, caused gastric pit closure (which would limit pepsin secretion) and the increased villus height and crypt depth in abomasal and intestinal tissues. These changes would slow the rate of protein hydrolysis and may limit absorption of amino acids and peptides, which are consistent with observations by Wang et al. (1996b).

Condensed tannins are clearly a “double edged sword” for feeding value. They are not digested by the microflora (McSweeney et al., 2001) and the carbon skeleton is not absorbed (Terrill et al., 1994), so high concentrations of CT reduce the DM potentially available for digestion. The CT protect protein from excessive degradation, but can also inhibit absorption of the protected protein. Understanding their effects on digestive physiology are central to obtaining benefits from temperate forages and overcoming adverse effects when browse is fed in hot climates.

6. Forages with CT for temperate agriculture

6.1. *Condensed tannin research in New Zealand*

A combination of field trials, digestive physiology and chemistry have sustained CT research over 20 years and have demonstrated clear benefits for lamb growth, wool production, fertility and tolerance of intestinal parasites (Table 1). This work evolved from demonstrations of high liveweight gain by lambs fed sainfoin or lotus major (John and Lancashire, 1981), after which Barry and colleagues showed high concentrations of CT in lotus major could lower intake, digestibility and performance (Barry and Duncan, 1984; Barry and Manley, 1984). Their work involved application of polyethylene glycol (PEG) to remove the effects of the CT, enabling comparisons between lotus “with and without CT”

(Barry, 1985). This technique was adopted by Waghorn et al. (1987) to show that the CT in birdsfoot trefoil reduced ruminal protein degradation and increased absorption of essential amino acids (AA) by 60%. That finding stimulated a more extensive investigation of forages containing CT that could benefit New Zealand farming. Sheep were used in field trials and metabolism experiments to elucidate effects of CT on digestive physiology with lotus major, birdsfoot trefoil and sulla. Benefits of these forages for production are summarised in Table 1.

Despite an improved understanding of CT on rumen digestion (McNabb et al., 1996; Waghorn, 1996; Min et al., 2005) much has still to be learned. Metabolism studies did show that CT from lotus major reduced fractional absorption of amino acid (AA) (Waghorn et al., 1994b) and that CT from birdsfoot trefoil reduced the rate of AA absorption from the small intestine (Wang et al., 1996b). Terrill et al. (1994) showed that the carbon core of CT was not absorbed during digestion and colourimetric analyses could not quantify CT added to digesta.

When mixtures of either lotus major or birdsfoot trefoil were fed to sheep with ryegrass pasture, clear differences were evident in the astringency or binding capacity of CT from the two species (Waghorn and Shelton, 1995, 1997). A detailed chemical analysis of CT purified from the two lotus species (Foo et al., 1996, 1997) was carried out to identify the cause of differences in reactivity (Table 2) and current research is attempting to relate CT structure to digestion and animal performance. The benefits of CT for animal performance have resulted in agronomic selections of birdsfoot trefoil for improved persistence under New Zealand conditions (W. Rumball, personal communication).

6.2. Relative feeding values

The response of ruminants to diets containing CT will depend on their physiological status (young, lactating, mature) which affects their nutrient needs, the overall diet quality (fibre, protein concentration) as well as the astringency of the CT. Many evaluations of temperate legumes containing CT have been undertaken with young growing (male) lambs or lactating animals because these are capable of responding to an additional supply of dietary protein. Ruminants will not improve performance in response to additional absorbed amino acids if amino acid supply is not limiting performance. For example, if animals are fed a fibrous diet (*e.g.* over 500 g/kg dietary DM), energy is likely to be first limiting for performance. The high proportion of fibre, especially tough stemmy material requires extensive chewing to clear the rumen. The yield of VFA will be low, and addition of CT to the diet may inhibit some fibre degrading bacteria. Any increase in AA absorption will only contribute to the energy balance, rather than protein synthesis.

Evaluation of forages containing CT for animal performance can be made by comparison with a "standard diet", which is often perennial ryegrass (*Lolium perenne*) dominant pasture in New Zealand, or with an equivalent legume such as lucerne or white clover. The effect of CT in forage can be evaluated by giving one group of animals PEG with the forage, either as a drench (twice daily) or sprayed on the forage. The use of PEG to remove CT effects has been very useful to elucidate nutritional effects, but it provided confusing results when used to evaluate the impact of CT on gastro-intestinal parasites in sheep fed lotus major or lucerne (Niezen et al., 1998a). These comparisons differentiate between the "legume effect" when a high quality (low fibre) forage is compared to grasses of lesser feeding value, and the impact of the CT itself. Feeding value is described as nutritive value (NV) × intake (Waghorn and Clark, 2004), and can reveal the performance expected from healthy productive ruminants.

Comparisons of daily liveweight gain, wool production and reproductive performance of sheep fed birdsfoot trefoil as a sole diet (Table 1) show an advantage of about 30%, relative to good quality ryegrass dominant pasture. Much of this response is attributed to the higher feeding value of legumes. However comparison of birdsfoot trefoil with lucerne demonstrated a 10% improvement in lamb liveweight gain, wool growth, ovulation rate and also milk production from sheep and cows. The CT in temperate forages does not increase intakes (*e.g.* Waghorn et al., 1987, 1994a) because CT slow rates of digestion in the rumen, so the benefits to animal performance represent a higher efficiency of feed utilisation, associated with increased amino acid absorption.

When either sainfoin or sulla was fed as a sole diet, liveweight gain was similar to white clover and about 20% greater than for lucerne (Table 1). Calculations showed metabolisable energy (ME) expenditure (mega joule; MJ) in relation to liveweight gain in lambs fed sulla was about 61 MJME/kg liveweight *versus* 68 for lucerne and 93 MJME/kg from ryegrass pasture (Burke, 2004). In previous trials, lamb daily gain was 12% lower when lotus major fed as a sole diet, compared to white clover (Purchas and Keogh, 1984), and a high concentration of CT in lotus major has reduced lamb growth by 25% (Table 1). Net absorption of amino acids from the intestine was reduced by CT in lotus major (Waghorn et al., 1994b), increased with birdsfoot trefoil (Waghorn et al., 1987; Wang et al., 1996b) and unchanged with Sainfoin and Sulla (Bermingham et al., 2001).

6.3. Parasitism and forages containing CT

The net nutritional benefit of CT in birdsfoot trefoil and negative effects with lotus major highlights the importance of concentration, astringency, and CT structure (Table 3). However the impact of CT in lambs infected with *Teladorsagia circumcincta* and *T. colubriformis* was quite different, with clear benefits associated with lotus major and sulla, compared to lucerne and ryegrass/white clover pasture (Niezen et al., 1998b). Daily liveweight gains (g) in parasitised and non-parasitised lambs were, lotus major 160 *versus* 232; sulla, 175 *versus* 226; lucerne 121 *versus* 243 and pasture 88 *versus* 165. The legumes containing CT were able to maintain higher daily gains in parasitised lambs, compared to lucerne and pasture. More important, the sulla was able to lower nematode numbers in the gastro-intestinal tract (Niezen et al., 1995), and investigations using quebracho tannin (Athanasiadoa and Kyriazakis, 2004) suggest the CT can either mitigate the effects of parasitism or reduce worm numbers. The conclusions drawn by Athanasiadoa and Kyriazakis (2004) in their summary of CT effects on parasitism, also parallel current priorities for nutrition research—the need to better understand CT structure to explain some of the variation in anthelmintic responses to CT.

6.4. Potential for forages with CT in temperate agriculture

The summary of research presented in Table 1 has established responses to CT and relativity between sources of CT, but animal performance under normal farming conditions may vary considerably from experimental field trials. In many farming situations grasses form the principal component of pasture. Grasses tend to have higher DM yields than legumes and can develop into highly productive persistent swards when grown with a legume which fixes nitrogen. This has been the basis for New Zealand agriculture where most pastures are a mixture of ryegrass and white clover.

If lotuses were able to persist in a grassy sward, then more astringent tannin, such as that in lotus major may provide a superior animal performance than birdsfoot trefoil, because the CT would be substantially diluted by the grass component of the diet. The greater astringency of lotus major compared to birdsfoot trefoil when fed as one third of a grass-based forage has been demonstrated (Waghorn and Shelton, 1997) and the challenge for plant breeders is to select a more persistent and competitive high-CT lotus for sowing with pasture grasses. Research is addressing the persistency of birdsfoot trefoil, with a recent development of a rhizomatous strain containing about 3× as much CT in the DM as c.v. Grasslands Goldie (Widdup et al., 2004).

6.5. Challenges for CT in temperate agriculture

The lower yield of lotus species and difficulties in establishing sulla (Waghorn et al., 1998) or improving the persistence of sainfoin (McMahon et al., 2000) presents challenges for researchers and producers alike. However the advent of anthelmintic resistance, consumer concerns about animal welfare, legislative requirements to lower greenhouse gas (GHG) emissions and to minimise nitrogen contamination of ground water, as well as increasing restrictions on use of antibiotics and other proprietary drugs indicates the potential value of CT for ruminant production. There is a need to change the focus of some agricultural systems away from production (at any cost?) to sustainable production with animal welfare and economic success remaining primary objectives.

For example, inclusion of legumes in pastures will lessen the need for nitrogen fertiliser use and urea fertiliser incurs a high GHG emission cost during manufacture (from methane and energy). Urea and other nitrogen fertilisers stimulate grass growth but can also result in forage with very high N concentrations (40 g/kg DM), leading to a high urinary N output, much of which is volatilised (including to nitrous oxides) or leached into waterways or ground water (Monaghan et al., 2004). High nitrogen intakes have implications for infertility in dairy cows, nitrate poisoning, bloat and occasionally laminitis and pulmonary emphysema and the metabolic cost of ammonia removal can reach 4% of ME intake. Growing legumes with pasture will reduce the need for nitrogenous fertiliser and the CT will divert excess nitrogen away from urine toward the faeces, which are degraded more slowly and retained in the soil (Somda et al., 1993).

These and other benefits associated with CT are listed in Table 4. The prevention of bloat in cattle would eliminate daily dosing with detergents as a bloat preventative, but it is the value of CT as a means of reducing the impact of intestinal nematodes in ruminants which has greatest advantages for producers in all regions. Although tanniniferous forages are able to sustain good productivity in parasitised animals, very low concentrations of semi purified CT are able to prevent larval development *in vitro* (Molan et al., 2002). Researchers must accept the challenge to understand the basis for *in vitro* anthelmintic activity so CT can be made more effective *in vivo*.

Table 4
Potential benefits of diets containing condensed tannins for animal welfare and environmental sustainability

Reduced need for anthelmintic drenches
Lower incidence of faeces adhering to wool and flystrike
Lower urinary nitrogen production and less energy costs for urea synthesis
Prevention of legume bloat
Potential to balance nutrient needs with a mixed diet by including legumes with condensed tannins
Possible benefits of CT for gastro-intestinal integrity (antibiotic effect?)
Reduced risk of laminitis and pulmonary emphysema
Reduction in energy losses to methane
Reduced nitrogen losses to N_2O and leachate
Reduced requirement for nitrogenous fertiliser

Condensed tannins have reduced methane production (g/kg dry matter intake) by about 15% in sheep fed lotus major and by a similar amount in dairy cows fed lotus major (Waghorn and Woodward, 2006). A similar reduction was demonstrated by addition of CT from Black Wattle (*Acacia mearnsii*) given to sheep (Carulla et al., 2005) and Puchala et al. (2005) reported very low methane emissions from goats fed Serecia Lespedezia (*Lespedeza cuneata*) *versus* grass forage (6.9 *vs.* 16.2 g/kg DM intake). These reductions may benefit production because less feed energy is lost during digestion, in addition to lowering greenhouse gas emissions.

Whilst inclusion of forages with CT in animal diets may not be profitable for temperate agriculture at the present time (Waghorn and Clark, 2004, 2006), changes in ruminant diets may be brought about by consumer demands and legislation. For example the value of CT for reducing environmental pollution bought about by excess use of urea, and improved animal health when forages containing CT are fed, will be apparent if artificial nitrogen is taxed and drug use is further limited. Consumers are increasingly concerned about the welfare of animals, and legislative changes affecting use of drugs and other inputs to animal production, should offer a strong incentive to maintain CT research.

7. Condensed tannins in hot climates

Farmers in tropical climates are faced with a very different situation to those in temperate regions. Ruminant feeding also differs from temperate regimes, in both feed quality and management of sheep and goats. Temperate systems have moved towards large farming operations, primarily with sheep and cattle, where animal numbers are measured in hundreds or thousands on individual farms. There are higher proportions of goats in hot climates, but animal numbers on individual farms are usually low, farming tends to be less intensive and many farmers will be poorly resourced.

In hot regions, ruminant diets are dominated by C4 grasses, as well as shrubs and fodder trees. The low feeding value of C4 grasses is a consequence of high fibre concentrations, low readily fermentable carbohydrate and protein contents and a higher bulk density (few air cavities) requiring more chewing for digestion (Waghorn and McNabb, 2003). Fibre concentrations can exceed 700 g/kg of the DM and become extensively lignified which is the primary deterrent to selection by sheep and goats. Mature or senescent C4 grasses will not meet maintenance requirements, so animals seek forage with a higher CP concentration and less fibre, such as leaves of browse.

Poor quality grass presents a strong drive to select more succulent forage, especially with goats (Ben Salem et al., 2000). However leafy material contains a range of secondary metabolites, including CT, which will always reduce the nutritive value of a diet with marginal or insufficient protein. Although the CT in browse may limit its feeding value, there are often no affordable alternatives.

7.1. *Management of dietary condensed tannins*

There are several methods for reducing the impact of dietary condensed tannins, but not all will benefit production. Drying or wilting browse is an inexpensive option, and can irreversibly bind the CT to protein in the forage. Drying may prevent CT from damaging the gastro-intestinal tract, but overall benefits of the protein to performance will usually be minor (Degen et al., 2000). Condensed tannins can be diluted with other forages but nutritional benefits will only occur if dietary CP concentration is increased, which is unlikely in hot environments and impractical for farmers with small flocks of sheep or goats.

A more promising mitigation for CT is through provision of a tannin-binding compound in the diet, such as PEG. This approach will improve animal performance, but the value of gains in productivity must exceed the cost of the PEG. The benefits of PEG have been evaluated in Mediterranean regions and elsewhere in Africa, with clear benefits for liveweight gain and lactation.

The cost of PEG is likely to limit its use by farmers and Ben Salem et al. (2005a) have shown that chopping and soaking leaves of Acacia (*A. cyanophylla* Lindl.) in solutions of wood ash can de-activate the CT and increase organic matter digestibility and nitrogen retention by sheep. Ongoing investigations (Ben Salem et al., 2005b) include soaking in water and water with urea to lessen the impact of tannins in Acacia leaves. These options are less costly for farmers in many regions but will require harvest and processing of foliage.

Options for mitigating effects of tannins are best achieved when the principal secondary metabolites in the diet are known, so clear management protocols can be devised. Protocols will differ for sheep and goats and must consider the CT in conjunction with other dietary components affecting animal performance. Genetic merit of the animals may also affect their response to PEG, and responses by native or unselected animals to PEG supplements may be less than anticipated (Gilboa et al., 2000). Conversely, high producing animals must be well fed in order that they may express their genetic potential.

7.2. *Effect of PEG on diet selection and performance*

A number of investigations have defined the effects of PEG (usually molecular weight 3500) on productivity, intake and choice of browse. PEG has been provided either as free choice, in drinking water, feedblocks (Ben Salem and Nefzaoui, 2003; Ben Salem et al., 2000), mixed with concentrate (Ben Salem et al., 2002) or given once or twice daily as an oral drench. Inclusion of 40 g/kg PEG in a forage based diet that included 56% carob pods, increased lamb growth threefold and increased DM and N digestibility by 15 and 20 percentage units, respectively (Priolo et al., 2000). In a separate trial, Priolo et al. (2002) demonstrated daily gains of 116 and 172 g by lambs given a similar diet containing 10 or 40 g PEG/kg DM. Nitrogen digestibility was 0.64 and 0.71 and they concluded the optimal PEG requirements for this type of diet (21 g/kg CT in the DM) exceeded 10 but was less than 40 g/kg of the DM. Atti et al. (2003) demonstrated a similar rate of muscle growth in lambs given concentrates or a diet containing *A. cyanophylla* with 20 g PEG/day, and showed browse with PEG was able to yield leaner carcasses at a lower cost.

When sheep or goats are offered *ad libitum* browse containing CT, provision of PEG will often increase intakes of the tanniniferous forage. In non-parasitised animals, rates of liveweight gain will increase, but cost-effective benefits of PEG supplementation will be best achieved with animals selected on the basis of genetic merit (Gilboa et al., 2000). They showed that a single daily dose of 10 g PEG, improved liveweight gain during pregnancy, kid birth weight and gains to weaning of Mamber goats. The same study showed Damascus × Anglo-Nubian goats produced 43% more milk (0.46 kg/day) when grazing scrubland (primarily *Q. calliprinos*, *Q. boisserii* (Reuter), *Pistacia palestina*, *Sarcopoterium spinosa*, *Rhamnus palaestina*) with PEG and concentrate supplements.

Other examples of PEG impact upon digestibility include increased in N digestion from 37 to 71% in goats offered *ad libitum* lentisk (*Pistacia lentiscus*) with 200 g concentrate/day (Decandia et al., 2000) and from 40 to 53% in a separate experiment with milking goats. In all instances, the amount and proportion of tanniniferous material eaten is increased when PEG is given, which suggests avoidance is not a consequence of palatability. Sheep and goats avoid excess CT because of the consequences for digestion.

Ben Salem et al. (2000) showed that goats consumed more browse than sheep and choice was affected by moisture and mineral content and avoidance of fibre. In other comparisons between goats and sheep, goats consumed more *Acacia saligna*, in terms of metabolic bodyweight (BW), than sheep and a daily administration of PEG (approximately 40 g/day) increased DM intake by 62 and 83% for the respective species (Degen et al., 2000). Villalba et al. (2002) showed that access to PEG resulted in a similar increase in intake of a pelleted tanniniferous (Quebracho) diet by lambs (39–70 g/kg $BW^{0.75}$) and kids (33–63 g/kg $BW^{0.75}$). Lambs consumed a similar ratio of PEG:CT (11:13 g/kg $BW^{0.75}$/day) but less PEG was consumed by kids (7:10 g/kg $BW^{0.75}$/day). These findings suggest animals are able to self-regulate their intake of PEG, and the lower PEG intake by kids relative to CT corresponds with a higher saliva production.

7.3. Anthelmintic value of CT

The benefits of forages containing condensed tannins for productivity by sheep carrying an intestinal parasite burden (Niezen et al., 1995, 1998b, Table 1) have also been demonstrated in deer (Hoskin et al., 2000) and in goats. Heckendorn et al. (2006) showed both Sainfoin hay and silage were effective in reducing adult *Haemonchus contortus* numbers in lambs ($P<0.05$) and the CT lowered the fecundity of *Cooperia curticei* ($P<0.001$). Trials with quebracho tannin, at up to 60 g/kg of DM intake, reduced faecal egg counts (FEC), worm fecundity and worm numbers in parasitised sheep in some but not all instances (Athanasiadou et al., 2000; Athanasiadoa and Kyriazakis, 2004). Quebracho tannin (at 50 g/kg of DM intake) also reduced FEC and sometimes worm fecundity and worm numbers in goats infected with either *T. colubriformis* and *Teladorsagia circumcincta* or *H. contortus* (Paolini et al., 2003a,b).

Min et al. (2004) fed parasitised goats (primarily *H. contortus*) alternating diets of Sericea lespedeza and a mixed pasture of ryegrass and crabgrass (*Digitaria sanguinalis*) on a 15-day rotation. The Sericea lespedeza contained 46 g extractable CT/kg DM and the alternating feeding regimen lowered daily faecal egg output from 173×10^4 (ryegrass/crabgrass only) to 45×10^4 (alternating feed) and reduced egg development to L3 larvae from 99 to 58%. More recently Shaik et al. (2006) demonstrated the efficacy of Sericea lespedeza hay for reducing ($P<0.01$) *H. contortus* and *Teladorsagia circumcincta* and *T. colubriformis* nematode numbers in goats. The impact of condensed tannins on larval development complements findings of Molan et al. (2002), so that the combined effects of lower egg output and development will lessen pasture contamination with infective larvae.

The benefits of CT for parasitised goats have been demonstrated with as little as 9 g/day from *Viscum verrocosum* (Madibela and Jansen, 2003) and by Kabasa et al. (2000) who showed substantial benefits of CT for pregnant goats grazing browse. They gave half of the goats a daily drench of 50 g PEG over the 6-month experimental period, during which the goats developed a gastro-intestinal burden initially of *T. colubriformis*, followed later by *H. contortus*. The goats spent 60–85% of their eating time selecting browse, which formed a substantial portion of their diet, and those receiving PEG had double the FEC relative to undrenched control goats. The PEG reduced daily gain from 92 to 70 g/day. Kabasa et al. (2000) concluded that CT played a significant role in reducing the negative effects of gastro-intestinal parasitism and suggested the goats selected a diet to provide optimal concentration (or type) of condensed tannins. They warned that increasing arable animal management would remove this capability.

The significance of gastro-intestinal worm mitigation cannot be under estimated, and reduced performance associated with a short exposure to high CT concentrations for parasite control may become part of a sustainable management strategy. These examples of gastro-intestinal parasite mitigation provides an important incentive for CT research, but the occasional variability in responses suggest more emphasis be placed on defining the chemical structure of the tannin being evaluated.

8. Future research priorities

8.1. Chemistry

Both the nutritional and anthelmintic potential of CT can only be realised when the composition, structure and biological function of CT (and other secondary metabolites) are better defined. Chemical analyses should be complemented by measurements of binding capacity with plant proteins and effects on enzyme activity or *in vitro* digestion, because the relationships between chemical structure and astringency are not yet clearly defined. Diligence in analyses and experimental design, will enable optimal CT to be identified for expression in temperate legumes by genetic engineering, conventional selection as part of plant breeding programmes, or for mitigation of gastro-intestinal parasites using existing forages.

8.2. Management through plant and animal selection

Medium-long term management of CT should be undertaken on the basis of astringency, which will require an improved understanding of condensed tannin chemistry and the concentration expressed in edible portions of plants. In high quality temperate forages, selection should focus on low concentrations of astringent CT, to minimise ruminal protein degradation, with minimal reduction in plant digestible DM content. The major challenge in temperate regions is the integration of these forages into grazing systems, or expression of CT in highly productive forages (*e.g*. lucerne or white clover). Selection of Sericea lespedeza to lessen the impact of CT on digestibility has been successful (Donnelly and Anthony, 1970) and future identification of browse with lower concentrations and/or less astringent CT, to improve the feeding value of diets where protein concentration my limit production, could be undertaken on the basis of animal trials or chemical analyses. Wiegand et al. (1995) demonstrated accessions of *Sesbania sesban* that were less detrimental to animal performance, but future benefits will only occur if these trees can be managed and sustained.

Opportunities for animal selection are available within sheep or goat populations. Goats produce more saliva and also proline-rich salivary proteins (able to bind and reduce the activity of CT; Robbins et al., 1991) compared to sheep, as evidenced by their propensity to browse tanniniferous plants rather than graze, but within each population some individuals will have a greater or lesser capacity for production when offered a mixed diet. Examples of potential differences between individuals which could benefit performance include a larger rumen capacity, so the slower degradation rate of tanniniferous forages would have less effect on feed intake (Waghorn et al., 1994a) and more extensive chewing enabling a more rapid clearance of poorly digested residues from the rumen. Other opportunities for exploitation include superior foraging and selection of less astringent dietary constituents, a longer intestine to improve fractional absorption of AA (Wang et al., 1996b) and resistance to gastro-intestinal parasites. A focus on tolerance to CT could have positive outcomes for sheep and goat production in hot climates but a combination of animal and management strategies is most likely to have the best outcome for producers.

9. Conclusion

The impact of CT upon ruminant performance will depend on the amount and astringency in the diet, animal nutrient requirements and other dietary components. There are potential benefits for incorporating CT into high quality temperate forages, but these are limited by the growth and persistence of forages expressing CT. Other benefits for improving animal health, reducing needs for chemical intervention and achieving sustainable farming have resulted in a substantial research effort to express CT in the foliage of lucerne or white clover. The impact of CT on rumen and intestinal function is similar in temperate and hot climates, but poor quality pasture in hot regions and the availability of browse inevitably results in anti-nutritional effects. Use of PEG to mitigate effects of CT offers good potential to improve sheep and goat production and potential anthelmintic effects offer a real benefit for farmers. Successful management of CT in all regions will depend on a combination of chemical analysis and animal experimentation.

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