

# Tannins for suppression of internal parasites

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**ABSTRACT:** It is increasingly evident that gastrointestinal parasite (GIP) control programs based on dewormers are failing because of increased dewormer resistance; thus, alternative GIP control strategies are necessary. Condensed tannins (CT) have biological effects that may aid in the control of GIP. The CT bind proteins and other molecules tightly at near-neutral pH, such as occurs in the rumen, with dissociation in the acidic pH of the abomasum, freeing them for digestion. Plant CT may have direct or indirect effects on GIP. Direct effects might be mediated through CT-nematode interactions, thereby affecting physiological functioning of GIP. Condensed tannins extracted from various forages can markedly decrease the viability of the larval stages of several nematodes in sheep and goats. Con-

densed tannins also may react directly by interfering with parasite egg hatching and development to infective stage larvae. Indirectly, CT can improve protein nutrition by binding to plant proteins in the rumen and preventing microbial degradation, thereby increasing amino acid flow to the duodenum. Several sheep studies have shown that improved protein nutrition decreases parasite infestation. This is assumed to be mediated by enhanced host immunity, which may be especially important with selection for immunity to GIP. Therefore, CT might counteract parasites by one or more of the aforementioned mechanisms, and mechanisms involved might differ between CT from different forage species. In conclusion, CT in forages have the potential to aid in the control of GIP.

Key Words: Digestive Tract, Forage, Nutrition, Parasites, Ruminants, Tannins

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## Introduction

Gastrointestinal parasites (GIP) cause marked production losses to livestock throughout the world (Sykes, 1994). Control of ruminant GIP over the past decades has been achieved by the use of anthelmintic drugs, but control of GIP is becoming more difficult due to the increased resistance of parasites to common anthelmintics, which has been reported in goats, sheep, and cattle (Prichard, 1994; Waller, 1994; Pomroy et al., 2002). Alternative parasite management strategies using forages containing condensed tannins (CT) have recently been suggested (Niezen et al., 1995; Barry et al., 2001; Min et al., 2002b). It seems possible that consumption of forage CT may reduce GIP numbers and improve animal performance through direct and indirect mechanisms. Alternative, nondrug GIP control strategies that are practical and realistic for introduction into farm production systems are required. This review, based on

published literature, summarizes data on CT and GIP and on the nutritional consequences of CT-containing grazed forages.

## Forages and Condensed Tannins

Tannins are usually classified either hydrolyzable tannins (HT) or CT (proanthocyanidins) based on their molecular structure. Hydrolyzable tannin molecules contain a carbohydrate (generally D-glucose) as a central core. The hydroxyl groups of these carbohydrates are esterified with phenolic groups, such as ellagic acid or gallic acid (Haslem, 1989). Hydrolyzable tannins can be further metabolized to compounds such as pyrogallol (Murdiati et al., 1992), which are potentially toxic to ruminants (Dollahite et al., 1962). Some rumen bacteria involved in this degradative pathways include *Eubacterium oxidoreducens*, *Streptococcus bovis*, *Syntrophococcus sucromutans*, and *Coprococcus* spp. (Tsai et al., 1976; Krumholz and Bryant 1986a,b). Plants that are considered to be toxic due to HT include *Clidemia hirta* (harendog; Murdiati et al., 1991), *Quercus ilex* (oak; Camp et al., 1967), *Terminalia oblongata* (yellow wood; Doig et al., 1990) and *Ventilago viminalis* (supplejack; Pryor et al., 1972).

The CT are the most common type of tannin found in forage legumes, trees, and shrubs (Barry and McNabb,

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**Table 1.** Characteristics of condensed tannins (CT) in different forage species<sup>a</sup>

Forage	CT, g/kg of DM	MW range	CT structure <sup>b</sup>
Temperate legumes			
<i>Lotus corniculatus</i> (birdfoot trefoil)	48	1,800 to 2,100	67:30
<i>Lotus pedunculatus</i> (big trefoil)	77	2,200	19:64
<i>Onobrychis viciifolia</i> (sainfoin)	29 <sup>2</sup>	2,040 to 3,060	81:19
<i>O. arenaria</i>	29–38	1,560 to 3,300	75:25
<i>O. vaginalis</i>	—	1,980 to 2,700	80:20
<i>O. antasiatica</i>	—	1,650 to 2,490	76:24
<i>Hedysarum cornarium</i> (sulla)	51–84	—	—
<i>Medicago sativa</i> (lucerne)	0.5	—	Trace D
Tropical legumes			
<i>Lespedeza cuneata</i> ( <i>Sericea lepedeza</i> )	46 <sup>c</sup>	14,000 to 20,000	Mainly PD
<i>Leuceanea diversifolia</i>	96	—	PC/PD
<i>Desmodium ovalifolium</i> 13089	232	—	—
Grass			
<i>Lolium perenne</i> (perennial ryegrass)	1.8	—	Trace D, C
Herbs			
<i>Chicorium intybus</i> (chicory)	3.1	—	—

<sup>a</sup>References: McLeod, (1974); Terrill et al. (1992); Koupai-Abyazani et al. (1993); Jackson et al. (1996); Foo et al. (1996; 1997); Min et al. (1997; 2001a), Bermingham et al. (2001).

<sup>b</sup>PC:PD ratio = procyanidin:prodelphinidin; D = delphinidin; C = cyanidin.

<sup>c</sup>Extractable CT.

1999). Structurally, CT are complexes of oligomers and polymers of flavanoid units linked by carbon-carbon bonds (Hagerman and Butler, 1981; Foo et al., 1986). The CT exist as oligomers of flavan-3-ols (catechin) or flavan-3,4-diols (epicatechin), and those occurring in temperate forages have a relative molecular mass of 2,000 to 4,000 comprising 10 to 12 oligomers of CT (Foo et al., 1986). Together, these differences can produce an infinite variety of chemical structures, which in turn affect the physical and biological properties of the CT. Condensed tannins accumulate in the vacuoles of cells in various tissues of many forage species. Structure and range of molecular weights (MW) for forage CT are summarized in Table 1. This review paper deals mainly with CT.

### Nutritional Effects of Condensed Tannins

Condensed tannins can complex with numerous types of molecules including proteins, polysaccharides, nucleic acids, and minerals (Spencer et al., 1988; Haslem, 1989). Condensed tannin complexes are mainly by hydrophobic/hydrogen interactions (Hagerman and Butler, 1981; Haslem, 1989). Formation of the CT-protein complex is influenced by many factors, such as pH, composition, and MW of both the CT and the proteins (Asquith and Butter, 1986). Although CT interact with carbohydrates, particularly starch, their affinity for carbohydrates seems to be much less than for proteins (Haslem, 1989). Moderate levels of CT (20 to 40 g of CT/kg of DM) bind to protein by hydrogen bonding at near neutral pH (pH 6.0 to 7.0) in the rumen to form CT-protein complexes, but dissociate and release bound protein at pH less than 3.5 in the abomasum (Barry et al., 2001). Thus, CT-containing plants can protect dietary protein against degradation in the rumen and

increase AA supply to the abomasum and small intestine, resulting in a improved nutritional status of the animal.

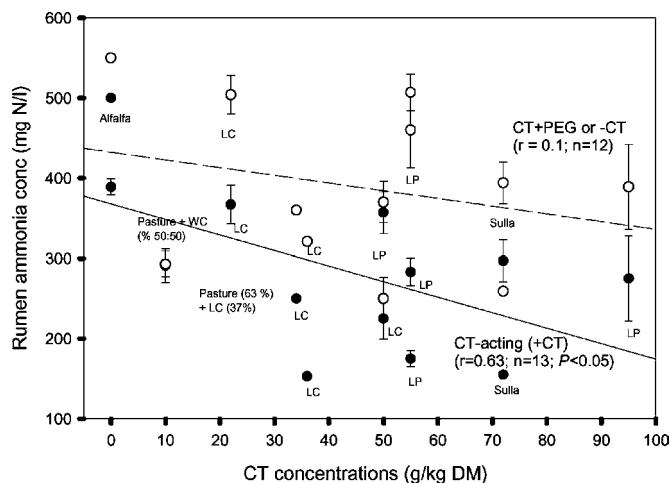
At similar CT concentrations (0.25 to 1.75 mg of CT/mg of total soluble plant protein), *Lotus pedunculatus* CT was more effective at protecting the plant protein from degradation by rumen microorganisms than *Lotus corniculatus* CT (Aerts et al., 1999). This effect of CT on plant protein degradation may be due to differences in the chemical structure influencing the reactivity of the CT (Table 1). The average MW of CT in *L. corniculatus* is 1,900, whereas that in *L. pedunculatus* is 2,200. In addition, the CT from *L. pedunculatus* contains a predominance of prodelphinidin (PD)-type subunits. Conversely, the CT from *L. corniculatus* is comprised predominantly of procyanidin (PC) subunits with a dominance of epicatechin (67%; Foo et al., 1996; 1997). The large number of free hydroxyl groups enables hydrogen bonding with proteins and other molecules, but the extent of the association appears to be affected by the size of the polymer, the predominance of prodelphinidin relative to procyanidin units, the types of terminal groups (2,3-*cis* or 2,3-*trans*), and the structure of potential binding sites (C4/C8 or C4/C6 interflavanoid linkages that effect the shape of the CT polymer chain; Hagerman and Butler, 1981; Foo et al., 1996; 1997). Therefore, the chemical structure of CT, as well as its concentration, needs to be considered in studies involving protein degradation and GIP control.

Barry and Forss (1983) defined CT associated with plant protein after mastication as bound CT, and the CT remaining in the supernatant after high-speed centrifugation as free CT. It has been suggested that high concentrations of free CT in the rumen can react with other sources of protein after chewing by animals, such as enzymes secreted by rumen bacteria, and so inhibit

rumen carbohydrate fermentation (Barry and Manley, 1986). Therefore, high CT concentrations such as those in *L. pedunculatus* (63 to 106 g of CT/kg of DM) substantially depressed feed intake, digestibility, and animal production in sheep (Barry and Duncan, 1984; Waghorn et al., 1994). Other forages with high concentrations of CT (over 50 g of CT/kg of DM) that have resulted in antinutritional effects when consumed include *Lespedeza cuneata* (sericea lespedeza; Windham et al., 1990), *Acacia aneura* (mulga; Pritchard et al., 1988), and *Eucalyptus melliodora* (eucalyptus; Foley and Hume, 1987). However, not all of the antinutritional effects of CT can be attributed to their high concentration in the diet. *Onobrychis viciifolia* (Sainfoin; 50 to 80 g of CT/kg of DM), *Hedysarium cornarium* (Sulla), and *L. cuneata* (52 g of CT/kg of DM), when fed to sheep and goats, had a higher nutritive value than similar forages without CT (Ulyatt et al., 1976; Niezen et al., 1995; Min et al., 2003a).

When ruminants are fed on high-quality fresh forages containing high concentrations of N (25 to 35 g of N/kg of DM), carbohydrate digestion in the rumen is efficient; however, degradation of forage N is excessive, resulting in surplus levels of ammonia (20 to 35%) in the rumen and absorption of that ammonia from the rumen, which is ultimately excreted as urea in the urine (Ulyatt et al., 1975). Therefore, a reduction of protein degradation in the rumen will increase the quantity of protein digested in the small intestine, potentially increasing animal production. It has been reported that CT in forages markedly reduces protein solubilization and degradation in the rumen and reduces ruminal proteolytic activity, but may inhibit extracellular microbial enzymes (proteinases, cellulases, and hemicellulases; Chung et al., 1998a,b; Min et al., 2001a; 2002a).

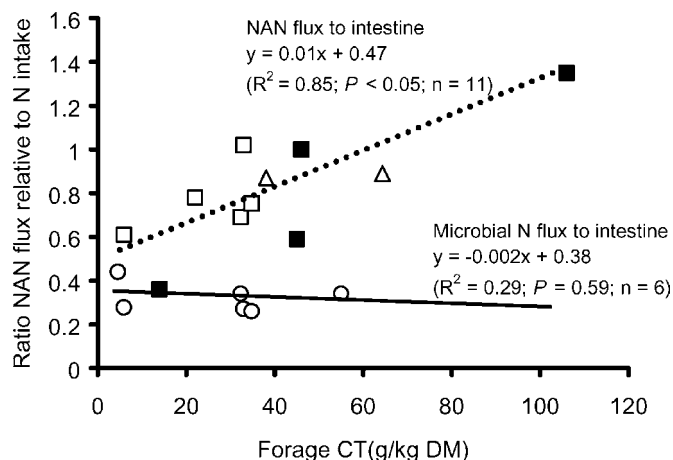
Figure 1 shows the reduction in rumen ammonia concentration as related to CT concentration compared with polyethylene glycol (PEG) supplementation or nonCT-containing forages. The specific effects of CT can also be assessed using PEG, which binds and inactivates CT. Figure 1 implies that CT in forages reduced rumen degradation of forage protein to ammonia (McNabb et al., 1996; Min et al., 2000). In situ and in vitro experiments have shown that this is due to the action of CT in *L. pedunculatus* and *L. corniculatus* slowing the rates of both solubilization and degradation of forage proteins by rumen microorganisms (McNabb et al., 1996; Min et al., 2000). In the absence of CT, 27% of the total N in *Trifolium repens* (white clover) forage was immediately solubilized, with the rate of rumen solubilization of the insoluble component being 15%/h (Min et al., 2000). These values show that the total N in *T. repens* forage was rapidly solubilized compared to the CT-containing forage *L. corniculatus* (23% total N immediately solubilized and 8%/h for the rate of rumen solubilization, respectively). In ruminants fed fresh forages, most proteins are rapidly solubilized, releasing 56 to 65% of the N concentration in the rumen as soluble N during mastication; consequently, a large



**Figure 1.** The relationship between condensed tannins (CT) concentration in fresh forage species and ruminal ammonia concentration in sheep. Animals were offered either a nonCT containing-forage, forage + polyethylene glycol (PEG) supplementation (○; nonCT), or CT-containing pasture without PEG (●; CT containing). WC = white clover, LC = *Lotus corniculatus*, LP = *L. pedunculatus*. The bars indicate the SEM when available. References: Barry and Manley (1984; 1986); Waghorn et al. (1987a; 1994); Terrill et al. (1992); Waghorn and Shelton (1992); Stienezen et al. (1996); Wang et al. (1996a). Min et al. (1998); and Douglas et al. (1999)

amount of soluble N is degraded by rumen microorganisms and N is lost as ammonia absorbed from the rumen (Ulyatt et al., 1975). The minimal concentration of CT (g/g of protein) needed to reduce proteolysis in laboratory studies is 1:10 (wt/wt; Tanner et al., 1994) or 1:12 (wt/wt; Jones and Mangan, 1977), with 5 mg of CT/kg of DM or greater being required to prevent bloat in cattle (Li et al., 1996).

Responses of rumen ammonia concentrations in sheep grazing CT-containing forages to PEG supplementation were due to the effect of PEG in preventing binding of CT to protein (Figure 1). Twice-daily oral PEG supplementation to sheep was sufficient to observe responses, but it is still not known if the response was maximal. However, sheep and goats exhibited different levels of tolerance to the effects of CT (Narjisse et al., 1995). Narjisse et al. (1995) reported that rumen ammonia in sheep was depressed by tannins extracted from *Quercus ilex* leaves (oak; 1 g of tannins/kg of BW), but was not affected in goats. The absence of a CT effect noted in goats should be considered with caution. The lack of effect of tannins in goats might result from the greater ability of their rumen microbial (*Streptococcus caprinus*) population to degrade tannins and their higher urea recycling and salivary secretion capabilities (Cocimano and Leng, 1967; Brooker et al., 1994). However, the diversity of tannin-tolerant rumen microorganisms is probably poorly represented by the few ruminal isolates that have currently been described.



**Figure 2.** Effect of forage condensed tannins (CT) on fraction of intake nitrogen reaching the small intestine. Figure shows the relationship between CT concentration (DM basis) in forage species DM (x-axis) and the ratio of nonammonia N (NAN) flowing at the abomasum or duodenum (□, *Lotus corniculatus*; ■, *L. pedunculatus*; △, Sainfoin; △, Sulla) and microbial N (○, *L. corniculatus* and *L. pedunculatus*) per unit of N consumed by sheep. References: Barry and Manley (1984; 1986); Waghorn et al. (1987a,b; 1994); McNabb et al. (1993); Wang et al. (1996b); Bermingham et al. (2001); and Min et al. (2001a).

Tolerance of protozoa, fungi, and bacteria to CT needs investigation, as does the role of tolerant microorganisms in the degradation of tanniferous forages. Goats produce more protein-rich saliva during eating than sheep (Dominigue et al., 1991). Gilboa (1995) also found that the parotid saliva of goats was relatively rich in proline (6.5%), glutamine (16.5%), and glycine (6.1%), which are known to enhance the affinity of proteins to CT (Mehansho et al., 1987). Furthermore, the concentration of protein in parotid saliva was significantly higher in goats (550 µg/mL) fed *Ceratonia siliqua* (carob; high in CT) than in goats (212 µg/mL) fed wheat straw (no CT), suggesting that exposure of goats to CT enhanced the secretion of proteins in parotid saliva (Gilboa, 1995). Hence, data on the effect of tannins on N digestion obtained with sheep and cattle may or may not be directly applicable to goats; more research is needed on the effects of forage CT in goats.

To further understand the effect of CT concentration on N digestion in the rumen, duodenal (abomasal) non-ammonia N (NAN) outflow per unit of N consumed has been plotted against CT concentration in fresh forages for sheep (Figure 2). Total NAN flux progressively increased with increasing CT concentration, whereas rumen microbial N outflow was little affected. This indicates that increasing CT concentration increased the amount of undegraded and total protein flowing to the small intestine.

Moderate levels of CT (20 to 40 g of CT/kg of DM) in forages (*L. corniculatus*) fed to sheep increased absorption of essential AA from the small intestine by 62%

(Waghorn et al., 1987b). Increased milk and wool production in sheep (Barry and McNabb, 1999; Min et al., 1999) and increased milk production in dairy cows (Woodward et al., 1999) were also observed when dietary forages contained CT (20 to 40 g of CT/kg of DM). Production of milk protein in dairy cows and sheep was increased by 40% with CT-containing forages. However, forages with high concentrations of CT (55 to 106 g of CT/kg of DM) may reduce productivity (Barry and Manley, 1984).

### Condensed Tannins and Gastrointestinal Nematodes

In most experiments, the effects of CT are determined by comparing CT-containing legumes to commonly grown forages that do not contain CT, such as *Medicago sativa* (alfalfa), *T. repens* (white clover), and *Lolium perenne* (perennial ryegrass). Alternatively, since PEG complexes with CT, thereby inactivating it, the effects of CT can be quantified by comparing nonPEG-treated animals (CT-active group) with animals given PEG (CT-inactive; control). However, Niezen et al. (1998b) reported that the use of PEG does not seem appropriate in parasitology studies. Total nematode burdens in lambs did not differ between ryegrass and *L. pedunculatus*, but were greatest in lambs fed ryegrass and given PEG, suggesting that PEG may have some unidentified effect on GIP numbers.

Parasitism of the abomasum and small intestine causes extensive protein losses in the digestive tract of sheep (Kimambo et al., 1998). Alternative, nondrug parasite-control strategies have recently been suggested based on using forages that contain CT (Table 2; Niezen et al., 1995; Barry et al., 2001). Condensed tannins may have direct effects on internal parasites themselves or may indirectly control the parasites by increasing the resistance and resilience of animals to

**Table 2.** The effect of grazing condensed tannins (CT)-containing forage (*Hedysarum coronarium*; sulla) on the growth and parasite status of anthelmintic-drenched (parasite free) and nondrenched (parasitised) lambs. *Medicago sativa* (lucerne) also was grazed as a control legume<sup>a</sup>

Item	<i>Medicago sativa</i>	<i>Hedysarum coronarium</i>	P-value <sup>b</sup>
Total condensed tannins, g/kg of DM	1.5	110	0.001
Live weight, g/d			
Anthelmintic drenched	230	247	NS
Non-drenched	37	207	0.001
Fecal egg counts, eggs/g			
Nondrenched	2,220	1,320	0.01
Total worm burden			
Nondrenched	18,676	10,553	0.01

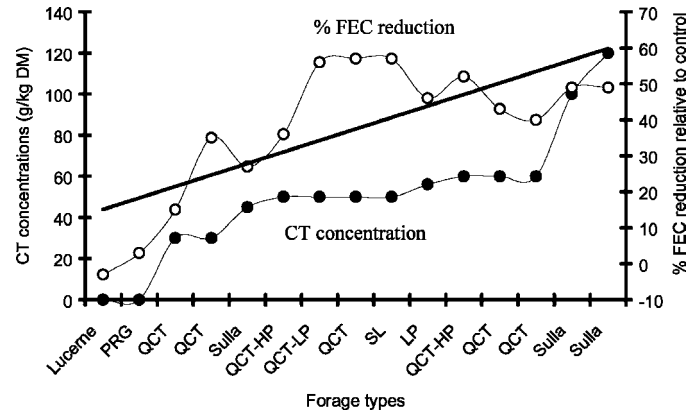
<sup>a</sup>Niezen et al. (1995; 1998a,b).

<sup>b</sup>NS = not significant.

GIP infections through improved protein nutrition. Possible direct effects could be mediated through CT-nematode interactions, which reduce nematode viability. It has been reported (Table 2; Niezen et al., 1995) that direct effects of CT on GIP may account for reduced fecal egg counts (FEC) and nematode burdens in lambs that grazed *Hedysarum coronarium* compared to *M. sativa* in New Zealand. Evidence in support of the direct affect of CT was provided by Molan et al. (2000) who demonstrated that the CT extracted from *L. pedunculatus*, *L. corniculatus*, *H. coronarium*, and *O. viciifolia* forages reduced the rate of larval development (eggs to L<sub>3</sub> larvae) by 91%, reduced the number of eggs hatching by 34%, and decreased the mobility of L<sub>3</sub> larvae by 30%.

Indirect effects on resistance and resilience could be mediated by changes in the supply of digested protein. Protein supplementation appears to be effective in enhancing specific immune responses for intestinal parasite infection (Bown et al., 1991). It has been shown that animals fed high planes of nutrition are better able to resist infection and disease, whereas disease is more severe in animals with low protein intakes (Bown et al., 1991). Protein supplementation has been shown to increase the resistance of sheep to *Haemonchus contortus* (Wallace et al., 1996). Hence, dietary CT may benefit parasitised ruminants by improved protein nutrition, which in turn may enhance animals' immune response to the parasite infection (Niezen et al., 2002; Min et al., 2003a). This offers exciting possibilities for the future. The effect of CT in *L. cuneata* (52 g of CT/kg of DM) on the immune response was compared with a control forage low in CT (crabgrass/tall fescue; 2.0 g of CT/kg of DM) in grazing Angora does (Min et al., 2003a). Immune response was greater ( $P > 0.01$ ) for *L. cuneata* than for the control at 12 and 24 h after injection of 250  $\mu$ g of phytohemagglutinin. Furthermore, grazing lambs on CT containing forage (*H. coronarium*) was associated with higher antibody titers of secretory-excretory antigens against adult worms (Niezen et al., 2002).

The FEC and parasite burdens at slaughter (Table 2) were considerably lower for lambs grazing *H. coronarium* (CT-containing forage) than for lambs grazing *M. sativa* (Niezen et al., 1995; 1998a,b). Dewormed lambs grew at similar rates when grazing *H. coronarium* or *M. sativa*. However, nondewormed lambs grew much better on the *H. coronarium*, indicating a reduced need for anthelmintic drugs to control GIP in grazing lambs. Recently, Min et al. (2003b) showed that GIP were controlled when Angora does were grazed (81 d) on *L. cuneata* (52 g of CT/kg of DM) in spring and summer, but not when goats were grazed on control forages (crabgrass/tall fescue; 2.0 g of CT/kg of DM). Tracer goats that grazed *L. cuneata* had a 76% reduction in total adult worm burdens compared with the control. The *L. cuneata* diet was also associated with a reduction in the numbers of *Haemonchus* (94%) and *Teladorsagia* spp. (100%) in the abomasum and *Trichostrongylus* (45%) in the small intestine.



**Figure 3.** The effect of forage condensed tannins (CT) concentration (●) on percentage fecal egg count (FEC) reduction (○) relative to control. Calculated as (CT active – CT inactive group)  $\times$  100/CT inactive group. PRG = perennial ryegrass/white clover, QCT = Quebracho CT, QCT-HP = QCT-high protein, QCT-LP = QCT-low protein, SL = Serricea lespedeza; LP = *Lotus pedunculatus*. References: Terrill et al. (1992); Niezen et al. (1995; 1998a,b); Jackson et al. (1996); Athanasiadou et al. (2000a,b; 2001), Butter et al. (2000); and Min et al. (2002b).

Fecal egg count reductions (percentage) from the action of CT have been plotted against CT concentrations for sheep and goats fed either CT-containing forages or drenched with CT extracts from plants (Figure 3). The results show that FEC were reduced by 50% with CT-containing forages (45 to 55 g of CT/kg of DM) relative to nonCT-containing forages. When CT concentration increased above 55 g of CT/kg of DM, the responses became variable, as shown in Figure 3. However, when CT concentration decreased below 45 g of CT/kg of DM, the FEC response was inconsistent. Therefore, beneficial effects of CT in plants for FEC occur in the range 45 to 55 g of CT/kg of DM. It is not yet fully understood how CT affects GIP, and this area merits further study.

The effect of CT in *L. cuneata* (46 g of CT/kg of DM) on FEC in goats has been studied using a crossover design with ryegrass/crabgrass (0.6 g of CT/kg of DM; Min et al., 2002b). Goats that consumed *L. cuneata* had significantly lower FEC (1,162 eggs/g) than goats that grazed on nonCT-containing control forage (2,722 eggs/g). This research (Min et al., 2002b) showed a 57% reduction in FEC and a 61% reduction in total fecal egg output in goats that consumed forage *L. cuneata* ( $66 \times 10^4$  eggs/d) compared with control forage ( $168 \times 10^4$  eggs/d). These results suggest that forage containing 5% extractable CT may substantially reduce the contamination of pastures with infective larvae and result in reduced need for anthelmintic drenches.

More controlled studies have demonstrated an effect of CT (0 to 60 g of CT/kg of pelleted food) from Quebracho extract (from the bark of the tropical dicotyledon *Schinopsis* spp.) on nematode egg production (Athanasiadou et al., 2000b; 2001). Per capita fecundity of worms

(FEC [eggs/g] divided by the total number of female worms recovered) of *Trichostrongylus colubriformis* was reduced in sheep drenched with 16% Quebracho CT (wt/wt) of food intake compared to worm fecundity in control sheep (0.055 vs. 0.181 eggs/female worm per day; Athanasiadou et al., 2000b; 2001). However, the effect of CT on worm fecundity could not be conclusively attributed to CT. Athanasiadou et al. (2000a) reported that utero fecundity of worms was not significantly different amongst sheep given different levels of Quebracho CT treatments. Niezen et al. (1998a) also showed that different forage types, including CT-containing forages, had different effects on the fecundity of worms (utero eggs per female nematode) among different major gastrointestinal nematodes. Therefore, the effect of CT in many other CT-containing forages on fecundity of worm needs to be assessed.

CT may enhance resistance of GIP infection through increases in protein supply, which are prioritized for tissue repair and immune response (Barry et al., 2001; Niezen et al., 2002). The CT could complex with nutrients and inhibit nutrient availability for larval growth or decrease GIP metabolism directly through inhibition of oxidative phosphorylation (Scalbert, 1991), causing larval death (Athanasiadou et al., 2001). Inhibition of the electron transport system by CT was observed with *Photobacterium phosphoreum* (Scalbert, 1991). Molan et al. (2000; 2002) have shown that CT extracted from several forages can disrupt the life cycle of nematodes by preventing their eggs from hatching and by preventing larval development to the infective stages. Molan et al. (2000; 2002) suggested that the extracted CT from forages (400 µg of CT/mL) are more potent inhibitors of egg hatching and larval development (87 to 100%) than of larval motility (21 to 39% inhibited). Furthermore, *in vitro* larval development was evaluated under conditions similar to those observed in field conditions, with CT in fecal material from digested forage showing that CT reduced larval development by 69% (Min et al., 2003b). Therefore, it seems that CT may counteract parasites by one or more of the above mechanisms, and that the mechanism involved may differ between different forage species. If CT binding were due to their physical characteristics, greater precipitation would be expected with higher MW CT molecules (Scalbert, 1991). Scalbert (1991) also pointed out that if the binding mechanisms of CT and flavanols are related, we might deduce that PD will be more inhibitory than PC. The CT from *L. cuneata* (Table 1) is predominantly of PD type of subunits. Therefore, chemical composition and molecular size of CT, as well as concentration, may be factors in GIP control.

### Implications

Condensed tannin-containing forages have the potential to help control anthelmintic-resistant gastrointestinal parasites. They have been shown to decrease fecal egg counts in sheep and goats and may decrease hatch

rate and larval development in feces. This reduces pasture contamination and ingestion of infective larvae and by itself might provide adequate control of gastrointestinal parasites.

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