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# Condensed tannins and the nutritive value of herbage

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**ABSTRACT** Many plant species contain condensed tannins (CT), but lotus is one of the few herbages of agricultural importance to contain CT. Lotus has a high nutritive value (NV) despite a moderate protein content and nitrogen digestibility, and this can be explained by the activity of CT during digestion. CT binds plant proteins in the rumen, reducing their solubility and degradation by rumen bacteria. Condensed tannins increase the passage of plant protein to the intestine, and have increased the availability and absorption of essential amino acids by 60% compared with equivalent CT-free forage. Condensed tannins prevent bloat. Dietary concentrations as low as 0.17% CT in the dry matter (DM) can affect protein solubility in tbe rumen, but concentrations up to about 2-3% of dietary DM are probably optimal for maximising NV. Values exceeding 5.5% of DM inhibit microbial activity excessively and depress voluntary intakes. Ruminant production of milk, meat and wool could be increased by 10-15 % if grazed pasture contained 2-3%CT. These levels would be achieved if white clover could be engineered to contain 7-8% CT in its foliage.

Keywords condensed tannins, lotus, nutritive value, herbage, ruminant digestion

## INTRODUCTION

Condensed tannins (CT) are present in many plant species, incuding some pasture legumes (Jones et *al.* 1976), but lotus cultivars are the only CT-containing plants now in common use in New Zealand. Other herbages containing CT include sainfoin (*Onobrychis viciifolia*), haresfoot trefoil (*Trifolium arvense* L) and birdsfoot trefoil (*Lotus corniculatus*) , 'Grasslands Maku' lotus (*Lotus pedunculatus)* and the common weeds crown vetch *(Coronilla varia* L.) and dock *(Rumex obtusifolius*). The presence of CT does not necessarily improve nutritive value of herbage for rurninants. High concentrations of CT, for example over 8- 10 % of dietary DM, markedly reduce nutritive value (NV) of *the* browse shrub mulga *(Acacia aneura)* (Pritchard *et al.* 1988) and of *Lotus pedunculatus* grown in cold wet conditions on acidic soils (Barry & Manley 1984).

In contrast both *Lotus corniculatus* and *pedunculatus,* and sainfoin, are of high nutritive value when grown under moderate fertility and fed to lambs (John & Lancashire 1981; Purchas & Keogh 1984). Ulyatt (1981) ranked both sainfoin and Maku lotus as 61-62 % better than perennial ryegrass, and second only to white clover for promoting lamb growth when fed *ad libitum.* However, we have been particularly interested in why the nutritive value is high, because the digestibility of these forages is lower than that of equivalent forages without CT (Table 1). In comparisons between sainfoin, low CT lotus and herbages without CT, the apparent digestibility of N in the CT-containing feed was 2-25% lower than the equivalent CT-free herbage, yet N retention or apparent absorption from the intestine was always substantially higher when fed at similar levels of intake (Table 1). The high nutritive value of sainfoin and lotus cannot be attributed to the digestible components of the plants, their digestibility or to level of intake (Ulyatt & Egan 1979; Egan & Ulyatt 1980; Waghom et *al.* 1987a; Mangan 1988). The explanation, therefore, must relate to the effects of digestion on products available for absorption and utilisation for growth.

In a number of trials at Biotechnology Division, DSIR, since 1984, *Lotus corniculatus (2.2%* CT in DM) and *Lotus pedunculatus* ('Grasslands Maku') (5.5 % CT in DM) were fed to sheep and dock (1.7 % CT in DM) was fed with luceme to cattle. The effects of CT on digestion were measured, and the likely mechanisms of action observed. We now have sufficient understanding of the effect of CT on digestion to be able to recommend an optimal range of CT concentrations in feed DM for improved efficiency of ruminant productivity, and are able to explain the high NV of these forages.

## RUMEN DIGESTION – THE ESSENTIAL FACTS

Grasses and legumes are digested initially by microbial degradation in the rumen, after which undigested material together with the microbes are further digested by enzymic hydrolysis in the intestine. About 60% of digestible DM is digested in the rumen. This includes a loss of about 70% of plant protein, and most of the digestible fibre. Some plant protein nitrogen (N) is incorporated into microbial N, but most of the degraded N is lost to the animal after conversion to ammonia, absorption and excretion as urea in the urine. Rumen digestion does provide about 70% of the available energy (metabolisable energy) to the animal, primarily as volatile fatty acids (VFA) which are by-products of bacterial metabolism and are absorbed from the rumen into the bloodstream.

The microbial population is essential for degrading plant structural components (cellulose, hemicellulose, pectin), enabling efficient productivity from herbage, and assisting with passage of fibrous food residues out of the rumen to the intestines. In the intestine the remaining plant protein is enzymically digested, along with microbial protein passing out of the rumen. The peptides and amino acides are absorbed into the bloodstream.

In sheep and cattle grazing fresh herbages, the first limiting nutrients for wool, meat and milk production are usually amino acids required for synthesis of the protein component of these tissues. Synthesis of microbial protein does not always compensate for the excessive loss of protein to ammonia from the digestion of fresh herbages in the rumen (Ulyatt & Egan 1979), and protein can become limiting.

## EFFECT OF CONDENSED TANNINS ON DIGESTION

### In vitro activity

Some aspects of CT activity are best examined in *vitro.* In 1977 Jones & Mangan showed that in homogenised preparations of sainfoin, the CT bound and precipitated fraction 1 (F1) protein at pH 4-7. This precipitate dissociated at lower pH values. CT was assumed, therefore, to form a stable complex with proteins in the rumen, which would dissociate under the acidic conditions of the abomasum (pH 1.3-3.0), enabling an enzymic digestion of the plant proteins in the proximal duodenum. A similar response has been obtained with lotus cultivars. A mascerate of lotus containing 1.5 % CT in DM precipitates 95 % of lotus protein (John & Lancashire 1981). Recently, Waghom & Jones (1989) demonstrated ***both in vitro*** and ***in vivo*** that CT from dock was able to precipitate F1 protein from luceme. Only 0.17% CT was required to precipitate 50% of the F1 protein in the mascerate.

### Effect on protein digestion in vivo

Chewing is less effective than masceration in releasing both CT and protein from plant cells and cellular organelles, but in *vivo* evidence for the protection of plant proteins by CT from degradation in the rumen is strong. When diets containing sainfoin, lotus or dock are fed to ruminants, the concentrations of ammonia in rumen digesta are much lower than normal. Concentrations of bacteria in the rumen are lower, bacteria in digesta flowing out of the rumen are fewer (Waghom *et al.* 1987a), and the concentration of soluble protein in rumen liquor is lower (Waghom & Jones 1989). The CT thus reduces both microbial degradation of plant protein and microbial growth itself. Recently we have shown that when sheep are fed ***Lotus pedunculatus*** (5.5% CT in the DM) about 60% of the lotus protein passed undergraded out of the rumen, in contrast to a usual passage of about 30% of plant protein with fresh forages (W.C. McNabb pers. comm.).

Protection of plant proteins increases their nutritive value because:

1. Protein quality: Plant proteins are of a higher biological value than microbial proteins. Plant

**Table** 1 The nutritive value of sainfoin and effect of condensed tannin (CT) in lotus on nitrogen retention and digestion, relative to CT-free lotus and legumes fed to sheep at similar levels of intake.

| Plant comparison | Response to CT (%) | Change in N digestibility (%) | Source |
|---|---|---|---|
| Sainfoin v. WC | + 18.4 Protein:Energy Abs[a] | -10 | 1 |
| Sainfoin v. WC | + 16.7 N digest in SI[b] | -8.4 | 2 |
| Early sainfoin v. WC | + 124 retained | -11.9 | 3 |
| Late sainfoin v. WC | + 19 N retained | -17.9 | 3 |
| Sainfoin (dry) v. Lucerne | + 56 N digest in SI[b] | -25 | 4 |
| Lotus; Maitland v. Empire[c] | + 130 N retained | -6.5 | 5 |
| Spring Maitland v. Empire | + 29 N retained | -12.0 | 6 |
| Autumn Maitland v. Empire | + 340 N retained | -2.1 | 6 |
| Maitland v. Maitland with PEG[d] | + 62 EAA absorbed | -10.2 | 7 |
| Maku v. Maku with PEG | + 42 N retained | -18.5 | 8 |

[a]An increase in the ratios of protein absorbed: non protein energy absorbed.
[b]An increase in nitrogen digestion in the small intentine.
[c]Empire has a very low CT content, and Maitland 1.5-3.5% CT in the DM.
[d]PEG removes the effect of CT as explained in text.

Abbreviations: N, nitrogen; SI, small intestine; WC, white clover; EAA, essential amino acids; PEG, polyethylene glycol.

References: 1, Ulyatt et al. 1976; 2, Reid et al. 1974; 3, Egan & Ulyatt 1980; 4, Thomson et *al.* 1971; 5, John & Lancashire 1981; 6, Waghom et al. 1987a; 7, Waghom *et* al. 1987b; 8, Waghom unpublished.

proteins have higher proportions of limiting amino acids, and are more suited to the requirements of milk, meat and wool protein synthesis.

2. Protein quantity: Reduced degradation of plant proteins usually increases the quantity of protein passing out of the rumen for digestion in the intestines.

The effects of CT on protein quality have been examined in detail by sampling digesta flowing out of the rumen (using abomasal cannulae) in two groups of sheep fed lotus. One group had an intraruminal infusion of PEG, which preferentially binds CT so that the feed is essentially free of CT. The other group had an intraruminal infusion of water. Apart from the lower ammonia and higher flow of N out of the rumen of the control (CT) sheep (Table 2), 50% more essential AA (EAA) flowed to the small intestine of control sheep compared with the PEG group (Table 3). A recent experiment with *Lotus corniculatus* has confirmed this finding and has also shown a 32% increase in both the availability and absorption of the first limiting amino acid for wool production, methionine, in control sheep (W.C. NcNabb pers. comm.). Therefore, condensed tannins have a significant effect on protein quality, and increase the quantity of protein available for absorption.

The reasons why EAA are preferentially protected from degradation in the rumen, but not the NEAA, are unclear. We suspect that either the structure of EAA make them more resistant to degradation than NEAA, or that their location within peptide fragments has made them less susceptible to enzymic attack.

## Effect of CT concentration in dietary DM

The positive aspects of CT on rumen protein digestion (Tables 2 and 3, Waghom *et al.* 1987a) must be considered in relation to the concentration of CT in the diet. A linear relationship has been established which shows that an increased concentration of CT in lotus (g/100 g DM; X) increased the ratio of non-ammonia-N flowing to the intestine: N intake (Y). $Y = 0.71 + 0.045X$. $r = 0.66$; $p<0.05$ (Waghom *et al.* 1987a).

However, high levels of protein protection were associated with reduced feed intakes. High concentrations of CT reduced the availability of protein N for microbial use, so that microbial growth was sufficiently reduced to lower the rate of plant fibre degradation in the rumen. This was evident in sheep fed *Lotus pedunclatus* containing 5.5 % CT in the DM . After 2 weeks of feeding about 1400 g DM/day, their intakes began to decline and after about 18 days their intakes were 10% below those of sheep fed the same diet with an intraruminal infusion of PEG. The sheep with the lower intakes had larger rumen volumes and a slower rate of clearance than when PEG was infused (Table 4). In contrast, DM intake of sheep fed lotus containing 2.2% CT in the DM did not decline after 24 days of feeding (Table 2).

**Table 2** Effect of 2.2 % condensed tannin (CT) in the dry matter (DM) of ***Lotus corniculatus*** on aspects of nitrogen (N) digestion in sheep, with and without an intraruminal influsion of polyethylene glycol (PEG).

| | Control sheep | PEG sheep | Significance |
|---|---|---|---|
| DM intake (g/d) | 1400 | 1461 | NS |
| DM digestibility (%) | 69 | 71 | NS |
| N intake (g/d) | 37.8 | 37.8 | |
| Rumen ammonia (mg N/l) | 367 | 504 | *** |
| Abomasal flow of NAN (g/d) | 29.5 | 25.8 | * |
| Ileal flow of N (g/d) | 13.5 | 8.8 | ** |
| Apparent Digestion of N (proportion of intake) | | | |
| Total | 0.70 | 0.78 | *** |
| Rumen | 0.12 | 0.21 | * |
| Small intestine | 0.52 | 0.56 | NS |
| Large intestine | 0.06 | 0.01 | NS |

Abbreviations: NAN, non-ammonia nitrogen, NS, not significant; + $P<0.10$; *, $P<0.05$; **, $P<0.01$; ***, $P<0.001$.

**Table 3** Ammo acid (AA) flow (g/day) through the digestive tract of sheep fed ***Lotus corniculatus*** (2.2% condensed tannin in the dry matter (DM)) at 1400 g DM/day with and without an intraruminal infusion of PEG.

| | Control sheep | | PEG sheep | | Significance of difference | |
|---|---|---|---|---|---|---|
| | EAA | NEAA | EAA | NEAA | EAA | NEAA |
| AA Intake | 112 | 98 | 112 | 98 | NS | NS |
| Abomasal AA flux | 95 | 69 | 63 | 60 | ** | + |
| Ileal AA flux | 26 | 31 | 19 | 18 | • | ** |
| [illegible] from the rumen | 17 | 29 | 49 | 38 | ** | + |
| Apparent absorption of AA from the small intestine: | 69 | 38 | 44 | 42 | • | * + |

Abbreviations: PEG, polyethylene glycol; EAA, essential amino acids; NEAA non essential amino acids.

**Table 4** Effect of 5.5% condensed tannin (CT) in the dry matter (DM) on intake and digestion of **Maku** lotus fed to sheep over a 25 day period with and without an intraruminal infusion of polyethelene glycol (PEG).

| | Control sheep | PEG sheep | Significance of difference |
|---|---|---|---|
| DM intake, day 8-14 (g/d) | 1320 | 1350 | NS |
| DM intake, day 15-25 (g/d) | 1220 | 1340 | * |
| DM digestibility (%) | 68 | 70 | NS |
| Rumen DM pool (g) | 484 | 400 | NS |
| Rumen DM fractional outflow rate | 1.66 | 1.93 | NS |
| Rumen ammonia (mg N/l) | 175 | 460 | *** |
| Nitrogen digestion (% of intake) | | | |
| Total | 66 | 81 | *** |
| Rumen | 13 | 26 | *** |

We lack the data to define the relationship between concentration of CT in DM and voluntary intake. However our current understanding, together with findings of Barry *et al.* (1986), suggest CT concentration should not exceed about 4.0% of plant DM if intakes are to be maintained. A concentration of 2-3 % CT in plant DM appears to be reasonable for adequate protein protection and a high intake.

Palatability is unlikely to mediate the effect of CT on intake. In the experiment where intakes declined in sheep fed *Lotus pedunculatus,* the stem fraction containing 2.2% CT in the DM was rejected. The leaflets, containing 8.5% CT, were nipped off the stems and eaten. Further, Jones & Mangan (1977) showed CT from sainfoin was unable to form insoluble complexes with submaxillary mucoprotein, so that the lubricating properties of the salivary mucoprotein, and palatability, were unaffected.

**Table** 5 Effect of dock (*Rumex obtusifolius)* in a **lucerne/grass** diet fed to cattle on intake, bloat and concentration of nitrogenous components of rumen liquor (mg N/l). (From Waghom & Jones 1989).

| | With dock | Without dock | Significance of difference |
|---|---|---|---|
| Condensed tannin in dietary DM (%) | 0.17 | 0 | - |
| DM intake (kg/day) | 6.77 | 7.33 | NS |
| Cow/days of bloat | 0 | 11 | - |
| N content of feed (% of DM) | 2.19 | 2.10 | - |
| Total N in rumen liquor | 392 | 449 | ** |
| Ammonia N in rumen liquor | 228 | 239 | NS |
| Soluble protein N in rumen liquor | 49 | 70 | * |

## CONDENSED TANNINS AND BLOAT

Pastures containing red or white clovers exacerbate bloat in cattle (and sheep). In contrast, bloat has not been recorded in cattle grazing lotus, sainfoin and other CT containing cultivars (Jones & Lyttleton 1971).

Because bloat had been observed to be less severe or prevalent in cattle grazing pastures infested with dock, we studied the effect of dock as 10% of a luceme-based diet fed to cattle (Table 5).

When the diet contained only 0.17 % CT in the DM, bloat was absent and both the total nitrogen and soluble protein content of rumen liquor were reduced. The ability of this level of CT to bind and precipitate 50% of the soluble protein was confirmed *in vitro* (Waghom & Jones 1989).

Very low levels of CT in herbage appear to affect protein digestion in the rumen and may considerably enhance both nutritive value and bloat control. More work is needed to establish the relationships between dietary CT content and bloat.

## POTENTIAL BENEFITS OF CT INCORPORATION INTO PASTURES

We are confident that incorporating low concentrations of CT into pasture DM would improve pasture quality and ruminant productivity. The concentration of CT in herbage eaten should not exceed 4%, and an upper limit should probably be 2-3% of DM. In a grass/clover pasture gains, in productivity of 10-15% are possible, but emphasise the need for a further trial involving CT supplementation of a grass-based diet fed to sheep.

CT would be best incorporated into pasture via white clover, the backbone of New Zealand farming. Lotus species are difficult to establish and are not persistent under high fertility. The flower petals of white clover contain CT (Jones *et al.* 1976), so the plant contains the genetic information for CT synthesis. Unfortunately, no evidence has been found for the expression of CT in white clover foliage, despite extensive screening. We suggest white clover is the ideal candidate for genetic manipulation in order to achieve foliar expression of CT.

Grasslands Division scientists should consider engineering a white clover plant containing up to 8 % CT in its foliage. We believe this could be acceptable to ruminant livestock, and if white clover accounted for 20-30% of pasture DM consumed, then dietary CT concentration would be 152.5%. Our estimates suggest productivity increases of 10-15% would be likely under this regimen, and bloat would be eliminated.

We believe that the results of applied ruminant research we have summarised provide a clear goal for plant breeders. The next challenge is for plant molecular biologists to insert genes into white clover, enabling CT to be expressed in the foliage.

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