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The nutritive value of Lotus for sheep

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ABSTRACT

The distribution of condensed tannins (CT) in plants, their mode of action and benefits to ruminant nutrition are briefly reviewed. Data are presented showing the CT in lotus species reduced rumen degradation of protein and increased its flow to the intestine, but an increased amino acid absorption only occurred with *Lotus corniculatus*, suggesting the CT in *Lotus pedunculatus* prevented enzymic hydrolysis of the protected protein. The extent to which CT in *Lotus pedunculatus* depressed nitrogen (N) digestion was similar when fed as a sole diet and when fed as a third of the diet with pasture. The implications of these results are that both concentration and type of CT are important in affecting nutritive value, and that these factors need to be resolved before an effective plant selection program can be undertaken.

Keywords Condensed tannin, lotus, sheep, protein digestion.

INTRODUCTION

Lotus is a perennial legume of comparatively minor significance in New Zealand agriculture. Interest in nutritive value of lotus relates to the presence of condensed tannins (CT) and their effect on the digestion of plant components by ruminants. Under some conditions condensed tannins can improve nutritive value of herbage for ruminants, but in other instances the effects are detrimental. For example Barry and Duncan (1984) and Barry and Manley (1984) have reported low intakes and digestibility with sheep fed *Lotus pedunculatus* grown under infertile cold conditions near Invermay, and in south eastern United States extensive selections have reduced the CT concentration by about 20% in *Sericea lespedeza* and increased its nutritive value for ruminants (Windham *et al.*, 1990). The CT content of Mulga (*Acacia aneura*) is about 12% of DM, and this reduces nutritive value to such an extent that this potentially valuable forage is of limited use for sheep (Pritchard *et al.*, 1988). Beneficial effects of CT have been demonstrated with sainfoin (*Onobrychis viciifolia* Scop.; Egan and Ulyatt 1980), *Lotus corniculatus* (Waghorn *et al.*, 1987a,b) and *Lotus pedunculatus* grown under high fertility conditions (Waghorn, unpublished; McNabb *et al.*, 1992). Current work is designed to identify the bases for improved nutritive value in lotus and to identify optimal concentrations and types of CT for ruminant nutrition which may ultimately be expressed in a suitable pasture species (for example white clover) using genetic engineering techniques.

The Lotus plant

Two species of lotus have been selected and are used in New Zealand. These are *Lotus corniculatus*, which includes the recent release of Grasslands Goldie, and *Lotus pedunculatus* cv Maku. *Lotus corniculatus* is suited to relatively dry conditions and moderate-low fertility. It is a low fertility lucerne substitute. In contrast Maku is a tetraploid cultivar best suited to high rainfall acidic soils. Lotus will out perform both white clover and lucerne in areas of low fertility and will produce well without phosphatic fertilisers, but lotus cannot compete with clovers and grasses under moderate to high fertility conditions.

Vegetative lotus comprises 50-60% leaf. Leaf dry matter has about 3-4 times the CT and half the fibre content when compared to stem dry matter (Waghorn *et al.*, 1990). The chemical composition of lotus plants is summarised in Table 1, and with the exception of the CT are similar to other legumes. Lotus stems are fibrous, difficult to breakdown by chewing and are rejected by stock as the plant matures.

TABLE 1 Chemical composition (% of dry matter) of *Lotus corniculatus*, Lotus *pedunculatus*, lucerne and red clover.

	Lotus corniculatus[a]	*Lotus pedunculatus*[b]	Lucerne[c]	Red[c] clover
Crude protein (N x 6.25)	16.9-21.8	19.8-25.8	21.2	26.9
Fermentable carbohydrate	14.5-17.3	18.1-18.2	15.8	16.1
Neutral detergent fibre	33.5-48.5	36.5-40.3	47.5	36.8
Ether extract	4.7	ND	2.8	4.1
Lignin[d]	9.9-11.4	8.8-15.2	10.3	6.5
Ash	8.8	6.5-10.0	9.9	11.7
Condensed tannin	0.25-3.5	4.5-10.6	ND	ND

[a] from John and Lancashire, 1981; Waghorn *et al.* 1987a,b.
[b] from Barry and Duncan, 1984; Waghorn unpublished.
[c] from Waghorn, 1986.
[d] assay probably includes condensed tannin.
ND not determined.

Animal performance

In trials where CT containing forages have been grown under good conditions, stock performance has been similar to that from clover or lucerne. Ulyatt (1981) ranked several herbages on the basis of lamb growth rate and both Maku lotus and sainfoin (which contains CT) ranked between white clover and lucerne. A comparison between white clover and *Lotus pedunculatus* (Purchas and Keogh,. 1984) showed that lambs fed pedunculatus grew slightly slower but in all cases the carcasses were leaner than those fed white clover. Egan and Ulyatt (1980) reported nitrogen retentions of 4.7 and 2.1 g/day in sheep fed sainfoin and white clover respectively. Current field trials (Douglas *et al.*, unpublished) are showing significantly greater rates of gain in both lambs and ewes fed Grasslands Goldie compared to lucerne. In one of two trials Clark (1991) reported significantly greater rates of gain in bulls grazing *Lotus corniculatus* compared to either red clover, chicory, fescue or ryegrass. A number of indoor trials have been carried out to determine the factors responsible for the rapid rates of gain, high nitrogen retention and lean carcasses associated with dietary CT. Results from ten trials involving either sainfoin or lotus grown under medium-high fertility conditions were summarised by Waghorn *et al.*, (1990) and in each instance an improved nitrogen absorption was associated with a reduction in nitrogen digestibility of 2-25%, compared to similar forages without CT. This apparent anomaly is explained by the effect of CT on reducing rumen protein degradation and improving the quantity and quality of amino acids reaching the intestine for absorption.

Fresh forages which do not contain CT have about 70% of their protein degraded by rumen microbes, and the resultant ammonia is absorbed from the rumen, converted to urea in the liver and either excreted in the urine or recycled to the rumen. Some ammonia is incorporated into rumen bacterial protein (which has a lower biological value than forage protein) so that the ruminant digests both microbial and forage protein in the intestine. Condensed tannins reduce the extent to which proteins are degraded in the rumen (Waghorn *et al.*, 1987b; McNabb *et al.*, 1992) so that a higher proportion of forage protein passes to the intestine in the presence of CT than is normally the case. Regression analysis of data summarised from several trials showed the slope of the line relating non ammonia nitrogen flux to the intestine relative to nitrogen intake was significantly ($P<0.05$) greater for forages containing CT (0.85) than for forages without CT (0.57; Waghorn *et al.*, 1987a). The increased passage can, but does not always, result in improved amino acid absorption, although few trials have measured this parameter, (Table 2).

Concentration and source of condensed tannin

Several surveys of CT concentrations in plants have been carried out. Concentrations of CT in foliage of 11 *Lotus corniculatus* cultivars ranged between 0.13 and 3.90% of DM, which was significantly lower than that for Maku lotus (5.80-9.76%; Lowther *et al.*, 1987). Sulphur application tended to reduce CT concentrations. Similar ranges were reported from analyses of leaves from 22 accessions of *Lotus corniculatus* (0.15-7.28; mean 2.09% of DM) and 10 accessions of *Lotus pedunculatus* (2.53-10.72; mean 5.99% of DM) by Kelman and Tanner (1991) in Australia. Barry and Forss (1983) reported a reduction in CT concentration of *Lotus pedunculatus* from 8-11% of DM when grown in acid soils without fertiliser to 4-5% with the addition of phosphorus and sulphur, due primarily to the improved dry matter yield.

Although high levels of CT in *Lotus pedunculatus* are detrimental to both intake and digestion by sheep, it is not only concentration, but also the type of CT which influences nutritive values. For example sainfoin contains 5-8% of CT in the dry matter (Jones, pers comm), but this is not detrimental to digestion. The differences between condensed tannins relate to molecular size and configuration (Mangan, 1988) with some sources of CT having relatively more reactive phenolic groups than others. These differences effect the CT-protein binding characteristics which in turn determines the effect of CT on nutritive value. However no direct comparisons of CT type on nutritive value have been carried out, and results presented here provide indirect evidence that the CT in *Lotus pedunculatus* is quite different from that in *Lotus corniculatus.*

Nutritive value of *Lotus corniculatus* and *Lotus pedunculatus*

A series of indoor feeding trials were undertaken to quantity the effects of CT from two sources (*Lotus corniculatus*, and *Lotus pedunculatus*) on digestion. In both instances the lotus was grown under high fertility conditions, so that CT concentrations were 2.2% of DM for *Lotus corniculatus* and 5.5% of DM for *Lotus pedunculatus*. The feeds were given to 15 month old wether sheep fitted with rumen and abomasal cannulae and held in metabolism crates for the duration of each trial. Half the sheep in each trial were given polyethylene glycol (PEG) as an intraruminal infusion to bind with and inactivate the CT so that the CT was unable to bind with forage protein (Jones and Mangan, 1977). Infusion rates were 50 g PEG/day with *corniculatus* and

TABLE 2 Digestion of *Lotus corniculatus* (2.2% CT in the DM) and *Lotus pedunculatus* (5.5% CT in the DM) when fed to sheep with and without an intraruminal infusion of polyethylene glycol (PEG) to inactivate the CT. Data are means with SEM.

	Lotus corniculatus			*Lotus pedunculatus*		
	Control	PEG	Sig.	Control	PEG	Sig.
DM Intake (g/day)	1,400 ± 42	1,460 ± 35	ns	1,220 ± 40	1,340 ± 28	*
DM Digestibility (%)	69 ± 0.8	71 ± 0.7	ns	68 ± 0.7	70 ± 0.8	ns
Rumen ammonia (mg/l)	367 ± 24	504 ± 57	***	175 ± 10	460 ± 47	***
Nitrogen digestibility (%)	70 ± 0.4	78 ± 0.8	***	67 ± 0.7	80 ± 15	***
Proportion of N digestion in the rumen	0.12 ± .01	0.21 ± .03	*	0.13 ± .05	0.26 ± .01	***
Essential amino acids (g/day)[a]						
Intake	112 ± 3.4	117 ± 2.8	ns	104 ± 4.5	117 ± 1.9	*
Flux to small intestine	95 ± 5.0	66 ± 5.4	**	126 ± 5.6	107 ± 1.5	*
Apparent absorption	69 ± 3.5	46 ± 5.4	**	83 ± 5.6	85 ± 1.3	ns
Non essential amino acids (g/day)						
Intake	98 ± 2.9	102 ± 2.5	ns	87 ± 4.6	99 ± 1.7	*
Flux to small intestine	69 ± 2.9	63 ± 3.1	ns	84 ± 4.9	78 ± 1.6	ns
Apparent absorption	37 ± 2.1	43 ± 3.3	ns	49 ± 4.6	57 ± 1.4	ns

ns, not significant; †, $P<0.10$; *, $P<0.05$; **, $P<0.01$; ***, $P<0.001$.

[a]Essential amino acids do not include sulphur amino acids.

100 g PEG/day with *pedunculatus*. This treatment enabled the effects of CT to be evaluated within each diet by comparing control (CT operating) and PEG (CT inactivated) treatments.

Digestibilities and nutrient absorption data presented in Table 2 summarise the effects of CT in *Lotus pedunculatus* and *Lotus corniculatus*. In both trials feed was offered at about 90% of ad libitum, and whilst this level of intake was maintained with corniculatus, intakes of control sheep given *pedunculatus* began to decline after about 10 days of feeding and were significantly lower than the PEG treatment from day 15 until slaughter on day 25. Digestibility of DM was similar for control sheep and those receiving PEG for both diets, and apparent digestion of nitrogen was significantly increased in sheep given PEG compared to controls.

The CT affected N digestibility by reducing net loss from the rumen, so that more N and amino acids passed out of the rumen to the intestine for enzymic hydrolysis and absorption (Table 2). The lotus species differed in the extent to which amino acids entering the intestine were absorbed. With *Lotus corniculatus* a similar proportion of essential amino acid (EAA) flux was apparently absorbed for both treatments (70-73%) so that the higher flow of EAA to the intestine of control sheep resulted in a higher net absorption (69 g/day) than those given PEG (46 g/day). The CT had only a minor effect on the flow of non essential amino acids (NEAA) to the intestine and there absorption (Table 2). In control sheep fed *Lotus pedunculatus* the flux of EAA to the intestine exceeded EAA intake, as a consequence of reduced rumen protein catabolism and gains in microbial protein synthesis from recycled endogenous urea. Some loss of EAA from the rumen was evident in the sheep receiving PEG so that net EAA flow to the intestine was lower than control animals ($P<.05$), despite a higher DM intake of those given PEG. However apparent absorption of EAA from the intestine was only 66% (78 g/day) in control sheep compared with 78% (83 g/day) in these given PEG, suggesting a possible partial inhibition of EAA hydrolysis prior to absorption in sheep where *Lotus pedunculatus* CT had bound to forage protein. A similar effect was evident with NEAA. Apparent absorption was 74% (57 g/day) in sheep given PEG compared with 57% (49 g/day) in the control animals (NS).

These data demonstrate a major difference between the two species of lotus which may be a consequence of either CT concentration or CT binding characteristics.

Nutritive value of lotus fed with pasture

If the potential benefits of CT for ruminant nutrition are to be realised under normal farming conditions, it is important that CT from one plant species is able to protect all dietary proteins from excess degradation in the rumen. The ability of CT in dock (*Rumex oblusifolius*) to bind with and precipitate lucerne protein has been demonstrated (Waghorn and Jones, 1989), and two experiments have been carried out in sheep fed a mixture of lotus and pasture.

The wethers in each trial were aged about 15 months, weighed about 44 kg and were not surgically modified. They were held indoors in metabolism crates and fed diets comprising lotus and pasture (mainly grass) in a 1:2 ratio for 35 and 42 days. One trial involved *Lotus corniculatus* (cv Grasslands Goldie) fed with pasture and the other involved *Lotus pedunculatus* fed with grass. Each trial involved 10 sheep in each of three treatments: lotus and grass (control), lotus and grass with twice daily drenchings of PEG, and grass alone. Intakes were restricted to that of the lowest treatment.

In the trial in which *Lotus pedunculatus* was fed, CT accounted for about 2% of dietary DM. Digestibility data were obtained with immature and mature forage (Table 3) and in each instance was lower ($P<0.001$) in the control sheep compared to those given PEG. When immature forage was offered, the extent of the depression in nitrogen digestibility in control sheep compared to those given PEG (65.3 v 77.5% respectively) was similar to that observed with *Lotus pedunculatus* fed as a sole diet and containing 5.5% CT in the DM (Table 2). With more mature forage PEG resulted in an increased N digestibility ($P<0.001$) compared to both the control group and those fed grass only (Table 3).

TABLE 3 Intakes and digestibility in sheep fed either *Lotus pedunculatus* or *Lotus corniculatus* with pasture (with or without polyethylene glycol, PEG) and pasture alone. Lotus was approximately 33% of DM when fed with pasture. Data are means with SEM.

	Lotus and pasture		Pasture	Sig.
	Control	PEG		
Lotus pedunculatus				
Immature forage				
DM intake (g/day)	1,368 ± 26	1,354 ± 10	1,290 ± 26	ns
DM digestibility (%)	72.0 ± 0.3	75.0 ± 0.4	75.3 ± 0.5	***
Nitrogen digestibility (%)	65.3 ± 0.7	77.5 ± 0.5	77.9 ± 0.8	***
Mature forage				
DM intake (g/day)	1,420 ± 26	1,457 ± 14	1,310 ± 39	*
DM digestibility (%)	65.8 ± 0.4	68.4 ± 0.4	69.2 ± 0.1	***
Nitrogen digestibility (%)	48.0 ± 0.9	62.5 ± 0.9	53.7 ± 1.2	***
Lotus corniculatus				
DM intake (g/day)	1,246 ± 20	1,240 ± 20	1,229 ± 22	ns
DM digestibility (%)	74.3 ± 0.7	75.0 ± 0.5	75.6 ± 0.4	ns
Nitrogen digestibility (%)	76.4 ± 0.7	79.8 ± 0.4	79.4 ± 0.3	***

ns, not significant; *, $P<0.05$; *** $P<0.001$.

The 12.2 percentage unit depression in nitrogen digestibility in control sheep fed *Lotus pedunculatus* and pasture (2.0% dietary CT) was similar to the percentage unit reduction (Table 2) when *Lotus pedunculatus* (5.5% dietary CT) was fed alone. This result has important implications for our understanding of CT and digestion, because a similar depression in N digestibility was attributed to two very different concentrations of *Lotus pedunculatus* CT. Further more the depression in N digestibility with *pedunculatus* and pasture was much greater than that in sheep given *Lotus corniculatus* (Table 2) which also contained 2.2% CT in the DM. It would appear that CT in *pedunculatus* differs from that in corniculatus in a manner not only related to its concentration in the diet. The reduced absorption of amino acids from the intestine of sheep from *Lotus pedunculatus* supports this difference, although the mechanism by which absorption was reduced is not understood.

A similar trial with *Lotus corniculatus* and pasture (Table 3) showed the CT concentration in this diet (0.7% of DM) did reduce N digestibility but this effect was comparatively minor. The reduction of N digestibility due to CT was less when *Lotus corniculatus* was fed with pasture (3.4 percentage units) than that in *Lotus corniculatus* fed as a sole diet (8.0 percentage units; Table 2). With *Lotus corniculatus* the response to CT appeared to be closely related to its concentration in dietary DM.

CONCLUSIONS

Condensed tannins are able to improve nutritive value of forage by protecting proteins from rumen degradation and increasing the flow and absorption of amino acids from the intestine. The effectiveness of CT is dependent upon its concentration in the diet and its binding characteristics with proteins. Although the CT from *Lotus pedunculatus* appear less desirable than those from *Lotus corniculatus* for improving nutritive value, optimal concentrations and types of CT for ruminant nutrition have not been established.

Most plants which contain CT are not competitive with ryegrasses and clovers in high fertility situations, so that either more competitive cultivars need to be selected, or CT need to be expressed in a competitive species, e.g. white clover, using genetic engineering techniques. If this option is taken then it is imperative that ruminant aspects of CT metabolism are fully understood so that expression of the gene constructs will give an optimal type and concentration of CT. Known benefits of CT include leaner carcases and elimination of bloat. Potential benefits to animal performance attributed to an improved protein nutrition would include more rapid and efficient growth, and an increased yield of milk and wool.

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