The role of condensed tannins in the nutritional value of *Lotus pedunculatus* for sheep

* 3. Rates of body and wool growth

By T. N. BARRY†

Invermay Agricultural Research Centre, Private Bag, Mosgiel, New Zealand

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1. *Lotus pedunculatus* (cv. Grasslands Maku) grown on acid low-fertility soil and containing high concentrations of condensed tannin (76–90 g/kg dry matter (DM)) was grazed by growing sheep for 31–42 d periods in three experiments. In Expt 2 an additional group of lambs grazed areas oversown with white clover (*Trifolium repens*) and red clover (*Trifolium pratense*). Lambs were transferred from grazing ryegrass (*Lolium perenne*) – white clover straight on to lotus in all experiments (unconditioned sheep). In Expt 3 a second group was included which had grazed high-tannin lotus for a pre-experimental period of 8 weeks (conditioned sheep).

2. Effects of condensed tannin on body and wool growth were assessed by studying responses to daily oral administration of polyethylene glycol (PEG; molecular weight 3350, 75–100 g/d). PEG forms a complex with condensed tannin, which is assumed to be inert in its passage through the digestive system, and so effectively reduces the nutritional effects attributable to high condensed-tannin concentrations.

3. Live-weight gain (LWG) in the absence of PEG was low (27–125 g/d) for sheep grazing high-tannin lotus, and PEG administration increased LWG by 41–61 g/d and increased wool growth. In Expt 3, responses to PEG supplementation tended to be less with conditioned than with unconditioned sheep, indicating that conditioned sheep had partially adapted to the high-tannin diet.

4. PEG supplementation had no effect on either LWG or wool growth of sheep grazing areas oversown with mixed clovers, confirming its effects as specific to forages containing condensed tannins. These experiments therefore conclusively show that high concentrations of condensed tannin induced by growing *Lotus pedunculatus* under low soil fertility conditions prevent maximum expression of LWG and wool growth in grazing sheep. These results contrast with high LWG (153–315 g/d) observed in growing sheep grazing the same lotus cultivar grown in high fertility soil and containing 20 g condensed tannin/kg DM, a level considered to be nutritionally beneficial.

Lotus pedunculatus (cv. Grasslands Maku) contains 20–30 g condensed tannin/kg dry matter (DM) when grown in high-fertility soils and 70–80 g condensed tannin/kg DM when grown in acid, low-fertility soils (Barry & Forss, 1983). High condensed-tannin concentrations increase amino acid absorption, depress rumen digestion of soluble carbohydrate (CHO) and hemicellulose, and depress voluntary intake (Barry & Duncan, 1984; Barry & Manley, 1984). Barry & Duncan (1984) reduced the total reactive condensed-tannin content of lotus through spraying the forage with polyethylene glycol (PEG; molecular weight (MW) 3350), which binds the tannin, with the tannin–PEG complex being excreted in the faeces and therefore not affecting ruminant digestion. The objective of this series of experiments was to assess if the high condensed-tannin concentration in lotus grown under acid, low soil fertility conditions was restricting body and wool growth in grazing animals. This was assessed through studying responses to daily oral administration of PEG.

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† Present address: Department of Animal Science, Massey University, Palmerston North, New Zealand.

EXPERIMENTAL

Forages

Areas of acid low-fertility hill-country soils were oversown with either Grasslands 'Maku' lotus or a mixture of white clover (*Trifolium repens*) and red clover (*T. pratense*). Soil pH was 4·5–4·8 and concentrations of available phosphorus and sulphur were very low at 6 and 4 μg/g soil respectively. Areas oversown with lotus were sprayed during winter with a selective weedkiller (Kerb, Rohm & Hass, USA) to control growth of spring grasses. Herbage produced from the initial spring growth (primary growth) was grazed in Expt 1, and material grown following the initial grazing (secondary regrowth) was grazed in Expts 2 and 3. Forages were fed in breaks, using electric fences, with the animals moved to a new break when all the leaf and about half the stem had been consumed. Each break lasted approximately 7 d.

Animals

All sheep were drenched with an anthelmintic plus 2·5 mg selenium as sodium selenate at the commencement of each experiment. Live-weight gain (LWG) was calculated from 24 h fasted weights taken at the start and end of each experiment. Wool patches of 122·5 mm × 122·5 mm were clipped on the left and right mid-sides of all sheep at the start of the experiment, and wool harvested from these areas at the end of each treatment and post-treatment period. Half the animals in each experiment were given a once daily drench of polyethylene glycol (PEG; MW 3350), made up in water as a 0·5 g/l solution, with the remainder being drenched with an equivalent volume of water at the same time.

Expt 1

Eighteen Romney × Cheviot wethers aged 15 months with a mean initial weight of 36·0 (SD 0·89) kg grazed leafy vegetative primary growth lotus for a 42 d period. This was followed by a 60 d period grazing ryegrass (*Lolium perenne*) – clover pasture, to measure any residual effects of the treatments on wool growth. Nine of the animals received 100 g PEG/d orally during the time they were grazing lotus. At the end of the post-treatment period the sheep were shorn, and fleece growth proportioned into that grown during the treatment and post-treatment periods using ratios of wool grown on the mid-side.

Expt 2

Twenty-four Romney wether lambs aged 7 months grazed areas oversown with either lotus or clover for 42 d. Mean initial weight was 25·5 (SD 1·50) kg. Twelve lambs grazing each forage received 75 g PEG/d. During this experiment the clover was in short supply and the lotus was mature secondary regrowth, showing some flower development.

Expt 3

Eighteen Romney wether lambs which had grazed high-tannin lotus for the previous 8 weeks (conditioned lambs) and eighteen lambs from the same source which had grazed ryegrass–clover during the previous 8 weeks (unconditioned lambs) were used. Age at the commencement of grazing experimental lotus was 6 months, and the mean (and SD) initial weights of conditioned and unconditioned lambs were 31·1 (1·81) kg and 28·7 (1·84) kg respectively. All lambs grazed vegetative lotus secondary regrowth as a single group for 31 d. Nine lambs from each of the unconditioned and conditioned groups received 75 g PEG/d.

All lambs then grazed high-tannin lotus as a single group for a post-experimental period of 32 d, after which the sheep were shorn and fleece wool growth determined as described in Expt 1.

Herbage sampling

Three cages measuring 0·35 × 0·50 m were placed on each area at the commencement of grazing each break and, at the end of grazing, forage was cut from the caged areas corresponding to what the animals had consumed. Grasses were removed and the legumes pooled from the three caged areas. This procedure was done on three of the breaks grazed during each experiment, and the three pooled samples per forage retained for chemical analysis.

Laboratory methods

The contents of total and free condensed tannin were determined on samples of fresh legume using the methods described by Barry & Forss (1983), free tannin being defined as that exceeding the binding capacity of the fresh mascerated plant. Analyses for total N and carbohydrates (Expt 3 only) were carried out as described by Barry & Manley (1984), using freeze-dried material. All wool samples were scoured, dried and results expressed as dry wool produced/d.

Statistical analysis

Statistical analysis was carried out using analysis of variance. In the case of wool growth, wool removed from the mid-side areas at the commencement of each experiment was used as a co-variate, and this resulted in a substantial improvement in precision through reducing the error mean square.

RESULTS

Herbage composition

Condensed tannin concentrations were uniformly high (76–90 g/kg DM) in the lotus used (Table 1) and contained appreciable concentrations of free tannin (7–12 g/kg DM). Total condensed tannin was present in only trace amounts in pooled samples of clover, whilst free tannin was not detectable. The lotus grazed in Expt 3 contained (g/kg DM) 90 soluble carbohydrate, 59 pectin, 78 hemicellulose, 208 cellulose, 163 lignin.

Expt 1

Oral PEG administration increased LWG of young sheep grazing primary-growth lotus from 125 to 166 g/d ($P < 0{\cdot}05$; Table 2), and tended to increase wool growth, with the effect over the complete 102 d period attaining significance at $P < 0{\cdot}07$.

Table 1. *Chemical composition (g/kg dry matter) of diets*

Expt no....	1	2		3
Diet...	Lotus (*Lotus pedunculatus*)	Lotus	White clover (*Trifolium repens*)	Lotus
Total condensed tannin	76·4	88·5	0·7	90·0
Free condensed tannin	8·1	6·8	0·0	12·4
Total nitrogen	28·5	28·1	32·9	31·4

Table 2. *Expt 1. Responses in live-weight gain and wool growth to oral administration of polyethylene glycol (PEG; molecular weight 3350, 100 g/d) in young sheep grazing lotus* (Lotus pedunculatus) *of high-tannin content*

(Mean values with their standard errors of difference for nine animals per group)

	Period of treatment (d)	Oral PEG supplementation		SED
		Without	With	
Live-wt gain (g/d)	1–42	125	166	16·8
Wool growth (g/d)	1–42	8·5	9·5	0·65
	43–102*	7·9	8·6	0·44
	1–102	8·1	8·9	0·40

* Post-treatment period grazing ryegrass (*Lolium perenne*) – clover (*Trifolium repens*).

Table 3. *Expt 2. Responses in live-weight gain and wool growth to oral administration of polyethylene glycol (PEG; molecular weight 3350, 75 g/d) in young sheep grazing lotus* (Lotus pedunculatus) *of high-tannin content and white clover* (Trifolium repens) *containing traces of tannin*

(Mean values with their standard errors of difference for twelve animals per group)

	Lotus		Clover		
Oral PEG supplementation...	Without	With	Without	With	SED
Live-wt gain (g/d)	27	70	28	26	9·2
Wool growth (mg/10^4 mm^2 per d)	81	104	77	83	5·4

Table 4. *Expt 3. Responses in live-weight gain and wool growth to oral administration of polyethylene glycol (PEG; molecular weight 3350, 75 g/d) in young sheep grazing high-tannin lotus* (Lotus pedunculatus)

(The sheep grazed either ryegrass (*Lolium perenne*) – clover (*Trifolium repens*) pasture (unconditioned sheep) or high-tannin lotus (conditioned sheep) during an 8 week pre-experimental period. Mean values with their standard errors of difference for nine animals per group)

Period of treatment (d)		Unconditioned		Conditioned		
	Oral PEG supplementation...	Without	With	Without	With	SED
1–31	Live-wt gain	45	106	68	83	15·4
32–64*	(g/d)	45	37	49	34	11·4
1–63		45	70	59	68	10·1
1–31	Wool growth	7·1	8·7	7·8	8·9	0·66
32–64*	(g/d)	7·6	8·5	8·3	8·5	0·69
1–63		7·4	8·6	8·1	8·7	0·63

* Post-treatment period, grazing high-tannin lotus.

Expt 2

LWG of young sheep grazing the sparse clover was low in Expt 2 (Table 3), and neither LWG nor wool growth was affected by PEG administration. LWG was also low in young sheep grazing mature lotus secondary regrowth but, in contrast to sheep grazing clover, both LWG ($P < 0{\cdot}001$) and mid-side wool growth ($P < 0{\cdot}01$) were increased by oral PEG administration.

Expt 3

As in Expt 2, LWG was low in unconditioned control sheep grazing lotus secondary regrowth (Table 4). PEG supplementation increased LWG and wool growth during the treatment period ($P < 0{\cdot}01$); there were trends for the responses to be greater with unconditioned than with conditioned sheep, but the interaction only attained significance for LWG ($P < 0{\cdot}05$). When LWG was calculated over the combined treatment + post-treatment periods, PEG supplementation produced no net increase in conditioned sheep but the stimulating effect was still retained in unconditioned sheep ($P < 0{\cdot}05$). Residual effects of PEG supplementation on wool growth were evident in the post-treatment period and, averaged over both periods, PEG supplementation increased overall wool growth rate ($P < 0{\cdot}05$) with the response appearing to be larger for unconditioned than for conditioned sheep.

DISCUSSION

The technique used in the present study relies on the assumption that effects of PEG are specific to condensed tannins contained in forages, and that in their absence PEG *per se* does not have beneficial or detrimental nutritional properties. This assumption is validated by the results in Expt 2 for sheep grazing areas oversown with a mixture of red and white clover.

Herbage mineral analyses were not performed in the present study, but lotus cut from the same area in other experiments contained 2·0–2·5 g phosphorus and sulphur/kg DM (Barry & Duncan, 1984). Although this is less than for ryegrass–clover pasture grown on well-fertilized soils in this area (4·5 g P/kg DM; 3·0 g S/kg DM), the values for lotus are not considered low enough to cause depressed intake from P deficiency (0·9 g P/kg DM; Gartner *et al.* 1982).

LWG

Findings from all three experiments conclusively show that high concentrations of condensed tannins prevent maximum expression of LWG when young sheep are introduced to grazing the cultivar of *Lotus pedunculatus* used in the present study. The mechanism of how high dietary tannin concentration depresses intake and productivity is unknown and is currently under research. Barry & Reid (1985) considered free and bound tannin contents to be indices of the detrimental and beneficial effects produced by forage condensed-tannins, and the depressions in productivity measured here may therefore involve effects produced by free tannin.

These results contrast with those obtained with growing sheep grazing the same cultivar of *Lotus pedunculatus* grown in high-fertility soils under warm conditions. Lotus is a poor competitor under these conditions, and such swards can only be artificially maintained through repeated herbicide application, to suppress competition from grasses and clovers. Nevertheless, over six comparisons, growth of lambs grazing pure lotus (116 g lignin/kg DM) was very high (153–315 g/d) and averaged 87% of that for lambs grazing pure white clover (190–354 g/d; John & Lancashire, 1981). When grown under these conditions, *Lotus pedunculatus* contains respectively 20 g/kg DM and trace amounts of total- and free-condensed tannins, and it therefore seems that this concentration is nutritionally beneficial and not detrimental.

Wool growth

Wool growth has long been known to be sensitive to protein absorption (Kempton, 1979) and, as the presence of condensed tannins in lotus and sainfoin (*Onobrychis viccifolia* Scop) increased both amino acid absorption and nitrogen retention (Ulyatt & Egan, 1979; John & Lancashire, 1981; Barry & Manley, 1984), it might initially be expected that oral PEG supplementation to reduce effects of condensed tannins would reduce and not increase wool growth. Part of the increase may be explained by the increase in forage intake which occurs when dietary reactive condensed tannin concentration is reduced following PEG application to high-tannin lotus (Barry & Duncan, 1984).

An additional explanation is that plasma growth hormone concentration is elevated in sheep given high-tannin lotus, and decreases by 0·32 μg (SE 0·065)/l for each 10 g/kg DM reduction in total reactive condensed-tannin concentration (Barry, 1984). Growth hormone stimulates N retention in ruminants (Trenkle, 1980), and injections of growth hormone into sheep simultaneously decrease wool growth and stimulate N retention, thus diverting amino acids away from wool synthesis into body protein deposition (Wallace, 1979). These changes in the partition of N deposition induced by growth hormone help to explain the reduced wool growth of sheep grazing high-tannin lotus, and the increase in wool growth that occurs when effects of tannins are reduced by oral PEG supplementation.

Condensed tannins and nutritive value

Dietary condensed tannins *per se* can be considered as nutritionally deleterious (McLeod, 1974) and a net benefit only occurs with ruminants given fresh-forage diets when the tannins react with forage proteins and reduce their solubility. The ideal dietary concentration would therefore seem to be the minimum amount of condensed tannin necessary to render the plant protein insoluble. Higher concentrations are likely to prove detrimental, especially if the tannin–protein complex formed from disintegration of such plants releases high proportions of free tannin. Observations at this Centre with *Lotus pedunculatus* suggest an ideal condensed-tannin concentration of 20–40 g/kg DM (T. N. Barry, unpublished results). The present study has conclusively shown very high concentrations (76–90 g/kg DM) to be nutritionally detrimental, as found by Van Hoven (1984) for game animals forced to eat browse plants under drought conditions in South Africa. Lowther & Barry (1985) found that LWG of lambs grazing areas oversown with lotus (90 g condensed tannins/kg DM) were initially low (60–100 g/d) and then increased (120–140 g/d), whereas LWG of lambs grazing areas oversown with white clover were consistently high (120–130 g/d). These results indicate adaptation to *Lotus pedunculatus* grown under conditions of low soil fertility, and results of the present study suggest that this involves partial adaptation to the high dietary concentration of condensed tannins.

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