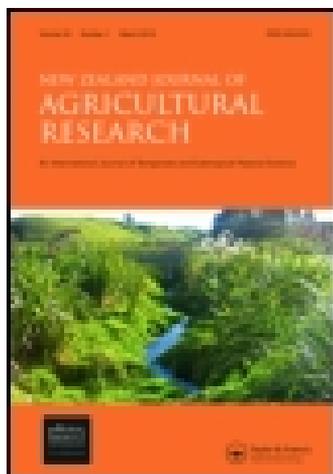


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Herbage intake, ingestive behaviour and diet selection, and effects of condensed tannins upon body and wool growth in lambs grazing *Lolium perenne* and *Holcus lanatus* swards in summer

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Abstract A comparative study was undertaken in New Zealand to investigate the effects of low concentrations of condensed tannins (CT) on diet selection, herbage intake, and performance in lambs grazing on four 0.2 ha paddocks each of perennial ryegrass (*Lolium perenne*) or Yorkshire fog (*Holcus lanatus*) with less than 10% white clover (*Trifolium repens*), continuously grazed at a constant height of approximately 6 cm from December 1992 to March 1993. The effects of CT on rumen metabolism and animal production were assessed by twice daily oral administration of polyethylene glycol (PEG; MW 4000) to half of the lambs on each sward.

Bite weight was greater for Yorkshire fog swards than for ryegrass swards during January (111 vs 85 ± 5 mg OM/bite, $P < 0.01$), but not in December. In both December and January, grazing,

ruminating, and idling times were similar between swards, while in January, the rate of biting in ryegrass swards was higher than in Yorkshire fog swards (64 vs 61 ± 1 bites/min, $P < 0.05$). The organic matter digestibility (OMD) of the herbage selected was higher in ryegrass swards in December (81 vs 78 ± 0.04 %, $P < 0.01$), but not in January (80 vs 79 ± 0.05 %). The herbage intake achieved by lambs grazing ryegrass swards was 23% higher than that achieved on Yorkshire fog swards in December (990 vs 800 ± 36 g OM/lamb/day, $P < 0.05$) whereas, in January, herbage intakes did not differ significantly. Lambs grazing on ryegrass swards had higher clean wool growth (1147 vs 1085 ± 15 µg/cm² per day, $P < 0.10$) and carcass weight (17.5 vs 16.3 ± 0.22 kg, $P < 0.05$) than lambs grazing on Yorkshire fog swards. The stocking rate maintained on ryegrass plots was 25% greater than on Yorkshire fog plots.

Low concentrations of CT were recorded in the diets of sheep on ryegrass and Yorkshire fog swards (≤ 0.2% on a DM basis). The low levels of CT had no significant effects on diet selection, herbage intake, grazing behaviour patterns, or lamb performance. However, the lambs grazing on Yorkshire fog swards showed small and non-persistent responses to CT in terms of wool growth and liveweight gain. The results of this study indicate that: (i) under high fertility conditions and intensive management, perennial ryegrass/white clover swards appear to have higher feeding value than Yorkshire fog/white clover swards for lamb production and (ii) the low CT concentrations (≤ 0.2% in the DM) observed in both swards did not influence lamb performance significantly.

Keywords *Lolium perenne* (perennial ryegrass); *Holcus lanatus* (Yorkshire fog); *Trifolium repens* (white clover); polyethylene glycol (PEG); condensed tannins (CT); herbage intake; diet selection; grazing behaviour and lamb production

INTRODUCTION

The results of a previous grazing experiment (Montossi et al. 1994) showed advantages to perennial ryegrass swards over Yorkshire fog swards in terms of herbage quality, herbage intake, and animal performance. However, these effects were not conclusive, and need to be investigated in animals of higher productive potential and nutrient demand over a greater range of seasons. Laboratory analyses of extrusa samples established the presence of limited concentrations of condensed tannins in perennial ryegrass and Yorkshire fog swards. Low concentrations of condensed tannins in Yorkshire fog have been related to probable nutritional benefits in animal production by protecting dietary protein from deamination in the rumen (Terrill et al. 1992a, 1992b) and potential effects on lamb parasitism (Niezen et al. 1993a). However, more experimental work is needed to establish the effect of low CT concentration on animal performance (Terrill et al. 1992a, 1992b; Montossi et al. 1994) to delineate an optimum range, and further grazing experiments are needed with sheep in different physiological states to further define production responses to dietary CT (Montossi et al. 1994; Wang et al. 1994). There is no definitive information on the effects of CT concentrations in *Holcus lanatus* on lamb production.

This study was designed to explore aspects of the plant-animal interface with particular reference to the effects of low concentrations of CT in *Holcus* and in perennial ryegrass, involving comparative evaluation of ingestive behaviour and voluntary herbage intake and their effects on wool growth, liveweight gain, and carcass weight in lambs grazing summer swards.

MATERIALS AND METHODS

Site preparation and management

The experiment was conducted at Massey University, Palmerston North, New Zealand (40°23'S), from December 1992 to March 1993 on a Tokomaru silt loam soil (Aeric Fragiaqualf) with Olsen P values in the range 20–30 µg/g. Long-term average annual precipitation for the site is 1000 mm, and mean ambient temperature ranges from 7°C (July) to 18°C (January). Five paired 0.2 ha paddocks of established Yorkshire fog (*Holcus lanatus* cv. Massey Basyn) or perennial ryegrass (*Lolium perenne* cv. Grasslands Nui) were used, each grown with white clover (*Trifolium repens*

cv. Grasslands Tahora). The plots had been continuously stocked with sheep for two years.

Nitrogen and phosphate fertilisers (50 kg of urea and 300 kg of superphosphate/ha, respectively) were applied to the experimental area in April 1992. Two additional applications of urea of 50 kg/ha each were made, one before the trial began and the other in the second week of January.

Sixty-four, four-month-old weaned, mixed-sex Suffolk × Romney lambs (mean weight 28.3 ± 2.0 kg) grazed the experimental plots from 3 December 1992 to 11 March 1993. The lambs were divided into 8 balanced sets according to fasted liveweight and sex (2 female and 6 castrated male), four sets to graze Yorkshire fog/white clover and four to graze perennial ryegrass/white clover swards. Ten additional lambs were slaughtered at the commencement of the trial to provide estimates of initial hot carcass weight. Experimental animals grazed the spare plots for two weeks before measurements commenced. The swards were maintained at approximately 6 cm surface height under continuous variable stocking management through the experiment. Additional adult sheep were used, mainly in ryegrass plots, to maintain the desired sward height (6 cm).

Half of the animals on each plot (1 female, 3 male) were drenched twice daily (0730 and 1730 hours) with polyethylene glycol (PEG; MW 4000) in order to prevent CT binding with plant protein in the rumen (Barry 1989). Based on previous experience by Terrill et al. (1992a, 1992b) of CT concentrations in *Holcus lanatus*, a twice-daily dose of 10 g PEG in 20 ml water per lamb was used for both ryegrass and Yorkshire fog treatments. The remaining lambs received an equivalent volume of water.

Sward measurements

Herbage mass was estimated monthly by cutting ten 0.1 m² quadrats per plot to ground level. Additional samples were bulked within each plot and dissected into categories for morphology (leaves, stem, live and dead tissue) and species, then dried and weighed.

Forty random sward surface height (SSH) readings were recorded twice per week in each plot, using a sward stick (Barthram 1986). These sward height estimates were used to adjust animal numbers. Five readings were also made inside each quadrat when herbage mass samples were collected, giving 50 readings for each plot. The bulk density of the swards was calculated by dividing the herbage

mass estimated for each quadrat cut by the corresponding SSH average (mean of 5 readings).

The vertical distribution of plant tissue within the sward canopy was measured monthly using an inclined point quadrat (Warren Wilson 1963) set at 32.5° to the horizontal. At least 100 contacts were recorded in each plot every month. Contacts were recorded for species, morphology (leaf, stem, petiole), and state (live or dead).

Animal measurements

Unfasted lamb liveweight was recorded weekly between 3 December 1992 and 10 March 1993. At the end of the trial on 11 March 1993 all the lambs were slaughtered and hot carcass weight was obtained immediately after slaughter. Total tissue thickness (GR) was measured on both sides of the hot carcass (Kirton 1989).

Wool growth was estimated at 6 weekly intervals by using a midside patch sampling technique (Bigham 1974). Wool samples were stored in untied plastic bags for further analysis. The weight of each greasy midside sample was recorded after conditioning at 20°C and 65% relative humidity for 48 hours, then samples were conditioned and scoured using the method described by Morris (1992). Clean wool weight and yield (expressed as the ratio of clean to greasy weight) were subsequently recorded.

Herbage organic matter intake measurements and grazing behaviour studies were undertaken simultaneously in two periods (December and January). Faecal output was estimated for all animals using intraruminal controlled release capsules of chromium sesquioxide (CRC; Captec (NZ) Limited, Auckland), according to the procedures described by Parker et al. (1989). The chromic oxide release rates were determined from capsules administered to 16 lambs (4 per treatment) three weeks before slaughter at the end of the trial. During these periods two pairs of castrated male sheep, fistulated at the oesophagus (OF), were rotated between plots on a daily basis and one extrusa sample was collected from each animal from each plot using the procedure described by Montossi et al. (1994). Laboratory analyses of extrusa samples were undertaken for CT (Terrill et al. 1992a), OM digestibility (Roughan & Holland 1977), and total nitrogen (N) using the Kjeldahl method. Herbage organic matter intake was estimated as specified by Parker et al. (1992) using estimates of faecal output and diet digestibility.

PEG administered (20 g/day) was deducted from faecal output values prior to calculating organic matter intakes, on the assumption that PEG is indigestible (Barry & Duncan 1984).

Grazing, ruminating, and resting activities were manually recorded for each lamb over one 24 hour period during each intake measurement, at intervals of 15 minutes. Rate of biting (bites/minute) was obtained using a 20-bites technique (Jamieson & Hodgson 1979) recorded by stop-watch during grazing periods at dawn, mid morning, early afternoon, and dusk. The weight of herbage in individual bites was determined by counting the number of bites taken by OF sheep during the collections of extrusa samples (Stobbs 1973). The botanical composition of the diet selected was assessed by suspending sub-samples of extrusa in water in a gridded tray and identifying the proportions of sward components (as a percentage of total contacts) recorded at grid intersections (Clark & Hodgson 1986).

Experimental lambs, fistulated sheep, and spare wethers were drenched at the beginning of the experiment and at 28 day intervals with Levamisol (Nilverm, Coopers-Pitman-Moore, New Zealand Ltd).

Over 15–16 January, a 24 hour evaluation of rumen ammonia concentration was carried out, sampling rumen contents at 4 hour intervals (0500, 0900, 1300, 1700, 2100, 0100 hours), using 12 wethers fistulated in the rumen (3 per treatment). The wethers grazed the spare plot of each sward and were drenched daily with PEG (20 g/wether) or water for 10 days before sampling. The rumen fluid samples (20 ml each) collected in the field were refrigerated at 4°C, subsequently centrifuged at 3000 g for 15 minutes, and then the residue was frozen until analysed. Rumen ammonia concentration was determined according to the method described by Waghorn et al. (1987).

Statistical analyses

The pasture and animal data were analysed using the statistical package SAS (SAS 1990), based on a Split-Split-Plot Design using 4 blocks, with swards (Yorkshire fog or perennial ryegrass) as the main plot, PEG (CT inactivated or operating) as the split-plot factor, and sex (female or male) as the split-split-plot factor. Means are presented with their standard errors (SEM). A point quadrat package (Butler 1991) was used in the analysis of inclined point quadrat data. All data were initially

tested for normality and homogeneity of variance. In cases where these assumptions were not valid, data were appropriately transformed.

Liveweight gain and wool growth were adjusted by co-variance for initial weight and for initial wool removed from the midside area of each animal, respectively. Estimates of carcass weight at the beginning of the experiment were derived from the initial slaughter group, and used as a covariate for analysis of final carcass weights. Animal and sward results generated from sequential sampling were analysed using the 'repeated measures' option of the SAS general linear models procedure.

RESULTS

Most of the interactions amongst swards, PEG supplementation, and sex were not significant for sward or animal variables. Therefore, the presentation of plant and animal results is concentrated principally on main effects and significant interactions.

Sward measurements

Sward surface height declined slowly from 7–8 cm to 4.5–5 cm on both pastures over the course of the trial. The additional grazing sheep required on ryegrass plots from December to February to achieve comparable sward height between pastures resulted in a 25% higher stocking rate overall for the ryegrass treatment.

At the commencement of the trial in December, ryegrass swards had significantly higher total herbage and dead herbage masses than Yorkshire fog swards, but there were no significant differences in green herbage mass between swards (Table 1). In January, there were no significant differences between swards in any of the sward variables studied. However, in February, total herbage mass on Yorkshire fog was higher than on ryegrass, reflecting the fact that dead herbage mass of Yorkshire fog was almost double that of ryegrass.

Sown grasses formed the major components of both Yorkshire fog and ryegrass swards throughout the experiment (Table 2). The proportion of white

Table 1 The effect of sward species on herbage mass (kg DM/ha) and on sward bulk density (kg DM/ha cm) from December to February.

	December			January			February		
	Ryegrass	Fog	SEM [†]	Ryegrass	Fog	SEM	Ryegrass	Fog	SEM
Herbage mass	2770	2210	189*	3790	3530	202	2460	3100	220*
Green herbage mass	1750	1560	127	2550	2260	132	1430	1080	98*
Dead herbage mass	1020	650	68**	1240	1270	82	1030	2020	130***
Herbage bulk density	380	370	24	580	670	31	560	730	49*
Green herbage bulk density	240	260	16	390	430	21	350	240	22**

[†]SEM = Standard error of the mean.

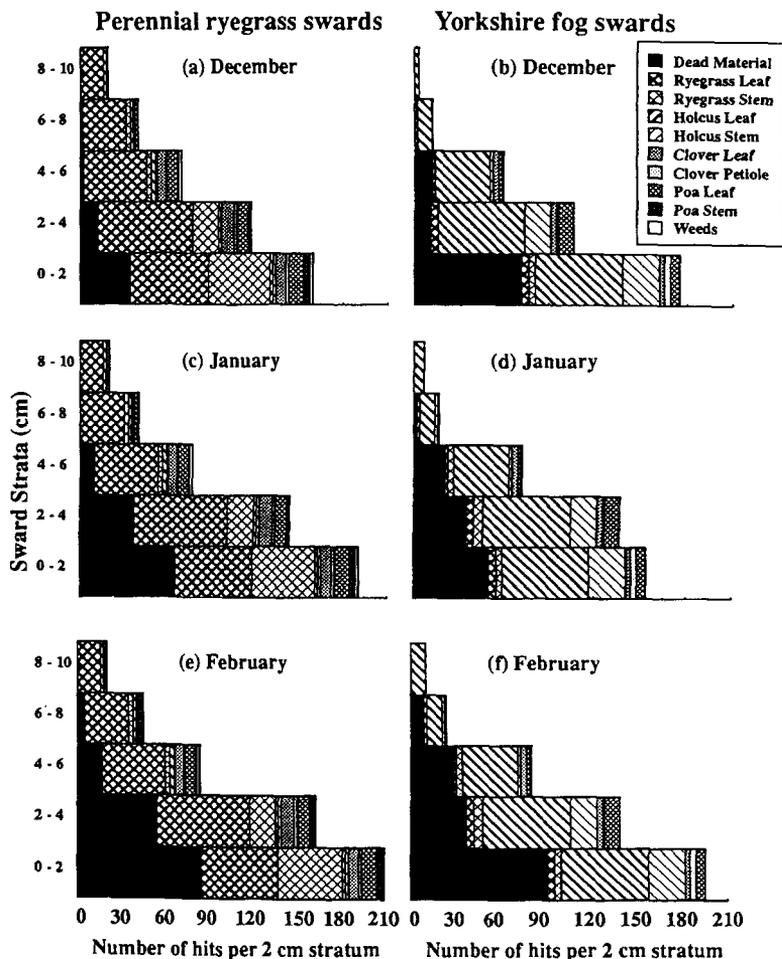
Significance: in this and subsequent tables [†] $P < 0.10$, * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$.
Number of observations contributing to the mean each month ($n = 40$).

Table 2 The proportions of components of ryegrass and Yorkshire fog swards estimated from hand separation (DM basis) from December to February.

Sward components (% of total DM)	December			January			February		
	Ryegrass	Fog	SEM [†]	Ryegrass	Fog	SEM	Ryegrass	Fog	SEM
Sown grass stem	16	15	2.5	23	13	1.4*	15	9	1.7
Sown grass leaf	32	29	4.0	31	18	2.0*	27	13	2.7*
Sown grass plant	48	44	5.8	54	31	3.0*	42	22	4.1*
Clover petiole	3.0	4.7	1.5	1.5	2.7	0.4	1.5	1.3	0.2
Clover leaf	4.2	4.1	1.4	2.5	5.7	0.8	3.5	2.7	0.4
Clover plant	7.2	8.8	2.8	4.0	8.4	1.2	5.0	4.0	0.5
Other grasses	8.5	19	6.2	7.1	25	2.8*	4.3	7.5	2.0
Weeds	0.6	0.2	0.4	2.1	0.0	1.4	7.7	0.2	5.3
Dead material	36	29	3.3	33	36	3.4	41	66	3.3*

Number of observations contributing to the mean each month ($n = 8$).

Fig. 1 Proportional distribution of plant species and morphology for ryegrass and Yorkshire fog swards during December, January, and February determined from inclined point quadrat contacts.



clover did not differ amongst swards or sampling periods. There was a higher content of grass leaf in ryegrass swards than in *Holcus* swards, and the dead material proportion was higher in *Holcus*. Weeds were a minor component and did not differ significantly between swards.

Comparisons of point quadrat data (Fig. 1) indicated that herbage mass was mainly concentrated at the base of both swards (0–4 cm height). Live leaf lamina was the major component of the uppermost layers (4–10 cm height) of both swards, particularly in ryegrass plots. However, stem frequency increased substantially from the top to the bottom in both sward profiles. Dead material was principally concentrated at the base of both sward canopies. White clover was distributed higher

in the sward canopy of ryegrass pastures than Yorkshire fog pastures.

Animal measurements

Separate identification of grass species in extrusa samples was difficult, so the results are based on comparisons of grasses versus white clover proportions and of live material versus dead material proportions. Leaf lamina and sheath were not distinguished. Weeds were not observed in ingesta samples for either sward. In both December and January, grasses and live material were the main constituents of the diet selected in both swards (Table 3). In both sampling periods, OF ingesta samples contained significantly higher proportions of grasses and white clover than the swards on

offer. When diet and sward comparisons are based on the composition of the upper layers of both swards (above 4 cm), rather than on the sward on offer, the differences become much smaller (Table 4).

In December, the OMD of the diet selected by OFs was 3% units higher in ryegrass swards than in Yorkshire fog swards, but in January there was no significant difference between diets (Table 3). In January, the N content of the ingesta samples collected in Yorkshire fog swards was significantly higher than that of ryegrass swards, but differences in December were not significant. The total, free, protein-bound, and fibre-bound condensed tannins in the diets selected did not differ significantly between swards or sampling periods (Table 3).

Rumen ammonia concentration (Table 5) was always higher in ruminal fistulated wethers (RF) grazing on ryegrass than on Yorkshire fog. Rumen ammonia values were increased by PEG administration in both swards, particularly 5–6 hours after

PEG supplementation, and this effect attained significance at $P < 0.05$ at 0100 h and at $P < 0.10$ at 1700 h and 2100 h.

Intake per bite was higher on Yorkshire fog swards than on ryegrass swards in December ($P < 0.10$) and January ($P < 0.01$) (Table 6). Rates of biting were higher on Yorkshire fog than on ryegrass in December ($P < 0.01$) but lower in January ($P < 0.05$). Grazing, ruminating, and resting times were not significantly different between swards in either sampling period.

There were no significant effects of sward species or PEG supplementation on the release rates of Cr_2O_3 in slaughtered lambs. Therefore, a common release rate of 188.5 mg Cr_2O_3 /day was used amongst treatments and periods. Overall, herbage intakes on ryegrass swards were higher than those on Yorkshire fog swards ($P < 0.05$ and $P < 0.10$ in December and January, respectively) (Table 7). There were no significant differences in herbage intakes from PEG supplementation or sex effects, or their interactions (Montossi 1996).

Table 3 Botanical and chemical composition of the diet selected from ryegrass and Yorkshire fog swards in December and January.

	December			January		
	Ryegrass	Fog	SEM	Ryegrass	Fog	SEM
Contacts (%) of						
White clover	7	4	0.7**	4	2	0.5**
Green material	94	89	1.0**	89	91	1.0
OM Digestibility	0.81	0.78	0.04**	0.80	0.79	0.05
Concentration (% DM) of						
N	3.69	3.73	0.06	3.74	3.99	0.04*
Free tannin	0.056	0.059	0.006	0.072	0.065	0.010
Protein-bound tannin	0.088	0.102	0.018	0.120	0.082	0.008
Fibre-bound tannin	0.021	0.025	0.001	0.061	0.026	0.010
Total condensed tannin	0.166	0.186	0.024	0.265	0.174	0.030

Number of observations contributing to the mean each month ($n = 16$).

Table 4 Relationships between the proportions of sward components in the upper layers (above 4 cm) of the ryegrass and Yorkshire fog sward canopies and the composition of the diet selected during December and January.

Components (%)	December				January			
	Ryegrass		Yorkshire fog		Ryegrass		Yorkshire fog	
	Sward	Diet	Sward	Diet	Sward	Diet	Sward	Diet
Grasses	94	93	94	96	91	96	92	98
White clover	6	7	6	4	9	4	8	2
Green Material	98	94	84	89	93	90	76	91
Dead Material	2	6	16	11	7	10	24	9

Table 5 Variation in rumen ammonia concentration (mg NH₃ per ml of rumen fluid) during 24 hours in rumen fistulated wethers grazing on Yorkshire fog and perennial ryegrass swards treated with zero or 20 g sheep/day of polyethylene glycol (PEG; MW 4000).

TIME Hours	Species (SPP)			Oral PEG supplementation		
	Ryegrass	Yorkshire fog	SEM	Without	With	SEM
0900	466	306	39*	361	411	39
1300	592	390	34**	459	524	34
1700	697	417	29**	513	600	29
2100	813	493	52**	580	724	52
0100	711	463	48**	503	671	48*
0500	370	262	17**	321	310	17

Number of observations contributing to the mean in each sampling time for main effects ($n = 6$).

Table 6 Effects of sward species on intake per bite (mg OM/bite), rate of biting (bites/minute), grazing, and ruminating and resting times (minutes).

Behavioural components	December			January		
	Ryegrass	Fog	SEM	Ryegrass	Fog	SEM
Mean bite size (mg OM/bite)	80	95	5.0	85	111	5.3**
Rate of biting (bites/min)	67	73	0.8**	64	61	1.0*
Grazing time (min) ¹	616	596	25	634	645	11
Ruminating time (min) ¹	228	224	16	457	458	8
Resting time (min) ¹	469	493	17	259	247	10

Number of observations contributing to the mean each month ($n = 32$).

¹Balance of 1440 min occupied in penning and drenching procedures.

Table 7 Effects of sward species, oral PEG supplementation, and sex of lamb on herbage intake (HI; g OM/kg LW^{0.73}.day), clean wool growth from midside areas ($\mu\text{g}/\text{cm}^2$.day), lamb liveweight gain (g/day), carcass weight (kg), and GR (mean value of left and right sides, mm) from December to March.

Animal parameters	Species			Oral PEG supplementation			Sex		
	Ryegrass	Fog	SEM	Without	With	SEM	Female	Male	SEM
Herbage intake (g OM/kg LW ^{0.73} .day)									
December	82	70	2.8*	76	75	1.7	78	74	2.0
January	98	85	3.5+	90	93	4.0	94	90	4.5
Clean wool growth ($\mu\text{g}/\text{cm}^2$.day)	1145	1085	15	1080	1145	25	1145	1090	35
Liveweight gain (g/day)									
8 Dec - 18 Jan	165	129	10+	136	158	15			
18 Jan - 6 Feb	190	208	28	190	207	16			
6 Feb - 15 March	64	68	10	72	60	10			
Overall	131	121	9	122	130	7	134	119	4.4*
Carcass weight (kg)	17.5	16.3	0.2*	16.8	17.0	0.4	16.6	17.1	0.5
GR (mm)	6.7	5.4	0.6	6.2	5.9	0.7	7.4	4.8	0.6**

Number of observations contributing to the mean each month for main effects ($n = 32$), and in the case of sex of lamb (male = 48; female = 16).

GR¹ = Mean value of left and right sides.

Lambs on ryegrass swards had higher wool growth from midside areas ($P < 0.10$) than those on Yorkshire fog swards (Table 7). There was no effect of PEG supplementation or sex on clean wool growth. However, although the results are not presented here, a significant sward species \times PEG supplementation interaction showed that the wool growth of non-PEG lambs on ryegrass swards was higher than those of the rest of the sward \times PEG supplementation combinations (Montossi 1996).

Lambs grazing ryegrass swards had greater rates of liveweight gain ($P < 0.10$) than lambs grazing Yorkshire fog swards in December/January, but not overall (Table 7). PEG supplementation had no effect upon liveweight gain. Carcass weight and GR values were higher for lambs grazing on ryegrass swards than those on Yorkshire fog, but only the difference in carcass weight attained significance ($P < 0.05$). PEG supplementation had no effect on these variables. Female lambs had significantly higher liveweight gain and GR values than castrated male lambs. There was no significant difference in carcass weight between sexes.

DISCUSSION

Swards

The continuous, flexible stocking management was adopted to minimise differences in sward conditions between treatments and over time. The higher stocking capacity of ryegrass swards, in contrast to Yorkshire fog swards, taken together with the higher herbage intakes observed on ryegrass plots (Table 7), is evidence of higher pasture growth of ryegrass swards. In other comparative studies, ryegrass has been found to be more productive than Yorkshire fog at higher levels of nitrogen fertilisation (Haggar 1976; Watt 1987; Frame 1992) or at high soil nitrogen status (Morton et al. 1992), particularly in summer, with an adequate supply of soil moisture (Haggar 1976). A decline in the contribution of the sown grass component in Yorkshire fog swards over time was also observed, with corresponding increase in ryegrass (Table 2). The higher proportion of dead material in Yorkshire fog swards is in accord with the results of other summer observations (Niezen et al. 1993a) as well as a late autumn comparison (Montossi et al. 1994).

Diet selection

In both swards, green material formed a higher proportion of the diet selected than in the whole

sward profile (Tables 2 and 3). In both sampling periods, white clover formed a lower proportion in the diet than in the total sward in Yorkshire fog swards, but not on ryegrass swards (Tables 2 and 3). Diet and sward composition (above 4 cm) were similar (Table 4). In temperate swards, there is evidence suggesting that the diet of oesophageally fistulated animals may reflect the composition of the top strata of the sward, indicating substantially unselective grazing (Milne et al. 1982; Illius et al. 1992; Clark 1993; Montossi et al. 1994). Though oesophageally fistulated animals were older than the experimental lambs, this is unlikely to have materially affected diet selection (Hodgson & Rodriguez 1971).

Dead material appeared in the extrusa samples collected from both swards in December and January, but to a greater extent in Yorkshire fog samples. This may be explained by the high proportion of this component in the whole sward profile, but particularly in the surface layers of the sward canopy of Yorkshire fog (Fig. 1). The presence of dead leaf and sheath material is reputed to reduce the acceptability of *Holcus lanatus* to sheep (Cameron 1979). The higher vertical distribution of white clover in the sward canopy of perennial ryegrass than of Yorkshire fog (Fig. 1), providing greater accessibility for the grazing sheep, may explain the higher proportion of clover in ryegrass extrusa samples.

The low concentrations of CT in extrusa samples were not expected to affect *in vitro* digestibility, and hence prediction of *in vivo* digestibility (T. N. Barry pers. comm.). In December, OF animals selected a diet 3 units more digestible from ryegrass swards than from Yorkshire fog swards (Table 3), in agreement with the results of Montossi et al. (1994) and of Morton et al. (1992). The higher OMD recorded for ryegrass swards reflects the important contribution of green grass leaf and white clover, and the lower proportion of dead material in the extrusa samples. The higher N content recorded in the extrusa from Yorkshire fog swards compared with ryegrass swards, particularly in January, is consistent with the reports of other researchers (Jacques 1974; Haggar 1976; Frame 1982; Harvey et al. 1984).

The presence of low concentrations of CT ($< 0.2\%$ on a DM basis) in *Lolium perenne* supports the evidence obtained by Montossi et al. (1994). The low CT concentrations in *Holcus lanatus* are in accordance with the results of other research reports (Terrill et al. 1992a, 1992b; Douglas et al.

1993; Montossi et al. 1994; Iason et al. 1995). In both sampling periods, the total and component CT did not differ significantly between sward species, in contrast with the observations of Montossi et al. (1994) where *Holcus lanatus* contained more total CT and protein-bound CT than *Lolium perenne*. Possible explanations for this discrepancy may be the presence of Yorkshire fog in ryegrass plots, or variations in growing conditions between experiments.

The experiments of Iason et al. (1995) and Douglas et al. (1993) indicated that the CT concentration of *Holcus* green leaf is approximately twice that of green stem. However, green grass leaf was the predominant component in the diet selected in *Holcus* swards. Therefore, it is unlikely that the low CT concentration of *Holcus* swards influenced the selective patterns of the oesophageal fistulated sheep in those swards.

Rumen ammonia

The increase in rumen NH_3 concentration in RF sheep with PEG administration (Table 5) provides additional evidence of the presence of CT in both ryegrass and Yorkshire fog swards, and is consistent with a reduced deamination of plant proteins when CT are present (Waghorn et al. 1987). Terrill et al. (1992b) also found that PEG administration resulted in increased rumen NH_3 concentration at low concentration of CT (0.47% on a DM basis). The high rumen NH_3 values recorded for both swards are probably related to the application of nitrogen fertiliser (50 kg/ha of urea) to the experimental plots four days before the rumen metabolism observations.

The level of PEG administration (20 g/day) was based on the experience of Terrill et al. (1992b), working with grass diets expected to have a comparable CT concentration to the Yorkshire fog grazed in this study. Retrospective calculation indicated that this level of use should have been more than necessary to inactivate the CT ingested on both swards in strictly quantitative terms. However, the variation observed in rumen NH_3 concentration amongst sampling times in both swards (Table 5) indicated that twice daily PEG supplementation may not have completely eliminated binding of plant proteins to CT in the rumen for a full 24 hr period (Terrill et al. 1992b).

Grazing behaviour and herbage intake

The higher mean bite weight of OF animals grazing on Yorkshire fog than on ryegrass swards,

particularly in January (Table 6), is in agreement with the results of Montossi et al. (1994) and Liu (1996). Possible explanations for this effect are either the higher bulk density, particularly of the green components (Table 1), or the lower tensile strength of *Holcus lanatus* leaves in comparison with those of perennial ryegrass (Evans 1967; Jacques 1974). Increases in bulk density (Burlison et al. 1991) and decreases in leaf shear breaking load (Poppi et al. 1987) have been positively correlated with bite weight.

With the exception of the contrast in bite rates between months, comparative patterns of grazing behaviour between treatments were similar in December and January. These results confirm that intake per bite is the most sensitive response to variations in sward characteristics (Hodgson 1985, 1990).

Lambs grazing on ryegrass swards had higher herbage intakes than those grazing on Yorkshire fog swards in December (Table 7). This result is in agreement with those observed previously for adult sheep in an autumn comparison (Montossi et al. 1994), where the evidence suggested that the most important limits were nutritional rather than behavioural in origin, and reflected differences in diet digestibility rather than in bite weight. This explanation also fits the results for January, where herbage intakes from the two swards were similar, reflecting the similar OM digestibilities observed in both diets (Table 3), despite the higher intake per bite recorded in Yorkshire fog swards (Table 6). When expressed per unit of metabolic weight (Table 7), intakes were similar to those recorded previously by Jamieson & Hodgson (1979) for comparable lambs grazing ryegrass swards of similar digestibility, under continuous stocking management, and higher than those observed on ryegrass swards in summer with ewes by L'Huillier et al. (1986). Risks of bias invalidate the calculation of herbage intake from the product of components of grazing behaviour, but comparisons between treatments for specific components are considered to be valid (Hodgson 1985).

In accord with the results of Terrill et al. (1992b), there was no evidence of a PEG effect on herbage intake in either grass species (Table 7).

Sward species and lamb performance

Lamb performance was generally better on ryegrass swards, where lambs had higher wool growth (5 to 8%), liveweight gain (8%), carcass weight (7%), and GR values (18–24%) than lambs from

Yorkshire fog swards, though not all of these differences attained significance (Table 7). Morton et al. (1992) and Niezen et al. (1993a) also showed higher lamb liveweight gains on perennial ryegrass than on Yorkshire fog. In contrast, Watkin & Robinson (1974) found similar nutritive value and animal performance on ryegrass and Yorkshire fog swards. In the current study, the superior intake of lambs grazing on ryegrass, particularly at the beginning of the trial, reflects the higher dietary OMD found in ryegrass than in Yorkshire fog swards, resulting in a greater liveweight gain. In addition to the better individual lamb performance, the stocking rates maintained on ryegrass swards until March were 25% higher than those on Yorkshire fog, indicating a greater lamb weight gain per hectare for ryegrass swards. The results of Niezen et al. (1993a) also support this finding under continuous stocking management.

Information comparing wool growth of lambs grazing on ryegrass or Yorkshire fog swards appears to be limited to the results of Watkin & Robinson (1974), who found greater fleece weights (5%) in favour of the ryegrass treatment.

Condensed tannins and lamb performance

Comparative information on the effects of low concentrations of condensed tannins in temperate grasses (< 1% on a DM basis) on lamb performance appears to be restricted to the results of Terrill et al. (1992b). In general, PEG drenching had no significant effect on the animal performance parameters studied despite the clear indication of greater rumen ammonia losses when it was used to prevent CT binding to plant protein. Montossi (1996) suggested that transitory effects of CT on lamb performance were observed in comparisons between PEG and non-PEG lambs grazing on Yorkshire fog swards over the first 4 to 5 weeks of the trial, but the low CT concentrations present in the diet of lambs grazing on ryegrass and Yorkshire fog swards were not enough to increase lamb performance in the longer term. Other researchers (Barry 1985; Lowther & Barry 1985) observed partial CT adaptation of sheep fed on *Lotus pedunculatus*. Furthermore, Robbins et al. (1987) found some buffering effects of sheep saliva against high dietary concentrations of CT. More research is warranted in this area before attempting to draw any general conclusion. The limited responses to PEG in the present experiment contrast with the results of Terrill et al. (1992b), where use of PEG increased lamb liveweight gain by 29% and wool

growth by 18%. However, the dietary levels of CT reported by Terrill et al. (1992b) were higher than those of the present study (0.47% versus 0.2% on a DM basis, respectively).

The higher wool growth of PEG lambs on ryegrass swards was not expected (Montossi 1996), but is supported by other results at this centre (Liu 1996). Recently, Niezen et al. (1993b) showed significant improvement in body growth rates resulting from PEG administration in lambs grazing on ryegrass swards. These results indicate the need for better understanding of the effects of PEG on ruminant digestion.

The accumulated experimental evidence (Montossi et al. 1994; Liu 1996) confirms the presence of low CT concentrations in perennial ryegrass and shows that this grass is not suitable as a "negative control" for testing the effect of CT on animal performance. Additionally, despite the similar concentrations of CT found in the diets of animals on both swards, animal performance data indicate that the relatively small and non-persistent responses to CT appeared in some degree to be more consistent in *Holcus* swards than in perennial ryegrass. This effect suggests a possible higher protein-binding capacity of CT in *Holcus* than that of perennial ryegrass, and deserves further study.

CONCLUSIONS

The results of the present study indicate that perennial ryegrass/white clover swards growing under high fertility conditions and intensive grazing management have higher feeding value in terms of lamb production and higher stocking capacity than Yorkshire fog/white clover swards.

The diet selected by oesophageally fistulated sheep consistently reflected the composition of the upper layers (above 4 cm) of both sward canopies, suggesting that differences in vertical distribution between legumes and grasses determined their selection by sheep within the sward canopy.

No evidence was found to suggest that the low CT concentrations ($\leq 0.2\%$ on a DM basis) of perennial ryegrass and Yorkshire fog influenced the selective behaviour of the lambs. Further, these low CT levels had no effect on herbage intake or on grazing behaviour patterns. The small and non-persistent effects of CT on animal responses observed in the present study show that dietary CT concentrations of 0.2% on a dry matter basis do not have any direct nutritional benefits to lamb production. More research is necessary to define

the minimal effective CT concentration in forage diets to improve ruminant production.

Given the traditional economic relevance of perennial ryegrass to New Zealand farming, this trial poses questions about the importance of CT in perennial ryegrass and the potential for improving the nutritional characteristics and ruminant production potential of the species from an increase in CT concentration resulting from plant selection or manipulation of soil nutrient status.

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