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Rumen digestion and rumen outflow rate in deer fed fresh chicory (*Cichorium intybus*) or perennial ryegrass (*Lolium perenne*)

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SUMMARY

Pure swards of chicory (*Cichorium intybus*) and perennial ryegrass (*Lolium perenne*) were grown at Palmerston North, New Zealand. They were cut daily and fed hourly at 2·25 kg dry matter (DM)/day to eight hand-reared, rumen-fistulated castrated red deer stags kept in metabolism crates during December 1994 and January 1995 (summer). Apparent digestibility, rumen fractional disappearance rate (FDPR), rumen fractional degradation rate (FDR), rumen fractional outflow rate (FOR) and mean retention time (MRT) were measured. The ratio of readily fermentable carbohydrate to structural carbohydrate was approximately three times higher in chicory than in perennial ryegrass. Apparent digestibility of DM was higher in deer fed chicory than in deer fed perennial ryegrass (0·785 *v.* 0·727), whilst apparent digestibility of neutral detergent fibre (NDF) was lower in deer fed chicory (0·679 *v.* 0·755), due to a reduced hemicellulose digestibility (0·667 *v.* 0·783). Relative to deer fed perennial ryegrass, those fed chicory had higher rumen FDPR values for DM (14·5 *v.* 8·6%/h), soluble carbohydrate (69·9 *v.* 54·7%/h), cellulose (15·5 *v.* 9·8%/h) and lignin (6·8 *v.* 3·8%/h). Rumen FDR in deer fed chicory was higher than those fed perennial ryegrass for cellulose (11·4 *v.* 7·0%/h) and lignin (2·7 *v.* 1·0%/h), but tended to be lower for hemicellulose. Rumen FOR was higher and MRT was lower for both liquid and particulate matter in deer fed chicory compared to deer fed perennial ryegrass.

It is concluded that rumen FDPR and apparent digestibility were much higher in deer fed chicory than in deer fed perennial ryegrass, due to faster degradation rates of most constituents in the rumen and faster outflow rates from the rumen. An exception was hemicellulose, where reduced rumen degradation rates and shorter rumen particulate MRT contributed to reduced apparent digestibility. Faster clearance from the rumen, due to both faster degradation and outflow rates may be used to explain the greater voluntary feed intake (VFI), as well as faster growth rate in deer grazing chicory compared to those grazing perennial ryegrass. Faster rates of lignin solubility in the rumen probably contributed to the more rapid breakdown of chicory in the rumen.

INTRODUCTION

Deer grazing chicory (*Cichorium intybus*) had higher liveweight gains (LWG) and VFI, both during lactation and post-weaning, than deer grazing perennial ryegrass (*Lolium perenne*)/white clover (*Trifolium repens*)-based pasture (Kusmartono *et al.* 1996*a*). Behavioural observations, both during indoor feeding (Hoskin *et al.* 1995) and under grazing (Kusmartono *et al.* 1996*a*) showed a similar time spent eating, but substantially less time spent ruminating by deer fed chicory than those fed perennial ryegrass. In indoor studies, deer fed chicory had a faster breakdown of particles to the critical particle size for leaving the rumen and faster fractional disappearance of total DM from the rumen than deer fed perennial ryegrass (Kusmartono *et al.* 1996*b*). Digesta clearance from the rumen has long been recognized as a major factor determining VFI and nutritive value of forages (Black *et al.* 1982) and explains the higher VFI on chicory.

Rumen fractional disappearance rate can be partitioned into two components; fractional degradation rate and fractional outflow rate. The objective of this study was to compare rumen digestion rate and

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rumen outflow rate in deer fed fresh chicory or perennial ryegrass.

MATERIALS AND METHODS

Experimental design

The experiment was conducted at Massey University Deer Research Unit, Palmerston North, New Zealand and was divided into two periods, each of 17 days duration. Period 1 (P1) took place 5–22 December 1994, whilst period 2 (P2) took place 10–27 January 1995. Red deer (*Cervus elaphus*) were fed either fresh chicory or fresh perennial ryegrass at 2·25 kg DM/day, given continuously at hourly intervals using automatic feeders. The trial was a changeover design, with the animals fed chicory in P1 being fed perennial ryegrass in P2, whilst those fed perennial ryegrass in P1 were fed chicory in P2. Each animal grazed its assigned pasture for 6–7 days before being brought indoors and placed in a metabolism cage. Each indoor period comprised an adjustment period (10 days) and data collection period (7 days), with apparent digestibility and rumen outflow rate being measured in the data collection period. To measure rumen liquid outflow rate, Cr-EDTA marker was continuously infused into the rumen during the last 5 days of the collection period. Lignin and acid detergent fibre (ADF) were used to measure rumen outflow rate of particulate matter. Rumen fractional outflow rate of liquid and particulate matter was then determined using the continuous infusion, total sampling method (Faichney 1975), with total rumen content of the two markers determined from emptying (baling) the rumen at the end of the infusion period.

Forages

Chicory (*Cichorium intybus* cv. Puna) was sown in January 1992, and was a pure crop, in the vegetative stage. Perennial ryegrass (*Lolium perenne* cv. Nui) was sown in 1991, and was a pure sward, c. 10 cm in height. Fertilizers applied included potassic superphosphate (9% P; 10% S and 7% K) dressed at 250 kg/ha, corresponding to 22·5 kg P/ha, to both forages in late autumn (April 1994). Urea was applied to each forage four times a year at 37 kg N/ha in late summer (February 1994), early spring (August 1994), late spring (October 1994) and summer (January 1995). Fresh forages were cut daily at 15.00 h using a mower; half was fed immediately after cutting and the remainder was spread on the floor in a cool building to prevent deterioration.

Animals and diets

Eight hand-reared, fistulated, castrated stags each fitted with an 83 mm diameter rumen cannula were used. Mean initial and final liveweights (±S.D.) of the animals were 130 (±6·8) and 129 (±8·9) kg for P1 and 136 (±7·8) and 132 (±7·3) kg for P2, respectively. The animals were kept individually in specially constructed deer metabolism crates similar to those described by Milne *et al.* (1978), to which they were well accustomed. One side of the cages was movable and could be used to adjust the floor area.

The animals were randomly allocated to two treatment groups each of four animals based on liveweight. Prior to being brought into cages, the animals were grazed on either chicory or perennial ryegrass for 6–7 days. A 10-day adjustment period allowed animals to adjust to indoor conditions, to the two diets offered, and to the handling procedures, including restriction of the movement caused by reducing the floor area.

During the adjustment and data collection periods, overhead feeders were set to deliver feeds at hourly intervals to achieve the steady state conditions required, and filling of the overhead feeders took place at 15.30 and 08.00 h. The daily DM offered of both feeds was kept at 2·25 kg DM/day, and the amount of fresh materials to be fed was calculated by taking triplicate samples of feed offered at 15.00 and at 08.00 h the following morning. Feed refusals were collected at 08.00 h for dry matter (DM) determination (100 °C; 18 h). During the experiment animals had free access to water and to mineralized salt blocks (Dominion Salt, Blenheim, NZ).

Digestibility trial

Feed offered and feed refusals were weighed and faeces were quantitatively weighed daily over the periods 16–22 December 1994 and 21–27 January 1995 in P1 and P2, respectively. The cages were designed such that there was no urine contamination of faeces, and any small amounts of faeces dropped on the floor were collected, so the total faeces was measured. Water intake was measured daily for each animal and the values were presented after being corrected for evaporative losses. Duplicate 200 g samples of feed offered were taken daily, pooled per week, and kept at −20 °C. Each animal's feed refusal was collected, pooled per animal per week, and kept at −20 °C. At the end of each period, duplicate subsamples of pooled feed offered and feed refusals were freeze-dried and ground for chemical analysis. Faeces were collected daily and separated from any hair and residual forage; 15% of total faeces excreted was pooled per animal, and kept at −20 °C. Later these were homogenized, triplicate samples were taken for DM determination (100 °C; 48 h) and duplicate samples were taken, freeze-dried and ground for chemical analysis.

Measurement of rumen outflow rate

Marker infusion

The inert liquid phase marker chromium ethylene diaminetetraacetic acid (Cr-EDTA) was prepared following the method of Binnerts *et al.* (1968) and adjusted to a pH of 6·5–7·0. The Cr-EDTA was made up to 10 litres with a final Cr concentration of 2 mg/g of solution. Following a priming dose of 50 g into the rumen, the Cr-EDTA solution was continuously infused into the rumen for 5 days at a rate of 28–32 g/h. The exact infusion rate was determined for each animal. The infusion was done using a peristaltic pump (PLG-multipurpose pump, Desaga, Heidelberg, Germany).

Rumen contents baling

The rumens were emptied on 22 and 23 December 1994 (P1) and on 27 and 28 January 1995 (P2) at the conclusion of the collection period. Rumen contents were weighed, thoroughly mixed, and subsampled before returning the warmed digesta back to the rumen. Subsamples of rumen digesta were taken for triplicate DM determination both by oven-drying and freeze-drying. Duplicate 200 g subsamples of rumen digesta were taken, freeze-dried and ground for chemical analysis. The process of baling took 20–25 min per animal. The animals remained standing and were not tranquillized during rumen baling.

Laboratory methods

All laboratory analyses were conducted using freeze-dried material, which had been ground to pass a 1 mm mesh diameter sieve (Wiley mill, USA). Organic matter (OM) content was measured by ashing in a furnace of 500 °C for 16 h and total nitrogen (N) was determined by the Kjeldahl procedure, using a selenium catalyst and sulphuric acid digestion. Hot water soluble carbohydrate (HWSC) and pectin were extracted using boiling water and ammonium oxalate respectively, and determined using the method described by Bailey & Ulyatt (1970). Neutral detergent fibre (NDF), acid detergent fibre (ADF) and lignin were determined by the detergent system of Van Soest (1994). Hemicellulose was calculated as NDF−ADF and cellulose was calculated as ADF−lignin. The DM of rumen digesta was determined by oven-drying (100 °C) for 3 days, and by freeze-drying for 6 days, until no further loss in weight occurred. Chromium analysis of rumen digesta was done using the method of Costigan & Ellis (1987).

Calculation of data and statistical analysis

Rumen fractional outflow rate (FOR) was calculated using the continuous infusion and total sampling procedure (Faichney 1975) as shown in Eqns (1) and (2). Liquid FOR was calculated with reference to the external marker Cr-EDTA. Particulate FOR was calculated using two internal markers (lignin and ADF) and it was assumed that any lignin or ADF digestion occurred in the rumen only; Eqn (2) assumes that there was minimal post-ruminal digestion of lignin or ADF.

Rumen fractional outflow rate (FOR):

Water (%/h)

$$= \frac{\text{Marker Cr infusion rate (mg/h)} \times 100}{\text{Rumen pool size (mg Cr)}} \quad (1)$$

Particulate matter (%/h)

$$= \frac{\text{Faeces lignin or ADF excretion rate (g/h)} \times 100}{\text{Rumen lignin or ADF pool size (g)}} \quad (2)$$

Rumen fractional disappearance rate (FDPR) and rumen fractional degradation rate (FDR) were calculated as shown in Eqns (3) and (4).

Fractional disappearance rate (FDPR; %/h) =

$$\frac{\textit{Intake (g/h)} \times 100}{\textit{Rumen pool size (g)}} \quad (3)$$

Fractional degradation rate (FDR; %/h) =

$$\textit{FDPR} - \textit{FOR (lignin)} \quad (4)$$

Rumen FDPR was calculated for dry matter, all carbohydrate constituents and lignin. Equation (4) was applied to the fibre constituents of each feed only, on the assumption that all fibre components left the rumen in the same particle as lignin and therefore had the same FOR. Rumen mean retention time (MRT) was calculated as the reciprocal of FOR (Faichney 1975).

Parameters measured were analysed using the General Linear Model (GLM) procedure (SAS 1987), for the changeover design; between animal and between feeding sequence variation were first removed, before analysing for dietary and period effects. Least Square Means (L.S.M.) analysis was used to test the differences between treatments.

RESULTS

Chicory contained significantly lower concentrations of DM, NDF, ADF, hemicellulose and cellulose ($P < 0·01$), but higher ash, lignin and pectin concentrations ($P < 0·01$) than perennial ryegrass (Table 1), with these differences being apparent in each feeding period. Water-soluble carbohydrate content and total N were similar for chicory and perennial ryegrass.

Dry matter intake (DMI) of deer fed chicory was slightly higher (*c.* 10%; $P < 0·05$) than for deer fed perennial ryegrass (Table 2). Apparent digestibility of DM was greater in deer fed chicory than those fed perennial ryegrass ($P = 0·06$). Fibre apparent di-

Table 1. *Chemical composition (g/kg DM) of perennial ryegrass and chicory*

	Period 1			Period 2		
	Perennial ryegrass ($n = 2$)	Chicory ($n = 2$)	S.E. (D.F. = 2)	Perennial ryegrass ($n = 2$)	Chicory ($n = 2$)	S.E. (D.F. = 2)
Dry matter (g/kg) ($n = 7$)	255	180	5·6	251	200	7·8
Ash	112	180	11·1	101	136	1·8
Total nitrogen	26·0	24·0	2·81	25·3	28·4	0·50
Water soluble carbohydrate (*a*)	134	108	8·9	107	106	9·3
Pectin (*a*)	14	85	13·0	14	106	3·0
Readily fermentable carbohydrate*	148	193	12·5	121	212	6·5
NDF	455	229	12·0	450	228	8·0
ADF	258	173	5·6	259	165	3·1
Hemicellulose (*b*)	197	56	6·5	191	61	4·8
Cellulose (*b*)	237	140	3·2	240	133	3·3
Ratio RFC:SC (*a*/*b*)†	0·34	0·99	0·084	0·28	1·09	0·028
Lignin	21	33	3·5	19	34	2·6

* Water soluble carbohydrate + pectin.
† Readily fermentable carbohydrate : structural carbohydrate.

gestibility was lower in deer fed chicory than perennial ryegrass, with the difference approaching significance for NDF ($P = 0·07$) and ADF ($P = 0·06$) and attaining significance for hemicellulose ($P < 0·05$).

For both forages, readily fermentable carbohydrate disappeared from the rumen around six times faster than total fibre (NDF). Fractional disappearance rate (FDPR) of chicory from the rumen was higher than that of perennial ryegrass, with the difference attaining significance for DM ($P < 0·05$), soluble carbohydrate ($P < 0·01$), cellulose ($P < 0·05$) and lignin ($P < 0·05$). Pectin FDPR was also considerably greater for chicory than for perennial ryegrass but, due to the variability encountered, the difference did not attain significance. There was no difference in FDPR value of hemicellulose between the two diets. Fractional degradation rate (FDR) of total fibre (NDF; $P = 0·06$), cellulose ($P < 0·05$) and lignin ($P < 0·01$) were higher in deer fed chicory than perennial ryegrass, whilst FDR of hemicellulose tended to be lower in deer fed chicory than those fed perennial ryegrass ($P = 0·11$).

Total rumen pool size and rumen liquid pool size tended to be lower ($P = 0·11$ and $P = 0·12$ respectively) for deer fed chicory than perennial ryegrass (Table 3). Dry matter percentage of rumen content was similar in deer fed either diet. Rumen liquid fractional outflow rates (FOR) were high for both diets. Rumen FOR of Cr-EDTA, lignin and ADF tended to be higher in deer fed chicory than perennial ryegrass but, due to the variability encountered, these approached significance at $P = 0·09$ and $P = 0·15$ for Cr-EDTA and lignin and attained significance at $P < 0·05$ for ADF. Nevertheless, effects on Cr-EDTA FOR were repeatable, with similar results being obtained when the calculation was based on Cr-concentration in total digesta (after ashing and digestion) or Cr concentration in the supernatant after high speed centrifugation (no ashing or digestion). The ratio Cr-EDTA FOR:lignin FOR was not different in deer fed either diet. Rumen mean retention time (MRT) tended to be lower for deer fed chicory than those fed perennial ryegrass, with the difference attaining significance for ADF ($P < 0·01$).

Total water intake was greater for deer consuming chicory than for those consuming perennial ryegrass ($P < 0·05$; Table 4), due to a much greater consumption of water in the forage ($P < 0·001$) as the amount of water drunk was lower in deer fed chicory than those fed perennial ryegrass ($P < 0·05$). Net rumen water balance (including salivary secretion) tended to be lower in deer fed chicory than perennial ryegrass, but with the variability encountered, the difference only approached significance at $P = 0·16$ when expressed per kg DM intake.

DISCUSSION

Fractional disappearance rate (FDPR) of DM from the rumen of deer fed chicory was significantly higher (14·5 *v.* 8·6%/h; $P < 0·05$) than those fed perennial ryegrass. This result agreed with the previous study of Kusmartono *et al.* (1996*b*) which reported a significantly higher FDPR value from the rumen of deer

Table 2. *Dry matter (DM) intake, apparent digestibility, rumen fractional disappearance rate and rumen fractional degradation rate of perennial ryegrass and chicory fed to red deer*

	Perennial ryegrass ($n = 8$)	Chicory ($n = 8$)	S.E. (D.F. = 6)
Intake			
kgDM/day	2·02	2·25	0·048
gDM/kg$W^{0·75}$/day	50·8	58·4	1·30
Apparent digestibility			
Dry matter	0·727	0·785	0·0140
Organic matter	0·744	0·820	0·0311
Neutral detergent fibre	0·755	0·679	0·0231
Acid detergent fibre	0·708	0·599	0·0349
Hemicellulose	0·783	0·667	0·0288
Cellulose	0·774	0·743	0·0331
Lignin	−0·001	0·235	0·1676
Fractional disappearance rate (%/h)			
Dry matter	8·6	14·5	1·29
Soluble carbohydrate	54·7	69·9	2·80
Pectin	40·4	58·0	10·44
Readily fermentable carbohydrate*	48·2	59·2	4·15
Neutral detergent fibre	8·3	10·2	0·97
Cellulose	9·8	15·5	1·52
Hemicellulose	7·8	7·3	0·81
Lignin	3·8	6·8	0·61
Fractional degradation rate (%/h)			
Neutral detergent fibre	5·7	6·7	0·72
Cellulose	7·0	11·4	1·11
Hemicellulose	5·0	3·2	0·67
Lignin	1·0	2·7	0·21

* Water-soluble carbohydrate + pectin.

Table 3. *Rumen pool size, rumen fractional outflow rate and rumen mean retention time for liquid and particulate matter in rumen red deer fed perennial ryegrass and chicory*

	Perennial ryegrass ($n = 8$)	Chicory ($n = 8$)	S.E. (D.F. = 6)
Rumen pool size (kg/kg DMI/day)			
Total*	5·32	3·89	0·530
Liquid	4·83	3·52	0·494
Dry matter (DM)	0·50	0·36	0·056
DM or rumen digesta (%)	9·28	9·49	0·884
Fractional outflow rate (%/h)			
Liquid			
Cr-EDTA (total digesta)	12·3	16·8	1·56
Cr-EDTA (liquid)	13·6	18·9	2·18
Particulate			
Lignin	2·78	4·08	0·551
Acid detergent fibre	2·02	4·30	0·506
Cr-EDTA/lignin	4·75	4·63	0·932
Mean retention time (h)			
Liquid			
Cr-EDTA	8·9	6·4	0·01
Particulate			
Lignin	49·0	37·7	9·61
Acid detergent fibre	52·5	27·9 4·66	

* DM + liquid.

Table 4. *Total water influx, rumen outflow and net water balance of deer fed perennial ryegrass and chicory*

	Perennial ryegrass ($n = 8$)	Chicory ($n = 8$)	S.E. (D.F. = 6)
Water intake (kg/day)			
Drink	4·9	3·3	0·43
Feed	7·2	14·4	0·25
Total	12·1	16·5	1·34
Rumen outflow*			
(kg/day)	28·1	30·5	2·74
(kg/kg DMI)	13·4	14·7	1·32
Net water balance			
(kg/day)†	16·4	12·8	2·92
(kg/kg DMI)†	7·9	5·3	1·24

* Liquid pool size × Cr-EDTA FOR.
† Rumen outflow − total water intake = salivary secretion + net water flux across the rumen wall.

fed chicory than perennial ryegrass (10·4 *v.* 5·3 %/h; $P < 0·01$). The difference in FDPR values between the two studies was probably due to the different measurement techniques used. Fractional disappearance rate values in the present study were obtained from a continuous infusion of marker (Faichney 1975) and continuous feeding, whilst in the study of Kusmartono *et al.* (1996*a*) FDPR values were obtained based on particle size reduction of rumen contents and twice daily feeding.

Whilst the initial plan was to offer deer identical amounts of both feeds, VFI recorded was slightly higher for chicory than for perennial ryegrass, due to some refusals for perennial ryegrass. This is unlikely to have influenced the results, as all data are expressed either in relation to the amount eaten or in relation to rumen pool size.

An objective of the present study was to determine factors responsible for higher FDPR of DM from the rumen of deer fed chicory compared to those fed perennial ryegrass. Results showed that the higher FDPR of DM in chicory than perennial ryegrass was due to both faster rumen FDR, notably of cellulose

Table 5. *Fractional outflow rate (FOR; %/h) of liquid and particulate matter in red deer, goats and sheep fed different diets during summer*

Author	Diet	Ash (g/kg DM)	Animal	FOR		
				Cr-EDTA	Lignin	Cr-EDTA/Lignin
Present study	Perennial ryegrass	112	Red deer	12·3	2·78	4·75
	Chicory	180	Red deer	16·8	4·08	4·63
Freudenberger *et al.* (1994*a*)	Perennial ryegrass/ White clover	108	Red deer	15·1	3·92	3·84
	Red clover	114	Red deer	13·3	2·52	5·51
Freudenberger *et al.* (1994*b*)	Lucerne hay	109	Red deer	12·4	2·78	4·50
Domingue *et al.* (1991)	Lucerne hay	94	Red deer	15·8	2·77	5·97
			Goats	10·8	3·66	3·07
			Sheep	10·4	3·32	3·24

and lignin, and also faster FOR of both liquid and particulate matter from the rumen. A major reason for greater FDPR on chicory must be higher the dietary concentration of readily fermentable carbohydrate (water-soluble carbohydrate + pectin) and its faster rate of disappearance from the rumen compared to deer fed perennial ryegrass.

Although water-soluble carbohydrate, pectin, cellulose and lignin were rapidly degraded in rumen of deer fed chicory, hemicellulose was degraded at a slightly lower rate relative to deer fed perennial ryegrass. This may be due to pH effects, as Church (1979) stated that degradation of hemicellulose was optimal at pH 6·0. Kusmartono, T. N. Barry & K. J. Stafford (unpublished) reported a lower mean rumen pH observed over a period of 24 h in deer grazing chicory (5·7) than those grazing perennial ryegrass (6·5) and the low pH may have restricted hemicellulose fermentation by rumen micro-organisms.

Effects on apparent digestibility of fibre can be explained through a knowledge of rumen FDR and FOR, given that 90% of the fibre that is digested in fresh forages is digested in the rumen (Ulyatt & MacRae 1974). In the case of cellulose, it seems that the faster rumen FDR on chicory is counteracted by lower particulate MRT in the rumen, allowing less time for microbial attack, resulting in the apparent digestibility of cellulose in deer fed chicory being similar to that of deer fed perennial ryegrass. However, in the case of hemicellulose, it seems that lower FDR and shorter MRT in the rumen combined to produce reduced apparent digestibility of hemicellulose in deer fed chicory relative to deer fed perennial ryegrass.

A higher proportion of lignin disappeared from the rumen faster in deer fed chicory than those fed perennial ryegrass (6·8 *v.* 3·8%/h; $P < 0·05$) and rumen lignin FDR was also greater for deer fed chicory (2·7 *v.* 1·0%/h; $P < 0·01$). This is probably related to the difference in lignin solubility between these two diets. Akin & Benner (1988) found that neither bacteria nor fungi could degrade lignin contained in a highly lignified cordgrass after being incubated for 7 days in rumen fluid at 39 °C. They argued that the loss of lignin from plant tissue was due to solubilization rather than direct fermentation (i.e. degradation). This argument is supported by data of Gaillard & Richards (1975) who found that the relatively high concentrations of dissolved (i.e. solubilized) lignins produced in the rumen are condensed and precipitated after passage from the rumen into the acidic conditions of the abomasum. As lignin is bonded to cellulose and hemicellulose within plant fibre (Van Soest 1994), greater rumen solubility of lignin in deer fed chicory may have made cellulose more accessible to rumen micro-organisms and contributed to the high cellulose FDR.

Rumen FOR of liquid and particulate matter were both measured using two techniques. The general agreement between the two methods for each forage further supports rumen FOR being faster for deer fed chicory than perennial ryegrass. Rumen FOR found in the present studies have been compared in Table 5 with other rumen FOR determined using similar techniques and at a similar time of the year. It can be seen that liquid leaves the rumen and flows into the intestines much faster than for particulate matter and that this ratio (i.e. FOR Cr-EDTA:FOR lignin) is consistently greater for red deer than for sheep or goats. Rumen frothy bloat is caused by a build-up of soluble protein in the rumen (Mangan 1959), and the high rumen liquid FOR of red deer probably explains why this species never gets bloated when grazing on rapidly digested forages such as red clover or chicory. Relative to perennial ryegrass, responses in rumen FOR seem to differ between red clover and chicory. Fractional outflow rate for red clover was lower than for perennial ryegrass, whereas with chicory FOR was higher. The higher ash content of chicory may be a contributing factor, with the deer increasing liquid FOR as a means of reducing a potential build up in

rumen osmotic pressure. This is supported by the greater total water intake of chicory-fed deer. Katoh *et al.* (1991) reported that deer have evolved a digestive system in which rate of digesta passage through the rumen is much faster than that for sheep and accommodated summer increases in VFI by stimulating rumen digestion through necessary changes in digestive characteristics.

Although not conclusive, the present studies have indicated that rumen net water balance (and hence salivary secretion) may be less in deer consuming chicory than those on perennial ryegrass. This seems feasible, as total time spent ruminating in deer fed chicory is only *c.* 10% of those fed perennial ryegrass (Kusmartono *et al.* 1996*b*), and salivary secretion rates are much greater during ruminating than during resting (Bailey 1961; Van Soest 1994). Salivary secretion rates in deer fed these forages need to be measured in the future studies. Lower salivary secretion rates in deer fed chicory could certainly explain the low rumen pH on this forage, due to a reduced buffering capacity.

It can be concluded that apparent digestibility of DM and OM was higher in chicory than in perennial ryegrass, but the reverse was found for hemicellulose apparent digestibility. More rapid FDPR of total DM from the rumen of deer fed chicory was due to higher FDR and faster liquid and particulate matter FOR and was related to the higher ratio of readily fermentable carbohydrate (RFC) to structural carbohydrate (SC) in chicory than in perennial ryegrass. This evidence may be used to explain the greater VFI and higher LWG of lactating and growing deer grazing chicory than perennial ryegrass/white clover pasture under field conditions (Kusmartono *et al.* 1996*a*).

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