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A study of voluntary intake and digestibility of roughages in relation to their degradation characteristics and retention time in the rumen

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Abstract

The voluntary intake, apparent digestibility, apparent mean rumen retention time of dry matter (DM), cell wall organic matter (CWOM) and the components of CWOM of wheaten straw (WS), oaten chaff (OC), lucerne hay (LH) and meadow hay (MH) were measured in rumen cannulated sheep using a 4×4 Latin square design. DM degradation characteristics (in sacco) of these roughages were also measured by incubating samples in nylon bags in the rumen of cannulated sheep, fed the same diets. Mean voluntary intake of organic matter (OMI) was more closely related to in sacco degradability at 24 h ($r^2=0.88$) and mean retention time of DM ($r^2=0.98$) than to in vivo digestibility ($r^2=0.70$). More than 90% of the variation in OMI could be accounted for by mean rumen retention time of CWOM, cellulose, hemicellulose and lignin. The intakes of WS and OC (378 and 515 g OM day^{-1}) were lower than those of LH and MH (1251 and 1288 g OM day^{-1}) because of their lower in sacco degradability and the slower rate of passage of indigestible fraction from the rumen.

Introduction

Straw and hay use in the production ration is limited by the ability of animals to achieve satisfactory intakes of digestible organic matter (DOM) when fed these materials. The causes of low intake of these roughages are poorly understood.

A high concentration of slowly fermented structural carbohydrates in straw and hay leads to a high degree of rumen fill (Van Soest, 1975), and probably contributes to restricting feed intake. Poppi et al. (1981) have indicated that intake is a balance of several forces, including rumen fill, which in turn are influenced by degradation rate in the rumen and outflow rate.

Thiago et al. (1979) reported that large differences in voluntary intake of forages had little effect on rumen dry matter (DM) pool size. Intake differ-

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ences were, however, related to differences in the rumen DM clearance rate by absorption and onward passage of undigested material. Similarly, Thornton and Minson (1972), using forage diets, found that the voluntary intake of dry matter (DMI) was inversely related to the retention time of the diet in the rumen. They concluded that the principle factor limiting DMI was the fibre component because of its positive relationship with retention time.

Hovell et al. (1986) reported that the DMI of hays were better related to potential degradability (POTDEG) and DM degradability (DMDEG) at 12, 24, 48 and 72 h than to in vivo digestibility. They concluded that degradation characteristics of forages may have useful application in predicting voluntary intake. Von Keyserlingk and Mathison (1989) showed that prediction of intake from neutral detergent fibre content and in sacco results were most accurate when 24 and 36 h dry matter degradability values were used. On the other hand, Ørskov et al. (1988) observed a poor relationship between intake and chemical composition of straw, but a more accurate prediction of feed intake from rumen degradation characteristics.

The objectives of this study were to determine feed characteristics and biological factors which are responsible for differences between feeds in the voluntary intake. This experiment examined voluntary intake, digestibility, apparent rumen retention time and degradation characteristics of four chaffed roughages — wheaten straw (WS) (*Triticum aestivum*), oaten chaff (OC) (*Avena sativa*), lucerne hay (LH) (*Medicago sativa*, second cut, pre-bloom) and meadow hay (MH) (primarily lucerne with couch (*Agropyron repens*) and barnyard grass (*Echinochloa* spp.).

Materials and methods

Roughages

Roughages were obtained from Leppington Farmers Co-operative, New South Wales, Australia. Table 1 shows the chemical composition of these roughages. Cell wall organic matter (CWOM) concentration ranged between 384.6 and 794.5 g kg^{-1} DM and large differences were found in CWOM, acid detergent fibre (ADF), cellulose (CELL), hemicellulose (HEMI) and lignin (LIG) contents of these roughages. The content of nitrogen (N), CELL, HEMI and LIG varied from 3.9 to 30.1 g kg^{-1} DM, 208.8 to 462.3 g kg^{-1} DM, 120 to 271.4 g kg^{-1} DM and 33.5 to 60.8 g kg^{-1} DM, respectively.

Determination of voluntary intake, digestibility and apparent mean rumen retention time

The voluntary intake, apparent digestibility and apparent mean rumen retention time of WS, OC, LH and MH were measured in 3 to 4 year-old

Table 1
Chemical composition, mean ±SE DM intake and digestibility coefficients of the experimental feed and mean ±SE metabolic body weight of sheep

Parameter	Wheaten straw	Oaten straw	Lucerne hay	Meadow hay
Feed composition (g kg^{-1} DM)				
OM	920.7	936.5	920.9	925.0
N	3.87	6.8	30.05	23.65
CWOM	794.5	622.7	384.6	495.2
ADF	523.1	369.9	264.6	327.8
CELL	462.3	336.4	208.8	276.0
HEMI	271.4	252.8	120.0	167.4
LIG	60.8	33.5	55.8	51.8
DM intake (g day^{-1})	411^{a} ± 131.1	550^{a} ± 65.3	1363^{b} ± 284.6	1392^{b} ± 160.6
Metabolic body weight (kg$^{0.75}$)	16.31 ± 0.06	15.21 ± 0.44	17.05 ± 0.66	18.22 ± 0.32
Digestibility coefficient (in vivo)				
DM	31.2^{A} ± 3.2	51.9^{B} ± 2.4	67.7^{C} ± 1.3	62.9^{C} ± 0.8
OM	33.2^{A} ± 3.7	53.4^{B} ± 2.5	69.2^{C} ± 1.0	63.6^{C} ± 0.8
CWOM	30.3^{a} ± 3.9	46.5^{b} ± 4.2	52.6^{b,c} ± 1.4	50.7^{b,c} ± 1.8

OM, organic matter; N, nitrogen; CWOM, cell wall OM; ADF, acid detergent fibre; CELL, cellulose; HEMI, hemicellulose; LIG, lignin.
Organic matter intake (OMI) = DM intake × OM/1000.
Digestible OMI (DOMI) = OMI × OM digestibility coefficient/100.
Superscript A, B and C on the same row denote significant differences ($P < 0.001$).
Superscript a, b and c on the same row denote significant differences ($P < 0.05$).

Merino wether sheep (mean ± SE live weight of 45.8 ± 0.8 kg) with rumen cannulae (70 mm) using a 4 × 4 Latin square design.

The animals were held in individual metabolism crates and fed ad libitum for 24 h with the use of automatic continuous feeders over a 15 day period. The amount of feed offered each day was adjusted to 1.2 times the voluntary intake of the previous day. DMI and faecal dry matter output were recorded using a 5 day measurement during each period. Samples of roughages offered, refusals and faeces were taken daily and bulked over the period.

At the end of the collection, the entire digesta from the reticulo-rumen of each sheep was removed through the fistula, weighed and a subsample taken. Faecal and rumen digesta subsamples were dried at 60°C for 72 h, ground through a 1 mm screen and analysed for ash, CWOM, CELL, HEMI and LIG contents (Faichney and White, 1983). Apparent mean rumen retention time of DM (MRTDM), CWOM (MRTCWOM), CELL (MRTCELL), HEMI (MRTHEMI) and LIG (MRTLIG) were calculated by dividing the weight of each fraction in the rumen by the mean hourly consumption of each fraction during the previous 48 h (Minson, 1966). The rate of passage of the

indigestible fraction from the rumen was a reciprocal of retention time of lignin in the rumen.

The apparent in vivo digestion coefficients for the roughages and their chemical components were obtained by calculating the difference between feed consumed and faecal output.

In sacco degradability

Feed samples were air dried and ground through a Christie and Norris hammermill (Checley Everitt & Associates, Vic., Australia) fitted with a 2.25 mm screen. Air-dried samples (2 g) were placed in each dacron bag (80 mm × 120 mm, 36 to 38 μm pores) manufactured from Nittral single thread woven with welded crossheads (Allied Screen Fabric, Hornsby, N.S.W.). One bag containing test roughages per time was incubated in the rumen of each of four cannulated sheep given the same basal diet as that of the test diet. Incubation times for LH and MH were 3, 6, 9, 15, 24, 32, 48 and 72 h, while for WS and OC the times were 4, 8, 24, 48, 72 and 96 h. The shorter incubation time of LH and MH was possible because no further degradation occurred after 48 h. The bags were introduced into the rumen in reverse sequence. Immediately after removal from the rumen, bags were immersed in a bucket of cold water, washed vigorously by hand under running tap water until water leaving the bags became clear. The bags were dried at 60°C for 48 h in a forced-draught oven. Disappearance of DM was measured as the loss of the bag contents.

The percentage disappearance (P) of dry matter followed the simple exponential relationship with time t, described by Orskov and McDonald (1979). DM degradation characteristics were derived from this relationship:

$$P = a\mathrm{DM} + b\mathrm{DM}(1 - \exp(-c\mathrm{DM}\, t))$$

The constant aDM represents the immediately soluble component and bDM represents the slowly but potentially degradable component which disappears at a constant fractional rate cDM per unit time. The POTDEG fraction was determined as the sum of aDM + bDM. The rate of DM degradation was calculated by regressing potentially digestible DM remaining in bags (expressed as natural logarithm) against time of fermentation.

Chemical analysis

Total nitrogen was determined by a Kjeldahl procedure (Association of Official Agricultural Chemists, 1980) using a Kjeltec Auto 1030 (Tecator AB, Sweden). OM was determined after ignition in a muffle furnace for 3 h at 600°C. CWOM and ADF were estimated by reflux according to Faichney and White (1983). HEMI was estimated as the difference between CWOM and

ADF, while CELL was estimated as the difference in mass between ADF and residue after digestion in 72% sulphuric acid. LIG was determined as the DM disappearance from the latter after ashing at 600°C for 3 h.

Statistical analysis

Analysis of variance was performed for a 4×4 Latin square design. Difference between means were tested with the least significant difference method. The relationship between different characteristics of roughages were obtained by simple linear and multiple regression analysis using Minitab (Ryan et al., 1985). All r^2 values are presented as the adjusted values from Minitab.

Results

Voluntary feed intake and in vivo digestibilities

The mean voluntary intake of DM (DMI), OM (OMI) and DOM (DOMI) for LH and MH were higher ($P<0.05$, $P<0.05$, $P<0.001$) than those for WS and OC (Table 1). These effects were significant both when intake was expressed on total intake and on metabolic live weight.

No significant differences in intake were observed between LH and MH or between WS and OC. Voluntary intakes of DM, OM and DOM ranged from 411 to 1392 g day^{-1} per sheep, 378 to 1288 g day^{-1} per sheep and 126 to 869 g day^{-1} per sheep, respectively. The digestibilities of DM (DMD) and OM (OMD) of LH and MH were significantly higher ($P<0.001$) than those of the WS and OC diets. In vivo DMD and OMD for the WS diet were significantly lower ($P<0.001$) than those of the OC diet. LH and MH did not differ in DMD or OMD. The digestibility of CWOM of WS was significantly lower ($P<0.05$) than those of OC, LH and MH diets.

Rumen digesta kinetics

The data on rumen pool and rumen retention time of DM, CWOM, CELL, HEMI and LIG are shown in Table 2.

Diets did not affect rumen pool size of DM, CWOM, CELL or HEMI. The rumen LIG pool of sheep fed WS or OC was smaller ($P<0.001$) than that of sheep fed LH or MH. The MRTDM of LH and MH was less ($P<0.001$) than those of WS and OC. The retention times of CWOM, CELL and HEMI of LH and MH in the rumen were also less ($P<0.05$) than those of WS and OC. A similar trend was observed in the retention time of lignin. From a knowledge of the rate of passage of indigestible fraction from the rumen, this study observed a significantly ($P<0.05$) faster rate of passage of the indigestible fraction of LH and MH from the rumen than that of WS or OC.

Table 2
Rumen digesta, rumen pool weights, rumen retention times of dry matter, cell wall organic matter and its components in the rumen of sheep offered experimental feeds (mean ±SE of four sheep)

	Wheaten straw	Oaten chaff	Lucerne hay	Meadow hay
Rumen digesta (g)	$4507^{a} \pm 773$	$4652^{a} \pm 862$	$4776^{a} \pm 237$	$5833^{a} \pm 168$
Rumen pool (g) for				
DM	$354^{a} \pm 90$	$515^{a} \pm 111$	$440^{a} \pm 41$	$555^{a} \pm 35$
CWOM	$264^{a} \pm 67$	$264^{a} \pm 85$	$285^{a} \pm 30$	$364^{a} \pm 30$
CELL	$145^{a} \pm 35$	$155^{a} \pm 24$	$183^{a} \pm 19$	$227^{a} \pm 14$
HEMI	$94^{a} \pm 25$	$120^{a} \pm 24$	$92^{a} \pm 12$	$123^{a} \pm 7$
LIG	$23^{a} \pm 4$	$16^{a} \pm 2$	$52^{b} \pm 9$	$56^{b} \pm 7$
Rumen retention time (h)				
DM	$26.0^{A} \pm 2.5$	$22.2^{A} \pm 1.7$	$7.3^{B} \pm 0.7$	$8.8^{B} \pm 0.4$
CWOM	$24.0^{a} \pm 2.2$	$18.9^{a} \pm 1.8$	$11.7^{b} \pm 1.3$	$11.6^{b} \pm 0.7$
CELL	$25.9^{a} \pm 1.7$	$16.9^{b} \pm 1.2$	$7.4^{c} \pm 0.7$	$8.8^{c} \pm 0.4$
HEMI	$25.2^{a} \pm 1.7$	$20.4^{a} \pm 2.6$	$12.0^{b} \pm 1.4$	$11.6^{b} \pm 1.1$
LIG	$29.0^{a} \pm 6.4$	$27.2^{a} \pm 8.4$	$15.0^{b} \pm 3.0$	$17.8^{b} \pm 2.7$

Superscript A, B and C on the same row denote significant differences ($P<0.001$).
Superscript a, b and c on the same row denote significant differences ($P<0.05$).
DM, dry matter; CWOM, cell wall organic matter; CELL, cellulose; HEMI, hemicellulose; LIG, lignin.

Nylon bag degradation

DMDEG of roughages from nylon bags incubated in the rumen of sheep, DM losses from nylon bags washed in water and constants of the fitted exponential equation are shown in Table 3.

The water-soluble component, small particles and total washing loss of DM from feeds placed in nylon bags then washed with water ranged from 6.9 to 24.6%, 0.6 to 1.3% and 8.2 to 25.2%, respectively. The soluble fraction (*a*DM) of the fitted exponential ranged from 0 to 33.6% of DM and was found to differ from the total washing loss in nylon bags from 0 h bags. A slowly but potentially degradable fraction, *b*DM ranged from 30.5 (OC) to 43.4% (LH).

The mean coefficient of determination (r^2) for a single exponential fitted to the degradation curve ranged from 0.87 (WS) to 0.96 (LH). The rate of degradation of *b*DM, *c*DM ranged from 0.043 to 0.141 (h^{-1}). The DMDEG after 24, 48 h and POTDEG of the experimental roughages ranged from 15.7 to 74.2%, 31.0 to 75.6% and 36.2 to 75.5%, respectively. The major loss of DM occurred in the first 24 h in the case of LH and MH as compared with WS and OC.

Table 3
Dry matter losses (%) of hay from nylon bags washed in water or incubated in the rumen given the same basal diet as test diet

Washing loss	Wheaten straw	Oaten chaff	Lucerne hay	Meadow hay
Water soluble	6.9	20.7	24.6	21.0
Small particles	1.3	0.9	0.6	0.7
Total	8.2	21.6	25.2	21.7
Dry matter degradability in the rumen				
24 h DMDEG	15.7±0.2	36.5±2.1	74.2±0.9	64.0±2.3
48 h DMDEG	31.0±1.2	50.1±2.4	75.6±1.0	68.2±2.7
Constants from fitted exponential				
*a*DM	0.00±nil	23.5±4.7	32.1±2.4	33.6±4.0
*b*DM	36.2±1.5	30.5±6.5	43.4±3.3	34.7±4.6
*c*DM	0.043±0.001	0.045±0.003	0.14±0.002	0.09±0.01
*a*DM+*b*DM	36.2±1.5	51.0±2.0	75.5±1.0	68.3±2.7

24 h DMDEG, dry matter disappearance in situ after 24 h; 48 h DMDEG, dry matter disappearance in situ after 48 h; *a*DM, soluble component (g per 100 g DM); *b*DM, slowly but potentially degradable component (g per 100 g DM); *c*DM, rate of degradation of *b*DM (h^{-1}).

Discussion

Prediction of feed intake by ruminants has been based on relationships between intake and either the degradation characteristics of DM in the rumen (Hovell et al., 1986; Ørskov et al., 1988; Von Keyserlingk and Mathison, 1989) or the chemical characteristics of the feed (Thornton and Minson, 1972). The study by Thornton and Minson (1972) concluded that the fibre component of the diet was the principal limit to intake of tropical grasses. Our study sought to refine this relationship by relating intake to the content of specific fibre components in roughage diets as well as degradation kinetics in the rumen.

Relationship between feed composition and OMI

Of the feed characteristics, the hemicellulose component of cell wall was the most closely correlated to OMI of the diet ($r^2=0.86$, $P<0.05$) (Table 4). LIG content, in contrast to the findings of Thornton and Minson (1972) was not related to OMI ($r^2=0.00$, $P>0.05$). This may have resulted from our study using four genetically diverse roughages, while the relationship of Thornton and Minson (1972) was derived from a limited range of *Panicum* spp. It appears that lignin composition, as well as its cross-linking of carbo-

Table 4
Correlation (r^2), and level of significance (P) of organic matter intake and rumen retention time of dry matter with different parameters

Parameter	Organic matter intake		Rumen retention time of dry matter	
	r^2	P	r^2	P
CWOM	0.75	0.87	0.85	0.051
CELL	0.66	0.119	0.78	0.078
HEMI	0.86	0.046	0.93	0.023
LIG	0.00	0.794	0.00	0.828
CWOM+N	0.84	0.235	0.93	0.151
24 h DMDEG	0.88	0.040	0.95	0.017
48 h DMDEG	0.83	0.058	0.91	0.032
*a*DM	0.59	0.147	0.65	0.128
*b*DM	0.00	0.463	0.00	0.425
*c*DM	0.65	0.123	0.75	0.087
(*a*DM+*b*DM)	0.80	0.070	0.87	0.042
(*a*DM+*b*DM)+*c*DM	0.64	0.341	0.82	0.248
OMD	0.70	0.107	0.78	0.077

CWOM, cell wall organic matter; CELL, cellulose; HEMI, hemicellulose; LIG, lignin; N, nitrogen; OMD, in vivo organic matter digestibility; 24 h DMDEG, dry matter disappearance in situ after 24 h; 48 h DMDEG, dry matter disappearance in situ after 48 h; *a*DM, soluble component (g per 100 g DM); *b*DM, slowly but potentially degradable component (g per 100 g DM); *c*DM, rate of degradation of *b*DM (h^{-1}).

hydrates, varies between plant type (Theander, 1989). Consequently, lignin content may not be significantly correlated with OMI across forage species.

The relationship between CWOM and OMI was not significant ($r^2=0.75$) and inclusion of nitrogen content did little to improve this ($r^2=0.84$) (Table 4). The variation accounted for by N is not surprising, considering that no N supplements were offered and availability of N for microbial growth commonly limits intake of low quality straw (Weston, 1967).

Relationship between degradation characteristics and OMI

Studies of feed degradation characteristics (*a*DM, *b*DM and *c*DM) in situ were undertaken to include the influence that animal and feeding environment factors have on intake. Mertens (1987) suggests that this approach may allow greater accuracy in predicting OMI. Ørskov et al. (1988) accounted for 90% of the variation in OMI by relating it to (*a*DM+*b*DM)+*c*DM. Carro et al. (1991) also observed that voluntary DMI of hays was significantly correlated with the soluble fraction in DM (*a*DM), and the rate of degradation of DM (*c*DM). In contrast, the OMI in our study was not significantly correlated to *a*DM, *b*DM or *c*DM when considered individually (Table 4). Inclu-

sion of cDM with (aDM+bDM) did not account for significantly more variation in OMI. Interpretation of the studies of Carro et al. (1991) is confounded because the sheep were maintained on a good quality hay rather than the test feed during in sacco studies. This is known to confound in sacco digestion kinetic estimates (Silva and Ørskov, 1988).

While OMI was poorly correlated to DM degradation characteristics, it was strongly related to DM disappearance in sacco after 24 h ($r^2=0.88$, $P<0.05$) (Table 4). This strong relationship between OMI and 24 h and 36 h in sacco digestibilities has also been found by Von Keyserlingk and Mathison (1989).

Relationship of rumen retention time of feed with OMI, in situ degradability to in vivo digestibility

A strong relationship existed between OMI and MRTDM ($r^2=0.98$, $P<0.01$). Thornton and Minson (1973) have previously implicated retention time of OM as an important limit to roughage intake. Because cell wall components constitute the majority of OM in roughages, the relationship between intake and retention of cell wall and cell wall components was assessed (Table 5). It was found that 96%, 91%, 97% and 97% of the variation in OMI could be accounted for by the MRTCWOM, MRTCELL, MRTHEMI and MRTLIG, respectively. The retention time of CWOM was strongly correlated ($r^2=0.87$, $P<0.01$) with the time that the indigestible portion of the diet was retained in the rumen as measured by the retention time of lignin. This strong relationship revealed that the retention of CWOM is influenced by the retention of lignin in the rumen.

MRTDM itself was negatively related to 24 h and 48 h degradability measured in sacco and positively associated with cell wall content of the roughage (Table 4). These findings indicate that it is the fibre component of these roughages, affecting degradability in the rumen, which may regulate the removal of OM from the rumen.

The observation that the retention of DM in the rumen was not related to

Table 5
Correlation (r^2) and level of significance (P) of organic matter intake with mean rumen retention time (MRT)

MRT	r^2	P
DM	0.98	0.006
CWOM	0.92	0.028
CELL	0.83	0.058
HEMI	0.95	0.016
LIG	0.94	0.019

DM, dry matter; CWOM, cell wall organic matter; CELL, cellulose; HEMI, hemicellulose; LIG, lignin.

lignin content of the feed ($r^2=0.00$) (Table 4) suggests it was not LIG but other feed or rumen factors, such as rumen ammonia level, limiting DM digestion.

In vivo digestibility of feed is frequently correlated with OMI (Hodgson, 1977; Freer, 1981) and MRTOM (Thornton and Minson, 1973; Hovell et al., 1986) but in our study OMD was not significantly related to OMI ($r^2=0.70$) or MRTDM ($r^2=0.78$) (Table 4). This was probably because WS and OC did not provide sufficient nitrogen to optimise rumen fermentation and a shift to hind-gut fibre fermentation may have occurred. This shift has been frequently observed in response to insufficient sulphur (Bird, 1972; Rees et al., 1974) and it seems reasonable that a similar response may have occurred on the low nitrogen OC and WS diets. Such a shift would have dissociated whole tract OMD from rumen retention time which limits intake. Consequently, while the relationships between rumen parameters and OMI discussed are meaningful, it was considered inappropriate to correlate further rumen parameters to whole tract OMD or to DOMI.

Conclusions

The voluntary intake of chopped forages by sheep was limited by the sheep's capacity to clear DM present in the rumen. OMI was not related to readily fermentable (soluble component) material but to retention time in the rumen of the cell wall and its components, cellulose, hemicellulose and lignin. The organic matter intakes of WS and OC were lower than those of LH and MH because of their lower in sacco degradability and the slower rate of passage of the indigestible fraction from the rumen.

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