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Dynamic of voluntary intake, feeding behaviour and rumen function in sheep fed three contrasting types of hay

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Summary — The purpose of this experiment was to analyse the dynamic relationships linking intake, feeding behaviour, and rumen content in sheep fed three types of hay representing contrasting nutritional situations. Six fistulated sheep received, ad libitum in a replicated 3 × 3 Latin square design, a late-cut mixed grass hay, an early-cut cocksfoot hay and an early-cut lucerne hay. Neutral detergent fibre content decreased from 684 to 637 and to 447 g/kg dry matter (DM), and in situ DM rate of degradation increased from 0.017 to 0.040 and to 0.092 h^{-1} for mixed grass, cocksfoot and lucerne respectively. Voluntary DM intake was 1000, 1484 and 1608 g ($P < 0.01$) for mixed grass, cocksfoot and lucerne respectively. Differences in voluntary intake among hays were mostly related to differences in the size of the principal meals and in intake rate, especially initial intake rate at the beginning of the meal. Cocksfoot was associated with a higher number of small meals. Early-cut hays needed less mastication time per g consumed than the late-cut hay. Rumen content before the meal was lower for the early-cut hays ($P < 0.05$). After the principal meal wet weight of rumen content was similar for the two grass hays but remained lower for lucerne. Faster clearance rate of rumen DM with early-cut hays ($P < 0.01$) after the principal meal was due to the higher disappearance rate of the degradable fraction. Intake of low quality forages seems to be primarily limited by a high content of undegradable and slowly degradable material in the rumen. Studying the dynamic of intake and rumen function is promising for development of mechanistic models to predict intake.

intake / feeding behaviour / rumen / hay / sheep

Résumé — Dynamique des quantités ingérées, du comportement alimentaire et du fonctionnement ruminal chez le mouton alimenté avec trois types de foin contrastés. L'objectif du travail était d'étudier la dynamique de l'ingestion, du comportement alimentaire, de l'encombrement du rumen et de la digestion chez des animaux alimentés avec des foins représentant des situations nutritionnelles contrastées. Six moutons fistulés (61 ± 3 kg) ont reçu, ad libitum selon un schéma en carré latin 3 × 3 répété, un foin de graminées récolté au premier cycle à un stade tardif, un foin de dactyle et un foin de luzerne tous deux récoltés au deuxième cycle à un stade précoce. La teneur en parois végétales a diminué de 684 à 637 et à 447 g/kg de matière sèche (MS) et le taux de dégradation ruminale de la MS mesuré in situ a augmenté de 0,017 à 0,040 et à 0,092 h^{-1} du foin de grami-

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nées au dactyle et à la luzerne. La quantité ingérée de MS a été de 1 000, 1 484 et 1 608 g ($p < 0,01$) pour le foin de graminées, de dactyle et de luzerne respectivement. Les différences de quantités ingérées s'expliquent principalement par la taille des repas principaux et par la vitesse d'ingestion, notamment la vitesse initiale en début de repas qui augmente de 6,96 à 8,84 et à 11,33 g de MS/min ($p < 0,05$) du foin de graminées au foin de dactyle et au foin de luzerne. De plus, le foin de dactyle se caractérise par une ingestion accrue lors des repas intermédiaires. Le temps de mastication par gramme de MS ingéré est nettement plus faible pour les deux foins récoltés à un stade précoce. Avant le repas principal, l'encombrement du rumen est plus faible pour les foins précoces (7,57 et 6,46 kg de contenu ruminal pour le dactyle et la luzerne respectivement et 8,41 kg pour le foin tardif de graminées, $p < 0,05$). Après le repas principal, l'encombrement du rumen est comparable pour le foin de graminées et le foin de dactyle (environ 10 kg), mais demeure plus faible pour le foin de luzerne. À partir de la détermination des fractions dégradables et indégradables du contenu ruminal, il apparaît que, après le repas, la vitesse de disparition de la fraction indégradable ne varie pas significativement entre les trois foins (environ 30 g de MS/h). La disparition plus rapide de la MS du contenu ruminal avec les deux foins récoltés à un stade précoce (66,4 et 65,3 g/h pour le dactyle et la luzerne respectivement et 44,9 g/h pour le foin tardif de graminées, $p < 0,01$) est due principalement à la disparition plus rapide de la fraction dégradable. Ces résultats vont dans le sens d'une limitation de l'ingestion de fourrages de faible valeur alimentaire par l'importance de la fraction indégradable et par la faible vitesse de dégradation de la fraction dégradable du contenu ruminal. Ils ouvrent des perspectives de modélisation dynamique de l'ingestion et de prévision de l'effet d'encombrement des fourrages.

ingestion / comportement alimentaire / rumen / foin / mouton

INTRODUCTION

Feed intake of forages has been assumed to be primarily limited by rumen fill (see review by Balch and Campling, 1962). More recently, the role of rumen distension in setting satiety has been confirmed (Anil et al, 1993) and the role of mechanical stimulation of the rumen wall has been suggested (Baumont et al, 1990a). Rate of degradation, rate of particle breakdown and rate of passage of food residues are the determinants of the level of rumen content. The concept of physical limitation has been used in several intake prediction systems (Mertens, 1994; Faverdin et al, 1995). Thus chemical (cell-wall content), biological (in situ degradation parameters) or physical (index of fibrousness) criteria have been used, singly or jointly, to predict voluntary intake of forages (see review by Dulphy and Demarquilly, 1994).

However, ruminants often do not use their maximum ruminal capacity continuously over the day when grazing (Thomson et al, 1985). In addition, forage palatability or appetite for the forage can be as important as rumen fill in the control of intake (Greenhalgh and Reid, 1971). Initial eating rate at the beginning of the meal seems a good criterion to evaluate the sensory response evoked by a feed (Baumont et al, 1990b) and the motivation of the animal to eat it (Faverdin et al, 1995). Ruminants are able to learn to prefer feeds of high nutritive value (Burrit and Provenza, 1992). Hence palatability and digestibility are related (Provenza, 1995).

The purpose of this experiment was to analyse the dynamic relationships linking intake, feeding behaviour, rumen fill and rumen function in sheep fed three types of hay representing contrasting nutritional situations. A late-cut mixed grass hay provided high amounts of fibre, low digestibility and slowly ruminal degradation. Early-cut regrowths of grass or lucerne hays provided higher digestibility, faster ruminal degradation with high or low amount of fibre respectively. Kinetics of intake, feeding and ruminating patterns, the use of ruminal capacity and digesta kinetics were investigated in sheep fed each of these three types of hays ad libitum.

MATERIALS AND METHODS

Animals, feeds and experimental design

Six 3-year-old Texel wethers (61 ± 3 kg) were each fitted with a polyamide cannula (id 75 mm) in the dorsal region of the rumen. During the experimental periods, the animals were housed in metabolism crates under continuous artificial light and allowed free access to water and salt block. The three hays used were a mixed grass cut at the end of the first cycle of vegetation, a cocksfoot (*Dactylis glomerata*) and a lucerne (*Medicago sativa*), both cut early in the second cycle of vegetation.

The animals were randomly assigned to the three hays in a replicated 3 × 3 Latin square design. Each of the three experimental periods lasted 5 weeks and consisted of a 2-week adaptation period followed by 1 week for measuring feeding behaviour and rumen fluid dynamics, and 2 weeks for measuring rumen content. The animals were fed ad libitum (10% refusals) and daily feed intake and water consumption were recorded throughout the experiment. Every day, at 09:00 h and at 21:00 h the animals were offered half of the daily amount of hay.

The kinetics of intake and feeding behaviour were recorded during the 3rd week of each experimental period for five consecutive days. On days 4 and 5 rumen fluid was sampled to measure rumen fluid fractional turnover rate. During the 4th and 5th weeks of each experimental period, rumen content was measured before (09:00 h and 21:00 h) and after (11:00 h and 23:00 h) the principal meals following the hay distributions.

Kinetics of intake and feeding behaviour

The daily pattern of intake was monitored by feed dispensers placed on sensors fitted with strain gauges. Weight variations of the feed dispensers were recorded by a microcomputer after digitalisation of the signal (Baumont et al, 1990b). Kinetics of DM intake during the principal meals (first meal after hay distribution) were determined by fitting the model $FI_{(t)} = a(1 - e^{-bt})$ to the data, where FI is the feed intake (g DM); t is the time after feeding (min); a is the asymptotic intake (g DM); and b is the rate constant of decrease (/h). Initial and final intake rates were calculated as the values of the first derivative of $FI_{(t)}$ at $t = 0$ (ab) and $t = T$ (abe^{-bT}), where T is the end of the principal meal. Jaw movements were recorded simultaneously using a polyurethane-foam-filled balloon placed under the jaw and connected to a microcomputer via a pressure transducer. Eating and ruminating activities were analysed as described by Brun et al (1984). Feed intake, eating time and rumination time data were summarised hourly for pattern analysis.

Rumen content and digesta kinetics

Total reticulo-rumen contents were determined by manually emptying the rumen. Rumen evacuations were carried out with an interval of at least 72 h to ensure normal digestion (Aitchison et al, 1986). The six animals were emptied simultaneously. After emptying, the rumen contents were weighed, homogenised and sampled for DM determination. Dried and ground (0.8 mm) samples of rumen digesta were preserved for further fibre fractions analyses and in vitro measurements of digestible fractions. Between rumen emptying after the principal meal and rumen emptying before hay was offered, the disappearance rate of digesta (g/h) expressed in DM, or in any of the different fractions measured, was calculated by the formula: disappearance rate = (initial content + amount ingested – final content) / duration. Daily fractional turnover rate (h^{-1}) of a given digesta fraction was calculated by dividing its daily intake by the mean rumen content of the fraction (Huhtanen and Kukkonen, 1995).

A 200 mL dose of a Cr-EDTA solution (Binnerts et al, 1968) was injected into the rumen 2 h before the morning hay distribution. Fifteen samples of rumen fluid (50 mL) were taken from 09:00 h over 36 h and stored at –20°C until analysed for Cr concentration. The rumen volume at time of injection and fractional turnover rate of rumen fluid were calculated by adjustment of the Cr-dilution curve (Warner and Stacy, 1968).

In situ hay degradability and in vitro measurements

In three different fistulated sheep fed a good quality lucerne hay, the degradability of the experimental hays was studied in situ using the nylon bag technique (Demarquilly and Chenost, 1969). After incubation times in the rumen of 2, 4, 8, 16, 24, 48 and 72 h the bags (two per incubation time and per sheep) were washed in cold water and placed in a pepsin solution for 48 h. The dry matter (DM) degradability data were fitted to the model proposed by Ørskov and Mc Donald (1979).

Whole digestive tract organic matter digestibility of the three hays was estimated by the method of Aufrère and Demarquilly (1989) using a cellulolytic enzyme. Ruminal digestible fractions of rumen digesta and of the hays were estimated after 48 h incubation of the samples in rumen juice kept at 39°C according to Tilley and Terry (1963). The residues were dried and kept for neutral detergent fibre (NDF) analysis.

Chemical analysis

DM contents of feed, digesta, in situ and in vitro residues were determined by drying samples at 80°C for 48 h. Ash content was measured by combustion of samples at 550°C for 6 h and total N was determined by the Kjeldahl method. Analyses of NDF, acid detergent fibre (ADF) and acid detergent lignin (ADL) were carried out on dried samples according to the method of Goering and Van Soest (1970).

Statistical analysis

Intake, feeding behaviour and rumen function data (n = 18) underwent analysis of variance, using the general linear model procedure of Statistical Analysis System (1987). In the model, effects of hay (2 df), animal (5 df) and period (2 df) were tested with 8 df in the error term. When the effect of the type of hay was significant ($P < 0.05$) differences between treatments were compared by Duncan's multiple range test. Analysis of feed intake, eating time and rumination time patterns (n = 18) was performed with the repeated measurements analysis of variance procedure with the same effects as previously described and using hour (24 levels) as the repeated measure factor. The effect of time of day (hour) and the interactions between time of day and the treatments were tested using the F-test adjusted by the Huynh-Feldt epsilon to allow for any unequal correlation between repeated measurements (Statistical Analysis System, 1987). When interaction between time of day and type of hay was significant, analyses of variance of contrast variables representing the differences between hours and the mean of all other hours were performed.

RESULTS

Hay composition and digestive characteristics

Protein contents of the cocksfoot and the lucerne hay were similar and both the organic matter digestibility and the ADF content of the two hays were close (table I). NDF content of the cocksfoot hay was slightly lower than that of the mixed grass hay, but was still much higher than NDF content of the lucerne hay. The lower digestibility of the mixed grass hay was related to its higher NDF and ADF content and lower crude protein content. The variations between hays in in vitro dry matter digestibility were consistent with those of organic matter digestibility estimated with the pepsin-cellulase method. In vitro NDF digestibility was close to DM digestibility for the grass hays, but markedly lower for lucerne. The two grass hays differed by their morphology. The mixed grass had a high proportion of stems and the cocksfoot a high proportion of leaves. The results of in situ degradability agreed closely with fibre fractions. The rapidly degradable fraction was negatively related to the NDF content and so positively related to the soluble content. The slowly degradable fraction was positively related to the NDF content and represented proportionally 0.74, 0.76 and 0.69 of the NDF content for mixed grass, cocksfoot and lucerne hay, respectively. Fractional rate of

Table I. Chemical composition (g/kg dry matter (DM)) and digestive characteristics of the three hays fed to sheep.

	Mixed grass	*Cocksfoot*	*Lucerne*
DM (g/kg fresh weight)	884	878	855
Organic matter (OM)	918	896	878
Crude protein (N × 6.25)	85	196	198
Neutral detergent fibre (NDF)	684	637	447
Acid detergent fibre	396	298	312
Acid detergent lignin	56.9	33.3	71.9
OM digestibility[a] (g/g)	0.541	0.658	0.638
In vitro digestibility[b] (g/g)			
DM	0.608	0.728	0.676
NDF	0.588	0.756	0.457
In situ degradable fractions[c]			
a (rapidly degradable)	312	404	506
b (slowly degradable)	503	482	306
Fractional rate of degradation (h^{-1})[c]	0.017	0.040	0.092

[a] Estimated from in vitro pepsin-cellulase digestibility according to Aufrère and Demarquilly (1989).
[b] From 48 h incubation in rumen fluid according to Tilley and Terry (1963).
[c] From fitting data to the model proposed by Ørskov and Mc Donald (1979).

degradation was lowest for mixed grass, consistent with its low digestibility. The fractional rate of degradation of lucerne hay was higher than that of cocksfoot hay.

Intake and feeding behaviour

Actual refusal levels were 13.2, 9.2 and 8.6% of the dry matter fed to the animals for mixed-grass, cocksfoot and lucerne respectively. Daily DM intake was significantly higher for the two early-cut hays than for the late-cut one, the highest value being observed for lucerne (table II). Compared to mixed grass, daily NDF intake was increased for cocksfoot but not for lucerne hay as a consequence of its low cell-wall content. Water intake was closely related to DM intake. The type of hay did not significantly affect the time spent eating each day, which averaged 275 min. Thus the increase in intake of the early-cut hays was a result of a higher intake rate.

No significant differences between morning and evening were found in the characteristics of the principal meals following distribution. Consequently, mean values of the morning and the evening meals were analysed for treatment effect. For the principal meals intake was increased with the two early-cut hays compared to late-cut mixed grass (+ 99 g DM, $P = 0.06$; + 254 g DM, $P < 0.01$ for cocksfoot and lucerne respectively). Differences in intake among the three hays for the principal meals were mainly attributed to differences in intake rates at the beginning of the meal, since final intake rates were not significantly affected by the type of hay. The principal meals

Table II. Effect of type of hay offered to sheep on dry matter (DM) intake, neutral detergent fibre (NDF) intake, water consumption and feeding behaviour.

	Mixed grass	*Cocksfoot*	*Lucerne*	*SE*
Daily DM intake (g)	1000 [a]	1484 [b]	1608 [b]	61
Intake rate (g/min)	4.10 [a]	5.57 [b]	5.76 [b]	0.39
Daily NDF intake (g)	684 [a]	945 [b]	719 [a]	34
Water intake (L)	3.37 [a]	5.83 [b]	6.37 [b]	0.13
Principal meals [d]				
DM intake (g)	445 [a]	544 [a]	699 [b]	31
Duration (min)	106 [ab]	92 [a]	116 [b]	5.1
Initial intake rate (g/min)	6.96 [a]	8.84 [ab]	11.33 [b]	0.82
Rate constant of decrease (/min)	0.0090 [a]	0.0105 [ab]	0.0122 [b]	0.0008
Final intake rate (g/min)	2.75	3.11	2.40	0.33
Small meals				
Number	2.0	5.0	3.1	0.9
DM intake (g)	110 [a]	396 [b]	211 [ab]	68
Rumination				
Number of periods	17.2	16.5	15.3	0.7
Daily duration (min)	499	430	450	20
Mastication				
Daily duration (min)	760	700	743	23
Min/g DM intake	0.79 [a]	0.48 [b]	0.47 [b]	0.04
Min/g NDF intake	1.16 [a]	0.75 [b]	1.05 [a]	0.06

[a, b, c] Means on the same line without a common superscript differ significantly ($P < 0.05$).
[d] Mean values of the morning and the evening meals following hay distribution.

accounted for proportionally 0.89, 0.73 and 0.87 of daily intake for mixed grass, cocksfoot and lucerne respectively. The number of additional small meals was highest for cocksfoot, which was eaten for the shortest duration after feeding. This increased number of small meals was associated with a significantly increased intake.

Neither the time spent ruminating daily nor the number of rumination periods was significantly affected by the type of hay (table II). Thus daily duration of mastication (eating and ruminating) did not vary significantly with the type of hay. However, the duration of mastication needed per unit of feed component was significantly affected by the nature of the hay. The two early-cut hays needed 0.30 min less mastication time per g DM eaten than the late-cut mixed grass hay. However, only the cocksfoot hay needed significantly less mastication per g of NDF eaten.

Experimental conditions with continuous artificial light and two hay distributions 12 h apart provided intake and feeding behaviour patterns that were cycled over a 12-h period (fig 1). Interaction between time of day and type of hay was highly significant for DM intake, time spent eating and time spent ruminating ($P < 0.001$ for the F-test adjusted by the Huynh-Feldt epsilon in the three cases). Patterns of DM intake (fig 1a) showed that the first hour following hay distribution contributed mainly to the daily intake differences between hays. The increased intake of cocksfoot hay during small meals occurred mainly 6 h after hay distribution (fig 1b). Patterns of time spent ruminating (fig 1c) showed that the occurrence of rumination after the principal meal was delayed with lucerne hay and that cocksfoot hay was ruminated less at the end of the 12-h period.

Rumen content and digesta characteristics

As a consequence of the 12-h cycled eating and ruminating patterns no significant differences between morning and evening were found for rumen content and digesta characteristics. Consequently, mean values of the measurements made before the morning and evening distributions, and after distributions were considered (table III). The wet weight of ruminal digesta before hay distribution was negatively related to DM intake; the lower the rumen content the higher the intake. The amount of DM in the rumen was closely related to the wet weight of digesta. In vitro digestibility of ruminal DM was 0.263, 0.323 and 0.190 ($P < 0.05$) for mixed grass, cocksfoot and lucerne respectively. The amount of undegradable DM in the rumen before hay distribution was lowest for cocksfoot and highest for mixed grass. The amount of NDF in the rumen was similar for the two early-cut hays and significantly lower than for mixed grass.

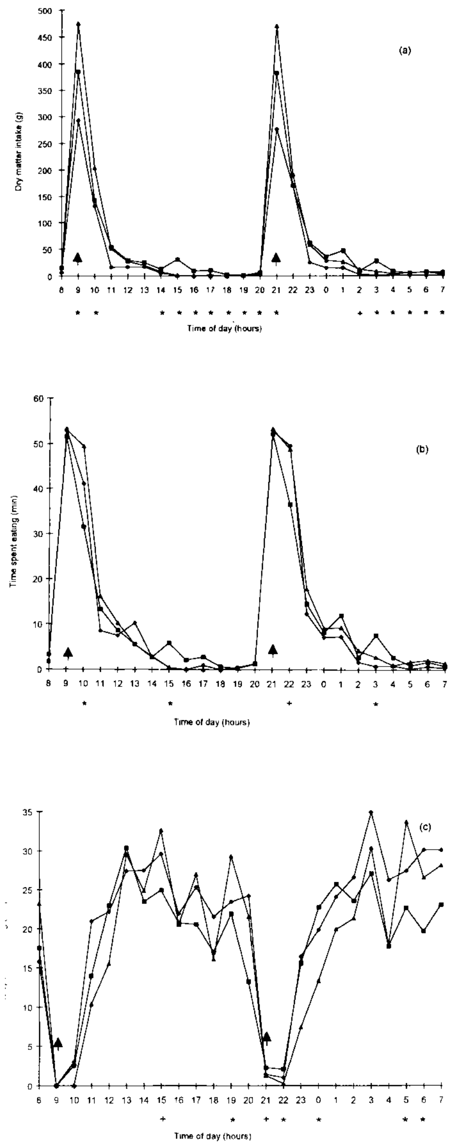

Fig. 1. Daily pattern of dry matter intake **(a)**, time spent eating **(b)** and time spent ruminating **(c)** in sheep offered late-cut mixed grass (◆), early-cut cocksfoot (■) or early-cut lucerne (▲) hay twice a day (🠕) at 09:00 and 21:00 h. Effect of the type of hay on contrast variables representing the differences between hours and the mean of all other hours are symbolised (* = $P < 0.05$; + = $P < 0.10$).

However, in vitro digestibility of ruminal NDF was not different among the hays (0.227, 0.215 and 0.166 for mixed grass, cocksfoot and lucerne respectively, $P > 0.05$). Hence the amount of undegradable NDF in the rumen before hay distribution was affected by the type of hay in the same manner as total NDF.

At the end of the principal meal, rumen fill expressed by the wet weight of digesta was equal for the two grass hays and significantly lower for lucerne (table III). However, when expressed by the amount of DM in the rumen, fill was similar for the three hays. In vitro digestibility of ruminal DM at the end of the principal meal was increased for the three hays and reached 0.289, 0.428 and 0.311 ($P < 0.05$) for mixed grass, cocksfoot and lucerne respectively. As a consequence of the high digestibility of ruminal DM for cocksfoot, the amount of undegradable DM was significantly lower. The amount of NDF in the rumen was lower for the two early-cut hays than for the late-cut mixed grass. Like that of DM, the in vitro digestibility of ruminal NDF was increased at the end of the principal meal and reached 0.263, 0.379 and 0.258 ($P < 0.05$) for mixed grass, cocksfoot and lucerne respectively. Ruminal NDF digestibility was highest for cocksfoot and similar for mixed grass and lucerne. Compared to mixed grass the amount of undegradable NDF in the rumen was significantly lower for cocksfoot and lucerne.

Fluid and digesta kinetics

Digesta kinetic calculations (tables IV, V) were based on the intakes recorded during the 4th and 5th weeks of each experimental period that were devoted to rumen fill measurements. Intakes were slightly higher than those reported in table II (1055, 1481 and 1651 g DM for mixed-grass, cocksfoot and lucerne respectively, $P < 0.05$), but the differences between hays were similar.

Disappearance rates of total DM or NDF are the result of microbial digestion and outflow from the rumen. Undegradable fractions estimated after in vitro incubation could disappear only by passage. Disappearance rate of DM between the end of a principal meal and the following distribution was significantly increased for the two early-cut hays (table IV). Variations in DM disappearance rate were related to disappearance rate of the degradable fraction of DM. In contrast, the disappearance rate of the undegradable fraction of DM was not significantly affected by the type of hay. Disappearance rate of NDF was only significantly increased for cocksfoot, the values being similar for lucerne and mixed grass. This was consistent with the low in vitro digestibility of the NDF of lucerne hay. As for DM, the variations in NDF disappearance rate were mainly related to disappearance rate of the degradable NDF.

Rumen fluid and DM fractional turnover rates were closely related and were significantly affected by the type of hay (table V). The higher DM and water intake, the higher fluid and DM fractional turnover rate. The increase in total DM fractional turnover rate was mainly related to an increase in turnover rate of the degradable DM and to a lesser extent of the undegradable DM. Compared to mixed-grass, the higher fractional turnover rate of NDF with cocksfoot was due to an increased turnover rate of the degradable NDF. In contrast, for lucerne the higher turnover rate of NDF is related to an increased turnover rate of the undegradable NDF.

DISCUSSION

Several relationships between voluntary intake and short-term degradability (Demarquilly and Chenost, 1969) or degradability fitted parameters (Khazaal et al, 1995) have been established. The three hays used in this trial differed widely in cell-wall content and

Table III. Effect of type of hay offered to sheep on rumen content and digesta characteristics.

	Mixed grass	*Cocksfoot*	*Lucerne*	*SE*
Before hay distribution [d]				
Wet weight of digesta (kg)	8.41 [a]	7.57 [ab]	6.46 [b]	0.36
Dry matter (g)				
Total content	896 [a]	800 [ab]	737 [b]	44
Undegradable content [f]	659 [a]	539 [b]	598 [ab]	26
Neutral detergent fibre (g)				
Total content	655 [a]	502 [b]	523 [b]	31
Undegradable content [f]	506 [a]	391 [b]	437 [b]	20
After the principal meal [e]				
Wet weight of digesta (kg)	10.10 [a]	10.25 [a]	9.30 [b]	0.26
Dry matter (g)				
Total content	1285	1302	1276	43
Undegradable content [f]	919 [a]	755 [b]	881 [a]	33
Neutral detergent fibre (g)				
Total content	938 [a]	845 [ab]	811 [b]	34
Undegradable content [f]	695 [a]	529 [b]	603 [b]	25

[a, b, c] Means on the same line without a common superscript differ significantly ($P < 0.05$).
[d] Mean values of the 09.00 h and 21.00 h rumen emptying procedures.
[e] Mean values of the11.00 h and 23.00 h rumen emptying procedures.
[f] Estimated after 48 h in vitro incubation with rumen fluid.

Table IV. Effect of type of hay offered to sheep on digesta disappearance rates (g/h) between end of principal meal and next hay distribution.

	Mixed grass	*Cocksfoot*	*Lucerne*	*SE*
Total dry matter (DM)	44.9 [a]	66.4 [b]	65.3 [b]	2.6
Degradable DM [d]	16.5 [a]	40.5 [b]	33.4 [c]	1.4
Undegradable DM [d]	28.4	25.9	31.9	1.8
Total NDF [e]	32.3 [a]	44.5 [b]	33.9 [a]	1.9
Degradable NDF [d]	11.8 [a]	28.2 [b]	14.6 [a]	1.2
Undegradable NDF [d]	20.6 [a]	16.3 [b]	19.3 [ab]	1.1

[a, b, c] Means on the same line without a common superscript differ significantly ($P < 0.05$).
[d] Fraction estimated after 48 h in vitro incubation with rumen fluid.
[e] Neutral detergent fibre (NDF).

Table V. Effect of type of hay offered to sheep on daily digesta fractional turnover rates (h^{-1}).

	Mixed grass	*Cocksfoot*	*Lucerne*	*SE*
Total dry matter (DM)	0.042 [a]	0.060 [b]	0.069 [c]	0.0021
Degradable DM [d]	0.092 [a]	0.112 [b]	0.175 [c]	0.0050
Undegradable DM [d]	0.023 [a]	0.027 [b]	0.031 [b]	0.0010
Total NDF [e]	0.040 [a]	0.061 [b]	0.047 [c]	0.0017
Degradable NDF [d]	0.095 [a]	0.141 [b]	0.096 [a]	0.0064
Undegradable NDF [d]	0.022 [a]	0.022 [a]	0.033 [b]	0.0012
Rumen fluid	0.071 [a]	0.099 [b]	0.111 [c]	0.0048

[a, b, c] Means on the same line without a common superscript differ significantly ($P < 0.05$).
[d] Fraction estimated after 48 h in vitro incubation with rumen fluid.
[e] Neutral detergent fibre (NDF).

in degradation parameters measured in situ. Differences in rate of degradation between hays were in agreement with the differences observed between early and late cut grasses and between grasses and legumes (Grenet, 1989).

Voluntary intake and feeding behaviour

Difference in voluntary intake between early and late-cut grass and between grass and legume hays agreed with the results of other studies using the same type of forages (Aitchison et al, 1986). Compared to mixed grass, the increase in intake during the principal meals accounted for proportionally 0.84 of the increase in daily intake with lucerne, but only for 0.41 with cocksfoot.

Rate of intake and not intake duration accounted for most of the difference in daily intake but also during the principal meals. Our results agree with the positive relation between amount ingested and intake rate (Moseley and Antuna Manendez, 1989). Moreover, the initial rate of intake at the beginning of the principal meals was closely correlated ($r = 0.702$, $P < 0.01$, $n = 18$) with daily intake. Such a correlation was also found in goats by Gill and Romney (1994). Kenney and Black (1984) found that in sheep preference is linked with initial intake rate and that they prefer feeds that can be consumed quickly. Initial intake rate integrates the organoleptic properties of the feed, but also of several physical properties such as ease of prehension and mastication (Baumont, 1996). The higher intake rate of leafy cocksfoot compared to mixed grass with high proportion of stems should partly be due to lower resistance to mastication. The cell wall of the cocksfoot hay was less lignified as indicated by the lower acid-detergent lignin content. The number of chews per gram ingested hay during the meal is significantly lower for early-cut than for late-cut grasses (Grenet, 1989). The highest initial intake rate observed with lucerne should partly be related to the possibility with legumes to sort the leaves that are very poor in cell-wall (Demarquilly and Andrieu, 1988) and in lignin (Jarrige et al, 1995b), from the stems. Thus animals are able to select the part of the plants that need least mastication. In another experiment using the same hays, the NDF content of the ingested fraction during the principal meal with lucerne was proportionally decreased by 0.20 compared to the NDF content of the hay but it was only decreased by 0.02 with mixed grass (Baumont et al, 1990b). NDF content of refusals was not modified with the leafy cocksfoot. Active diet selection with lucerne can affect the NDF content of the first meal after feeding. However, with a level of refusal of 10% it is of minor importance on daily NDF intake. The more rapid decrease in intake rate during the meal with lucerne can also be partly explained by the active diet selection. As eating proceeds the animals spend more time searching for leaves and eat an increasing proportion of stems that need more mastication.

The other factor that accounts for the increased intake with early-cut cocksfoot compared to late-cut mixed grass hay was an increased intake between the principal meals. This is in accordance with the decrease in the number of small intermediate meals observed with grasses at successive stages of vegetation (Dulphy and Faverdin, 1987). For late-cut forages the low intake during the principal meal is not compensated by the small additional meals.

Consistent with the data summarised by Jarrige et al (1995a) the early-cut hays needed less mastication per g DM consumed than the late-cut one. This indicates a higher efficiency of mastication for the former. However, on a NDF basis the efficiency of mastication was similar for lucerne and mixed grass. This is probably because the NDF of lucerne hay is mainly located in the stems that are rich in lignin (Jarrige et al, 1995b).

Physical limitation of intake and digesta kinetics

For mixed grass hay that had the lowest crude protein content, intake of PDI can be estimated to 53 and 69 g/day for PDIN and PDIE respectively. This is sufficient for a maintenance requirement of 55 g/day PDI. The energy maintenance requirement of sheep is 95 kcal of metabolizable energy or 26 g of digestible organic matter per kg $BW^{0.75}$ (Bocquier and Thériez, 1989). Voluntary intakes of digestible organic matter were 22.8, 40.1 and 41.2 g/kg $BW^{0.75}$ for mixed grass, cocksfoot and lucerne respectively. Thus the maintenance requirement was not fully reached with mixed grass and rumen fill observed with that hay should be close to the maximum capacity of the animals.

Rumen content before hay distribution was highest with mixed grass and was also high at the end of the meal. Also, the fact that after the principal meal the wet weight of digesta was similar for the two grass hays suggests the ruminant stops eating once a certain level of distension is achieved. This could explain the relatively short duration of the principal meal with cocksfoot. The similar amount of DM in the rumen at the end of the principal meal for all three hays (fig 2) is in accordance with a physical limitation of intake. However, even at the end of the principal meal, the wet weight of digesta remained significantly lower with lucerne. Hence it is questionable whether rumen distension limits the meal size with lucerne. Intake should be limited by chemical products due to a high degradation rate or simply by lack of motivation to eat the remaining lucerne, which contains a high proportion of stems. Other studies have found lower rumen content with legumes than with grasses (Thomson et al, 1985; Grenet, 1989). What exactly are the signals involved in the physical limitation of intake remains partly unknown. Addition of balloons filled with water (Campling and Balch, 1961; Anil et al, 1993) has shown that ruminants sense the volume and weight of digesta. Other trials performed with long fibres of polypropylene (Welch, 1967) or with blocks of expanded polystyrene (Baumont et al, 1990a) have suggested the role of mechanical stimulation of the rumen wall in the cessation of eating by causing the

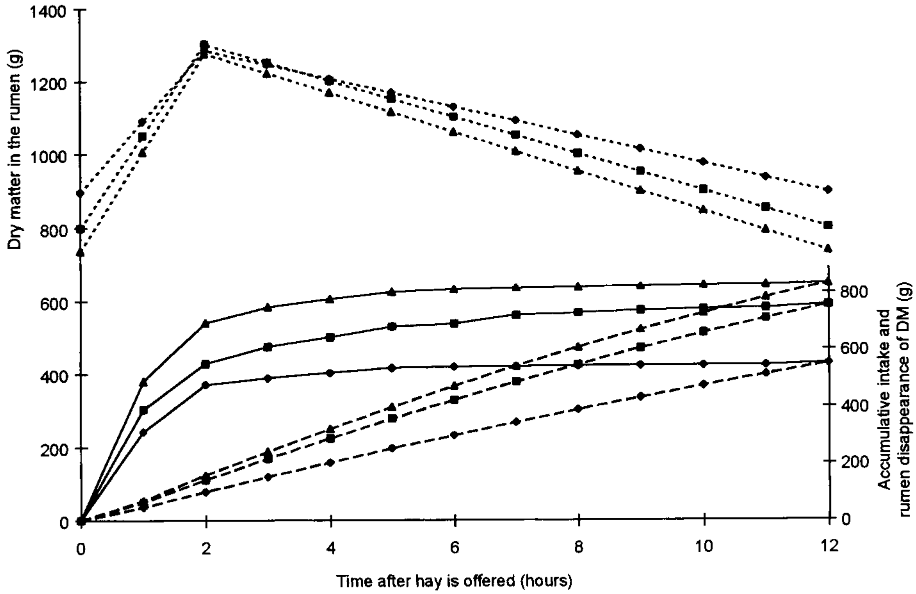

Fig.2. Dynamic of dry matter in the rumen (......) as related to intake (____) and digesta disappearance (_ _ _) in sheep offered late-cut mixed grass (◆), early-cut cocksfoot (■) or early-cut lucerne (▲). The kinetic of digesta disappearance is estimated from rumen content and fractional turnover rates presented in tables III and V respectively.

onset of rumination (Campion and Leek, 1996). The rapid increase after principal meals in time spent ruminating with the two grass hays supports this.

Figure 2 illustrates the dynamic of rumen content, intake, and disappearance of digesta in the three nutritional situations studied. This approach allowed the development of a non-steady state mechanistic model of intake and chewing activities of sheep (Sauvant et al, 1996). The space available in the rumen at the beginning of the meal contributes to the amount that can be eaten before a high level of distension is reached. The level of rumen content before hay distribution is mostly determined by the disappearance rates of DM. A partition between degradable and undegradable digesta was made to assess which fraction was mainly limiting rumen clearance. The choice of a 48 h incubation time for the determination of the undegradable fractions was made to fit roughly with the ruminal residence time of the indigestible residues and thus approximate the fractions that are actually degraded or not degraded in the rumen. However, it can be argued that 48 h of incubation will underestimate the true digestible fraction and overestimate the indigestible fraction (Mertens, 1993). Other studies performed in vitro (Aitchison et al, 1986; Deswysen and Ellis, 1988) have chosen longer incubation times. In this trial digestibilities of rumen contents were lower than in the study by Aitchison et al (1986), but this is mostly explained by differences in the digestibilities of the hays. The most striking feature is that the clearance rate of ruminal DM and NDF after a meal depends primarily on the disappearance rate of the degradable fractions.

Disappearance rates of the undegradable fractions were fairly constant among hays. This suggests that outflow rate of the undegradable feed residues depends on the physiological control of outflow (Mathison et al, 1995) rather than on the type of hay.

Undegradable fraction of digesta can only leave the rumen by passage, when the degradable fraction is submitted to microbial digestion and passage. Thus, in a similar manner to that done by Huhtanen and Kukkonen (1995), in vivo fractional rate of degradation can be estimated by the difference between fractional turnover rates of degradable and undegradable DM. Thus in vivo fractional rate of degradation of degradable DM can be estimated to 0.069, 0.085 and 0.144 h^{-1} for mixed grass, cocksfoot and lucerne respectively. Although these values are markedly higher than the in situ fractional rate of degradation, the differences between hays are consistent. Fill effect of ingested feed is proportional to its residence time in the rumen. It will in turn depend on the size of the undegradable fraction and on the degradation rate of the degradable fraction. Dynamic measurements, such as those of in situ degradability parameters, are promising to predict fill effect and to a lesser extent forage ingestibility (Faverdin et al, 1995).

In conclusion, intake of late-cut grass hay with high proportion of stems seems to be primarily limited by physical constraints that are related to a high content of undegradable and slowly degradable material. Rate of intake is probably reduced by the lengthy masticatory work the animals have to do before swallowing. High rumen fill before the principal meal should limit its size. Thereafter, despite a high rumination activity rumen clearance is slow due to the high proportion of undegradable digesta and the low disappearance rate of the degradable fraction. Thus mechanical stimulation of rumen wall could keep the animals ruminating and reduce the likelihood of eating additional meals. With early-cut leafy grass or lucerne hays intake is probably limited to a lesser extent by physical constraint as indicated by the plateau of digestible organic matter intake for these two hays. The combined study of the dynamic of intake and rumen function is promising for development of mechanistic models to predict intake.

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