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Original article

Influence of the method of forage conservation on feeding behaviour, intake and characteristics of reticulo-rumen content, in sheep fed *ad libitum*

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Summary — The influence of silage conservation methods on eating behaviour and the characteristics of reticulo-rumen contents was studied in sheep by comparing 3 forages, a silage without additive (WAS), one with additive (FAS) and hay (H), prepared from the same cut green forage. The sheep were rumen fistulated. WAS was very badly and FAS poorly preserved while the hay was dried under favourable conditions. The forages were fed *ad libitum* and the dry matter (DM) intake was 1 054, 1 241 and 1 469 g/day for WAS, FAS and H respectively. There was a single feeding in the morning. At the main meal, DM intake was 270, 317 and 388 g/day and ingestion rate 4.76, 4.56 and 4.16 g of DM/min for WAS, FAS and H respectively. There was slight recovery in ingestion around 16-19 h with hay and FAS but not with WAS. With hay, rumination lasted much longer than with the silages and began sooner after the end of the main meal. In contrast, overall rumination efficiency was the same for hay and FAS. There were fewer contractions of the reticulo-rumen with both WAS and hay. The amounts of reticulo-rumen contents were comparable for the 2 silages and higher for hay. The amounts of NH_3 in the contents were the same with WAS and hay but greater with FAS. With WAS, contents were richer in butyric, valeric and caproic acids. The DM turnover rate of the contents was the same for FAS and hay and lower, but not significantly, for WAS. Accordingly, with silage, satiety seems to be rapidly reached but there was no evidence that organoleptic factors were involved. There were no problems with the digestion rate of silages. However, the factors limiting silage intake persisted throughout the diurnal cycle, and reticulo-rumen fill was affected. The more poorly preserved the silage the more these factors reduced the duration and volume of the meals, or both.

intake / feeding behaviour / rumen content / forage conservation / sheep

Résumé — Influence de la méthode de conservation du fourrage sur le comportement alimentaire, l'ingestion et les caractéristiques du contenu réticulo-ruminal, chez le mouton nourri à volonté. *L'influence du mode de conservation sur les activités alimentaires et les caractéristiques du contenu réticulo-ruminal a été étudié chez le mouton par comparaison de 3 fourrages (un ensilage*

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sans conservateur WAS, un ensilage avec conservateur FAS et un foin H) préparés à partir du même fourrage vert sur pied. Les moutons étaient munis d'une fistule du rumen. L'ensilage WAS a été très mal conservé et l'ensilage FAS a eu une qualité de conservation médiocre alors que le foin avait été séché très correctement. Dans ces conditions, les quantités de MS ingérées ad libitum *ont été respectivement égales à 1054, 1241 et 1469 g/j. Les fourrages ont été distribués en une seule fois le matin. Lors du grand repas les quantités de MS ingérées ont été de 270, 317 et 388 g/j alors que les vitesses d'ingestion étaient respectivement de 4,76, 4,56 et 4,16 g de MS/min. Au cours de la journée une très légère reprise de l'ingestion a été observée vers 16–19 h pour le foin, également pour l'ensilage FAS, mais pas pour l'ensilage WAS. Avec le foin, la durée de rumination a été nettement plus élevée qu'avec les ensilages et cette rumination a démarré toujours plus vite après la fin du grand repas. Par contre, l'efficacité globale de la rumination a été la même pour le foin et l'ensilage FAS. Il y a eu moins de contractions du réseau avec l'ensilage WAS, mais également avec le foin. Les quantités de contenu du réticulo-rumen ont été comparables pour les 2 ensilages et plus élevées pour le foin. Dans les contenus réticulo-ruminaux les teneurs en NH_3 ont été identiques pour l'ensilage WAS et le foin, mais plus élevées pour l'ensilage FAS. La plus importante augmentation au cours du repas a été observée avec l'ensilage WAS. Avec cet ensilage, les contenus ont été plus riches en acides butyrique, valérianique et caproïque. Enfin, le taux de renouvellement de la matière sèche des contenus a été identique pour l'ensilage FAS et le foin et plus faible, mais non significativement, pour l'ensilage WAS. L'ingestion d'ensilage entraîne donc un rassasiement rapide des animaux sans que, apparemment, des facteurs organoleptiques ne soient en cause. Il n'y a pas non plus de problèmes dans la vitesse de digestion des ensilages. Par contre, les facteurs limitant l'ingestion des ensilages ont un effet permanent tout au long du nycthémère. Cet effet limite le remplissage du réticulo-rumen. Les facteurs en cause réduisent d'autant plus la durée et/ou le volume des repas que les ensilages sont plus mal conservés.*

ingestion / comportement alimentaire / rumen / conservation de fourrage / mouton

INTRODUCTION

In Europe, grass silage is increasingly preferred to hay as animal feed. The variations in intake between these two types of forage depend on how finely they are chopped, how well they are preserved and on their dry matter (DM) content. All these factors have been thoroughly studied (Demarquilly *et al,* 1981; Dulphy and Michalet-Doreau, 1981; Dulphy and Demarquilly, 1991). However, despite the large number of published reports, the mechanisms involved in the regulation of silage intake have not yet been completely elucidated. Two main approaches, descriptive or experimental, emerge from studies in this field. The first is based essentially on 3 complementary methods of investigation: 1) examination of the regressions between the intake and characteristics of silage (Wilkins *et al,* 1971; Demarquilly, 1973); 2) observation of eating behaviour (Deswysen *et al,* 1978; Dulphy *et al,* 1984); 3) observation of the extent of reticulo-rumen fill (Campling, 1966; Dulphy *et al,* 1975a; Thiago and Gill, 1986). The second approach is based on the study of the effects of experimental modifications to silage characteristics: chopping of silage after removal from the silo (Dulphy and Demarquilly, 1973) and addition of different acids of nitrogen compounds at the time of feeding (Hutchinson and Wilkins, 1971; Martin Clancy *et al,* 1977; Buchanan-Smith and Philipp, 1986; Buchanan-Smith, 1990).

In sheep receiving grass silage, the amounts of DM ingested during the main meal after distribution were low (Dulphy, 1985) but this was offset by an increase in the number of small meals taken during the day, if green forage (Dulphy *et al,* 1984) or hay (Dulphy *et al,* 1975a) were taken as controls. These findings suggest that the animals did not use their rumen capacity to the full (Thiago and Gill, 1986).

In the present trial we studied both the behaviour of the animals and the physical as well as the chemical characteristics of ruminal digestion in relation to the nature of the preserved forage. For that purpose we compared 3 preserved forages, all prepared at the same time from the same green plant, but with very different characteristics: poorly preserved silage, well preserved silage and a good hay. Our objective was to try to understand the daily voluntary intake of these 3 forages by the analysis of the kinetics of intake, of the eating and ruminating activities, of the extent of the rumen fill and of the characteristics of reticulo-rumen content. This approach is not common in the literature and is used here to study the effects of silage (by comparison to hay) and of quality of silage preservation.

MATERIAL AND METHODS

Animals and feeds

In July 1990, a cocksfoot meadow in the second cycle of vegetation was mown to prepare three differently preserved forages: a direct-cut silage, without additive and harvested with a precision chop forage harvester (WAS); the same forage, but treated with 4.4 l of formic acid (FAS); and hay (H), field cured in favourable conditions.

The 3 forages were distributed from September to December to six 4-year-old castrated Texel sheep (initial live weight 60 ± 3 kg) fitted with a rumen cannula 75 mm in diameter.

The required amounts of silage were removed from the silo twice a week and stored at +4 °C. Throughout the experimental period the animals were maintained with lights off from 21.00 h to 07.00 h and with lights on for the rest of the time, to achieve a constant photoperiod. The animals were fed *ad libitum* (10% refusal) with a single feeding a day at 8.30 h. They had free access to the forages, water and salt licks.

Experimental design

The experimental design was a replicated 3 x 3 Latin square, using 2 sheep simultaneously per treatment. Each of the 3 periods lasted 5 weeks, divided as follows: 1 week of adaptation to the diet; 1 week of adaptation to the metabolism crates; 1 week of measuring digestibility, the kinetics of intake during the day and eating and ruminating behavior; 2 weeks with the animals still in metabolism crates, during which 4 complete emptyings of the reticulo-rumen were performed.

Measurements

The digestibility of the 3 forages *in vivo* was determined by collecting the total faecal production. Concomitantly, but in 3 different sheep receiving a good quality lucerne hay, the kinetics of the DM degradation of the 3 forages was studied *in situ* (Demarquilly and Chenost, 1969) at incubation times in the rumen of 0, 4, 8, 16, 24, 48 and 72 h. On removal from the rumen, the nylon bags (2 per incubation period and per sheep) were washed in cold water and placed in a pepsin solution for 48 h.

Daily intake was calculated by measuring the difference between the amounts offered and refused. Mangers were placed on sensors fitted with strain gauges (Baumont *et al,* 1988) coupled to a computer so that the intake could be determined for each meal throughout the day without disturbing the animals. At the same time, eating and ruminating behaviour was observed according to the technique of Ruckebush (1963), as adapted by Baumont *et al* (1988). The pressure signals transmitted by a balloon filled with polyurethane foam were immediately read into the computer and analyzed with software developed by Brun *et al* (1984). Likewise, we recorded the motility of the reticulo-rumen by means of another balloon placed in the dorsal sac of the rumen and connected to a pressure transducer.

The total reticulo-rumen contents were withdrawn by hand at 8.30, 10.30, 15.30 and 20.30 h. Emptyings were made at intervals of at least 72 h, to allow digestion to return to normal (Aitchison, 1985). For a given time, all animals were treated together. All these contents were weighed and sampled after homogenization to determine DM content (48 h at 80 °C), dry samples being kept for analysis, particle size, and to measure pH, VFA (volatile fatty acids) and ammonia content, osmotic pressure and viscosity in the fluid.

The disappearance rate of digesta was calculated in g/h between 2 different times according to the formula: disappearance rate = (initial content + amount ingested–final content) / duration.

Chemical analyses

During the measurement periods, a representative sample of silage and hay was taken at each feeding. The DM content of the samples was determined after drying at 80 °C for 48 h and corrected for silage according to the recommendations of Dulphy *et al* (1975b), which take into account losses in volatile DM during oven drying. Crude protein content was determined in undried silage. The other analyses were made on samples after drying: ash was determined after incineration for 6 h at 550 °C, nitrogen by the method of Kjeldahl and total cell walls (NDF) according to Goering and Van Soest (1970).

The fermentation characteristics of the silages (pH, VFA, lactic acids, ammonia and soluble nitrogen) were determined in fluid expressed under pressure. Ammonia was immediately assayed according to the method of Conway (1957) and soluble nitrogen by that of Kjeldahl. The fluid sample for lactic acid assay was conserved frozen without additives and then analyzed by the method of Noll (1974). Another fluid sample was treated with orthophosphoric acid and stabilizing agent and frozen for VFA and alcohol assay (Jouany, 1981).

The characteristics of the reticulo-rumen contents were determined either overall (particle size) or on dry matter, or on fluid filtered through a 1-mm mesh grid. Particle size was estimated after sieve separation in a liquid flow according to the method of Grenet (1970). The dry samples were ground (0.8 mm grid) for estimation of the plant cell walls. In the fluid, VFA were analyzed according to the method of Jouany (1981) and ammonia by the method of Berthelot (fluid treated with NaCl and frozen). In the fluid, we also estimated osmotic pressure by cryometry, and viscosity from the flow time into a capillary tube (Dardillat and Baumont, 1992).

Statistical analysis

Statistical significance of the feed intake, eating and ruminating activities, motility of reticulo-rumen, extent of rumen fill, characteristics of the reticulo-rumen contents and some parameters of the digestion were tested using an analysis of variance with the effects of animal (5 DF), type of forage (2 DF) and period (2 DF) and with 8 DF in the error term. The calculations were performed using the general linear model procedure of the Statistical Analysis System Institute (SAS, 1985).

RESULTS

Chemical composition and digestibility of forages

Table I shows the chemical composition of the 3 forages. The 2 silages were very wet. Overall, ash content was rather high and crude protein rather low for regrowths (Andrieu *et al,* 1988). *In vivo* digestibility of the silage with additives was slightly higher than that of the other 2 forages (+ 3.6 points for OM). The kinetics of digestion *in sacco*, in the rumen, were almost identical: the variables A and B, calculated from the model of Ørskov and Mac Donald (1979) were comparable for the 2 silages. In contrast, the value of B was lower for hay. The degradation rate C was highest for silage with FAS and lowest for WAS.

Table II shows the fermentation characteristics for the 2 silages. The silage without additive contained practically no lactic acid but a high level of VFA, including 9 g of propionic lactic acid, 5.5 g of valeric acid and 10.5 g of hexanoic acid per kg DM.

Intake, eating behaviour and motility of the reticulo-rumen

Silage intake was considerably smaller than hay intake (table III). Although the intake of silage with additive was markedly higher (+ 18%) than that of silage without, there was no significant difference between the 2. In relation to the metabolic

Table I. Characteristics of forages studied.

	Silage without additive WAS	*Sillage with additive FAS*	*Hay H*
Chemical composition			
Dry matter (DM) contents (g/kg)	157	170	880
Contents in g/kg of DM			
Ash	128	117	112
Crude protein	125	119	103
Total cell walls (NDF)	601	594	658
Digestibility in vivo *(%)*			
Organic matter	64.3[b]	67.9[a]	64.3[b]
NDF	66.6[b]	69.3[a]	66.5[b]
Digestibility in sacco (parameters of the adjusted curve) (dry matter)			
A	31.3	30.0	32.7
A + B	76.3	77.8	68.5
C	0.034	0.041	0.039

NB : For different treatment results followed by different letters are significantly different.

Table II. Fermentation characteristics of the silages.

		Silage without additive	*Silage with additive*
pH		5.55	4.14
$N.NH_3$ % total N		26.9	11.4
Soluble N % total N		54.7	44.7
Lactic acid	g/kg DM	2.4	20.9
Acetic acid		34.6	33.2
Butyric acid		32.7	3.5
Total VFA		92.5	41.5
Total alcohol		2.9	4.5

weight of the sheep, the amounts ingested were 48.8, 57.6 and 66.2 g of DM/kg W0.75 respectively for WAS, FAS and H.

The daily time spent eating hay was longer than with the silages (+ 25%) but there was less difference between ingestion rates (+ 12% between WAS and H, which is not significant).

Intake during the main meal was significantly higher for hay than for the silages, + 22 and 44%, compared to FAS and WAS respectively. The rates of intake were comparable, although slightly lower for hay, so that the duration of the main meals differed significantly according to the treatment. In contrast, these rates were much higher for silages at the beginning of the main meal. For hay, they were regular throughout the meal.

There was no significant difference between the number of secondary meals a day.

Table III. Intake, eating and ruminating behaviour of animals.

	Silage without additive WAS	*Silage with additive FAS*	*Hay H*	*RSD**
Day				
DM intake (g)	1054[b]	1241[b]	1469[a]	142
Duration (min)	303[b]	325[ab]	393[a]	57
Ingestion rate (g/min)	3.50[a]	3.85[a]	3.92[a]	0.4
Main meals				
DM intake (g)	270[b]	317[b]	388[a]	38
Duration (min)	58[c]	72[b]	93[a]	9
Ingestion rate (g/min)				
Total meal	4.76[a]	4.56[a]	4.16[a]	0.60
First 15 min	6.80[a]	5.93[a]	4.07[b]	0.73
First 30 min	5.80[a]	6.07[a]	4.50[b]	0.68
Number of secondary meals	10.2[a]	10.5[a]	9.5[a]	2.2
Rumination				
Daily duration (min)	417[c]	457[b]	535[a]	28
Number of cycles	506[b]	569[a]	612[a]	37
Duration of cycles (sec)	50[ab]	48[b]	52[a]	2
Time between distribution and beginning of rumination (min)	182[a]	161[a]	138[a]	37
Time between end of main meal and beginning of rumination	124[a]	89[ab]	45[b]	41
Chewing				
Daily duration (min)	720[b]	782[b]	927[a]	76
Efficiency (g/min)	1.47[b]	1.59[a]	1.60[a]	0.08

* RSD: residual standard deviation of the analysis of variance (8 ddl).

The daily duration of rumination varied significantly, with a difference of 28% between WAS and H.

Figure 1 shows the daily pattern of eating and rumination at 1 h intervals. The results confirm the importance of the main meal for hay intake. They also show a significant recovery in hay intake between 16 and 19.00 h. There was a similar recovery for FAS only at 18.00 h, but not for WAS.

Although forage was distributed only once, there were 2 peaks of rumination in the day (fig 1). With hay, the latency time was shorter and rumination always began more quickly (table III). The rumination cycles had an average duration of 50 s and although the difference in times between FAS and H was significant, the values measured were very similar.

The time spent chewing daily was comparable on the 2 silages (on average 750 min) but significantly higher (23%) with hay. In contrast, chewing efficiency was the same for FAS and H and slightly lower

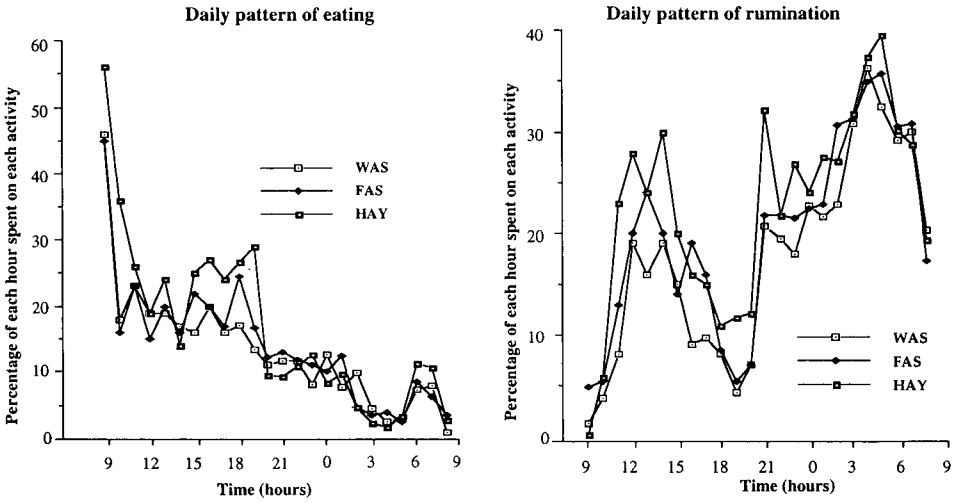

Fig 1. Evolution of feeding behaviour during the day.

(–8%) for WAS. However, if we report the time spent ruminating per unit DM digesta present in the reticulo-rumen we obtain the same figure for the 3 forages: 0.36 min/g DM digesta.

Table IV shows the number of contractions of the reticulo-rumen per min. Overall, this number was higher for FAS and lower for hay. If the numbers are offset by taking account of the real duration of each activity, we find 1 741, 1 830 and 1 752 of type A contractions per day for WAS, FAS and H respectively. The values for the total contractions were 2 893, 3 181 and 3 052.

Table IV. Number of contractions per min of the reticulo-rumen according to the type of activity.

	Silage without additive WAS	*Silage with additive FAS*	*Hay H*	*RSD*
Type A contractions				
Main meals	1.70^{a}	1.78^{a}	1.49^{b}	0.06
Small meals	1.51^{ab}	1.57^{a}	1.45^{b}	0.05
Rest	1.04^{ab}	1.07^{a}	1.01^{b}	0.04
Rumination	1.23^{a}	1.28^{a}	1.23^{a}	0.06
Type A + B contractions				
Main meals	3.40^{a}	3.56^{a}	2.93^{b}	0.15
Small meals	2.80^{ab}	2.99^{a}	2.74^{b}	0.14
Rest	1.66^{b}	1.83^{a}	1.74^{ab}	0.11
Rumination	1.87^{b}	2.02^{a}	1.96^{ab}	0.10

Extent of reticulo-rumen fill and physical characteristics of the contents

Table V shows the amounts of fresh matter, DM and total cell wall contents. There was no significant difference between the 2 silages: an average of 10 266 g fresh matter for WAS and 10 668 g for FAS (+ 4%) and 1 153 g DM for WAS and 1 224 g for FAS (+ 6%). The values for hay were much higher, with significant differences at 10.30 and 15.30 h compared to silages (on average, 11 988 g fresh matter and 1 479 g DM over the day). On the basis of total cell wall contents, the reticulo-rumen contents were higher with hay (on average, 994 g *vs* 775 and 814 g with WAS and FAS).

The DM level of the contents was highest with hay, but overall there was little difference between the forages (table VI). The levels were low before the morning meal (107 g/fresh kg) and remained steady at 119 and 123 g after the main meal and in the evening respectively (fig 2). The cell wall levels of the contents were very similar with only slight variations during the day: an average maximum of 677 at 15.30 h and a minimum of 656 g/kg DM at 20.30 h.

There was little difference between the 2 silages in the size of ruminal particles (table VI), except for a slight inversion between the small particles (0.05–1 mm) and the soluble compounds with the latter being a little higher with the well preserved silage. In contrast there were fewer large particles with hay (–9% left on the 8 mm mesh sieve) but more medium-sized particles (+ 70% on mesh between 1–8 mm) and hence more particles ≥ 1 mm (fig 2). When observed with the naked eye, these particles generally seemed to be larger for hay than for the silages, but no precise measurement was made.

Table V. Influence of the nature of the forage on reticulo-rumen fill.

In g	*Silage without additive WAS*	*Sillage with additive FAS*	*Hay H*	*RSD*
Fresh matter				
8.30 h	8689[a]	9266[a]	9930[a]	1151
10.30 h	10941[ab]	10773[b]	12298[a]	1032
15.30 h	10561[b]	10931[b]	12854[a]	1296
20.30 h	10874[a]	11702[a]	12870[a]	1515
Dry matter				
8.30 h	943[a]	993[a]	1088[a]	147
10.30 h	1269[b]	1267[b]	1529[a]	96
15.30 h	1123[b]	1220[b]	1602[a]	171
20.30 h	1279[b]	1416[ab]	1697[a]	256
Total cell walls				
8.30 h	639[a]	663[a]	722[a]	101
10.30 h	856[b]	851[b]	1037[a]	70
15.30 h	760[b]	821[b]	1095[a]	122
20.30 h	846[b]	923[ab]	1120[a]	181

Table VI. Mean characteristics of reticulo-rumen contents.

	Silage without additive WAS	*Silage with additive FAS*	*Hay H*	*RSD*
DM content g/kg	111[b]	113[b]	122[a]	9
NDF content g/kg DM	672[a]	665[b]	670[ab]	10.7
pH	6.60[a]	6.50[b]	6.37[c]	0.16
N-NH_3 mg/l	100[b]	138[a]	99[b]	34
VFA mmol/l	92[b]	95[b]	106[a]	9
Acetic acid (%)	68.6[b]	70.2[a]	69.4[ab]	2.2
Propionic acid (%)	16.6[c]	17.9[b]	18.8[a]	1.2
Butyric acid (%)	11.5[a]	8.8[b]	9.6[b]	1.6
Valerianic acid (%)	2.8[a]	2.7[a]	2.0[b]	0.5
Caproic acid (%)	0.6[a]	0.4[b]	0.3[c]	0.2
Particles retained on sieve (%)				
8 mm mesh	213[a]	215[a]	194[a]	42
Between 1–8 mm mesh	82[b]	86[b]	143[a]	23
Between 0.05–1 mm mesh	360[a]	336[b]	330[b]	35
< 0.05 mm (g/kg DM)	345[b]	362[a]	334[b]	26
Osmotic pressure (mOsm/ml)	264[b]	261[b]	281[a]	9
Viscosity (m.Pa/s)	1.07[b]	1.01[b]	1.26[a]	0.18

The viscosity of the centrifuged rumen juice (fig 2) was practically the same for the 2 silages but a little higher (+ 21%) for hay. On average, viscosity went from 1.20 before the meal to 1.08 afterwards and then to 1.06 and 1.12 at the subsequent emptyings. Likewise, the osmotic pressure of the rumen fluid (fig 2) was similar for the 2 silages but higher (+ 7%) for hay.

Chemical characteristics of the reticulo-rumen contents

There was a significant difference in pH between the forages, and the level was lower for hay than for silages (table VI). On average, pH decreased regularly from 8.30 h (6.71) to 20.30 h (6.29) (fig 3). Ammonia contents were the same for WAS and H but higher for FAS. At 8.30 h, the level was 132 mg/l and at 10.30 h 137, after which it decreased. The most clear-cut effect of the main meal (an increase in ammonia level of 47 mg/l in 2 h) was observed with the WAS (fig 3).

VFA contents were about the same for the 2 silages and slightly higher for hay. The levels increased gradually throughout the day, from 84 mmol at 8.30 h to 109 mmol at 20.30 h (fig 3). Overall, the proportions of acetic and propionic acid were lowest with WAS. In contrast, it was this silage that had the highest amounts of butyric, valeric and caproic acid. The proportions of valeric and caproic acid were lowest with hay. The most notable modifications were observed with WAS after the main meal, at which time the proportions of acetic, propionic, butyric, valeric and caproic acids reached levels of 65.5, 15.3, 13.7, 3.5 and 0.8% respectively.

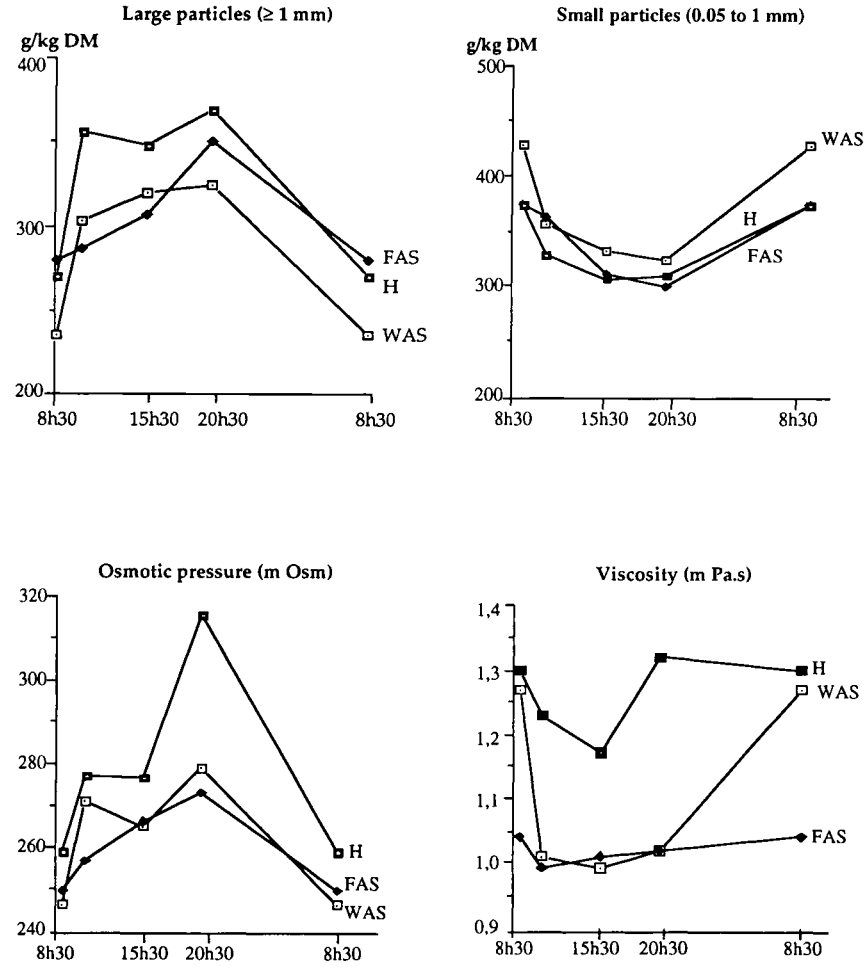

Fig 2. Evolution of the characteristics of the reticulo-rumen contents during the day (particles, osmotic pressure and viscosity).

Rate of disappearance of digesta

During the day there was no great difference in the rates of DM disappearance between the 3 forages (average of 48 g/h) but a marked increase at night for hay (table VII). The disappearance rates of the plant cell walls were also very similar except again for an increase with hay during the night. The DM turnover rate of the contents during the nycthemeral cycle was therefore the same for FAS and H and lower, but not significantly for WAS. The variations in the cell wall turnover rates, although slightly greater, were still not significant.

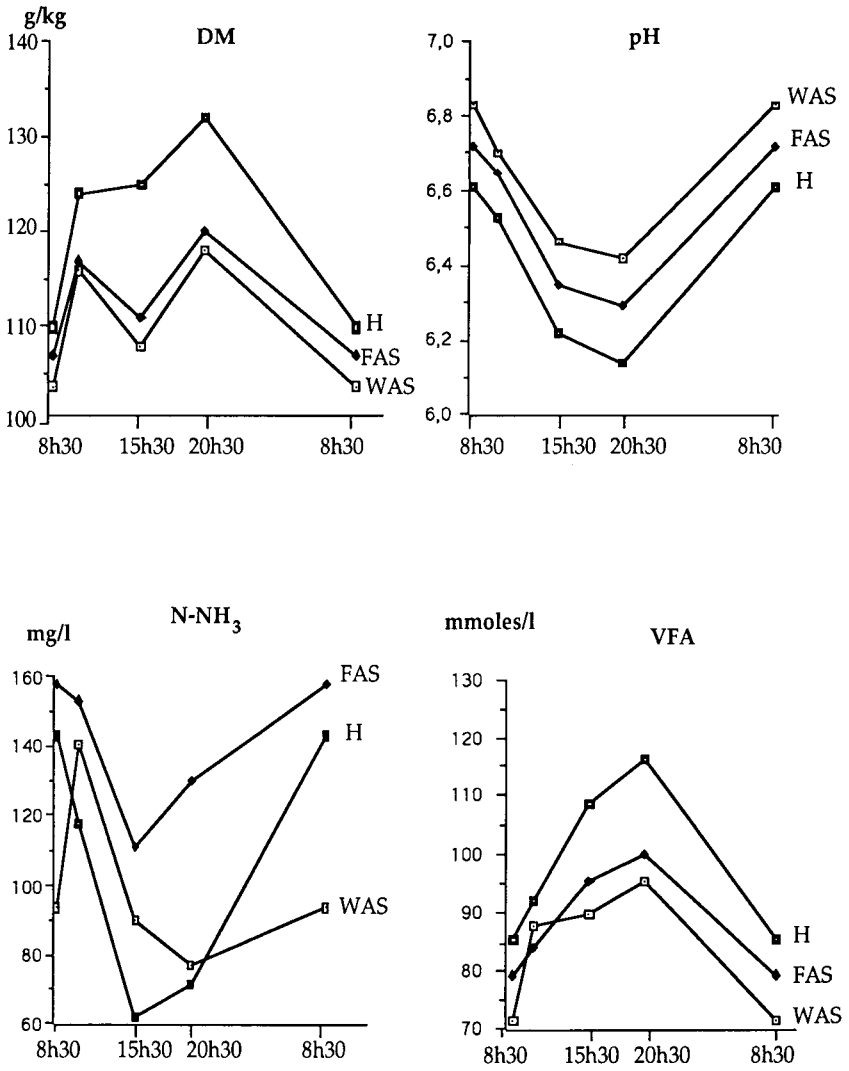

Fig 3. Evolution of the characteristics of the reticulo-rumen contents during the day (dry matter, pH, $N\text{-}NH_3$ and volatile fatty acids).

DISCUSSION

The green forage from which the silages and hay were prepared was rich in water and probably poor in soluble carbohydrates (Jarrige, 1981). As a result, the silage with additive was of mediocre quality and that without was very poorly preserved. Hence, in contrast to what is usually observed (Dulphy and Demarquilly, 1991),

Table VII. Rate of disappearance of reticulo-rumen contents and turnover rate.

	Silage without additive WAS	*Silage with additive FAS*	*Hay H*	*RSD*
DM disappearance rate (g/h)				
Day (8.30 h – 20.30 h)	44.8[a]	49.9[a]	48.8[a]	19.2
Night (20.30 h – 8.30 h)	43.1[b]	53.5[ab]	73.6[a]	19.2
Disappearance rate of plant cell walls (g/h)				
Day	28.9[a]	32.5[a]	31.1[a]	11.6
Night	26.8[b]	33.4[ab]	48.0[a]	13.4
Turnover rate of contents				
DM (%/h)	3.89[a]	4.30[a]	4.21[a]	0.63
NDF (%/h)	3.48[a]	3.85[a]	4.13[a]	0.58

the intake of the silages was far lower than that of the hay. Likewise, the difference between the 2 silages themselves was greater than the standard dissimilarity (Dulphy and Michalet-Doreau, 1981). The difference corresponds however to that predicted by the equations given by these authors, in which the intake of the silage is in relation to the pH or the proportion of ammonia nitrogen. Finally, in comparison with the tables of Andrieu *et al* (1988), we obtained high, normal and low intake respectively for H, FAS and WAS.

Differences in intake were observed from the main meal. With the WAS, the sheeps' appetite was quickly satisfied, as observed in a previous study (Dulphy, 1985) and in agreement with the findings of Gill *et al* (1988) in young cattle. However, contrary to what has often been reported (Dulphy *et al,* 1975a; Martin Clancy *et al,* 1977; Dulphy *et al,* 1984), the animals did not compensate for rapid satiety by increasing the number of their meals.

Yet the number of meals taken with the silage diets was not so different from that usually reported (Dulphy *et al,* 1984). With hay it was higher (Dulphy, 1972; Dulphy *et al,* 1975a), perhaps because there was just 1 feeding per day. The same increase in the number of meals with a hay diet has been observed elsewhere (Dulphy *et al,* 1988). These findings therefore suggest that the effects of the factors limiting intake of the 2 silages were persistent throughout the diurnal cycle, since there was a lower intake at each small meal.

There are several factors involved in the regulation of silage intake: oral (taste, odour, prehensibility; *cf* Buchanan-Smith, 1990), digestive (rate of digestion, functioning of the reticulo-rumen; *cf* Martin Clancy *et al,* 1977; Sissons *et al,* 1986) and metabolic, *via* mechanisms that maintain the homeostasis of the animals.

One approach to organoleptic problems is to study the rate of ingestion, a variable which often sharply discriminates between the different types of silage. The rate decreases when the silage particles are longer (Dulphy and Demarquilly, 1973) and if there is no additive (Dulphy *et al,* 1984).

Strangely, in the present trial, this rate was not affected by the silage conservation method. Moreover, the silages were injected during the main meal at a faster rate than the hay. Problems of palatability did not therefore seem to limit intake of the 2 silages studied. In this respect, Buchanan-Smith (1990) stresses the negative role of acetic acid, of which there were similarly moderate amounts in our 2 si-lages. In agreement with the findings of the same author, we observed no effet of ammonia or of butyric, valeric and caproic acids.

Three aspects of digestion can be studied; the efficiency of rumination, the rate of digestion and reticulo-rumen fill. The efficiency of rumination was a little lower with the silage containing no additive. The reasons for this are difficult to determine since there was little difference between the digestion rates and digestibilities of the 3 forages. The digestion rate may have been a little slower for WAS. However, these observations are not sufficient to explain the differences in intake. Elsewhere, per unit of rumen digesta, the efficiency of rumination was exactly the same for the 3 treatments. For the same silage, the latency time between the end of the main meal and the beginning of rumination was much longer. The intake of poorly preserved silage therefore tended to 'disturb' rumination more than that of silage with additive. However, this may simply have been due to the fact that rumen fill was lower with silage than with hay.

Our findings showed that reticulo-rumen fill was greater for hay than for silages, and are consistent with previous reports (Campling, 1966; Thiago and Gill, 1986; Waldo *et al,* 1966), confirming that the animals' rumen capacity, at least in these trials, was not a factor that limited silage intake. In ratio to the metabolic weight of the animals, the average amounts of fresh content reached highest levels of 510, 540 and 600 g per kg $BW^{0.75}$ respectively for the 3 forages. These values were high compared to those of several other reports (Dulphy *et al,* 1975a; Baumont *et al,* 1988; Dulphy *et al,* 1988) but comparable (595 g) for hay to the results of Baumont *et al* (1990). The fact that the forage was well or poorly preserved had little effect on rumen fill, in contrast to results of a trial performed by Dulphy *et al* (1975a).

The fall in silage intake therefore resulted in a decrease in the reticulo-rumen contents. For WAS, a lower turnover rate of the contents was also observed. However, there is no evidence that the intake of the 2 silages studied was limited by a decrease in the animals' digestive capacity.

Given the composition of the grass silages, 2 series of compounds may be involved in metabolic changes: acids, or the products of the decomposition of nitrogen matter (Miettinen *et al,* 1991), or both. Because of this, it is often difficult to identify the compounds involved and to determine where and how their effects are achieved.

Certain end-products of the fermentation of finaly chopped silages quickly satisfy the animal's appetite before the rumen is filled. Several compounds may play a role: VFA, nitrogen compounds and probably lactic acid also (Morgan and L'Estrange, 1977; Thomas *et al,* 1980). Since the phenomenon occurs with all silages, the acids must be involved. Satiety is even more quickly reached if the silage is poorly conserved, so compounds from the degradation of nitrogen have an effect. When they are given well-preserved silage, animals may offset early satisfaction of hunger by eating more often, and in sizeable amounts, so that they ingest as much silage as hay (Dulphy and Demarquilly, 1991). This did not happen in our trial because the silage with additive was of mediocre quality. With poorly conserved silages, which hence are rich in VFA or am-

monia or in both, 2 sets of mechanisms may come into play simultaneously. The time spent eating and the amount ingested per meal may decrease, as in our experiment, in proportion to the poor state of conservation of the silage. The receptor areas are probably situated in the stomachs. The animals' lack of appetite, as evidenced by a slow intake rate, can also shorten the duration of meals or reduce the amount ingested for the same time spent eating (Dulphy *et al,* 1984; Buchanan-Smith and Philipp, 1986). The number of meals themselves may also decrease. While this decrease is only slight with well chopped silages, it is clear-cut in those with long particles (Dulphy and Demarquilly, 1973). The limiting effects of chemical or physical factors last longer in the rumen in this case, or eating may be delayed by the animals' lack of motivation. The latter possibility is supported by the findings of Gatel (1984) and Baumont *et al* (1990), who observed that the unpalatability of diets could be largely responsible for short-term satiety. In the present trial, however, this factor did not seem to be important.

An interesting question is how these end-products of the silage limit intake. We can suggest a direct action on chemical receptors, but it is also possible that silage feeding may elicit a signal which does not permit the rumen to fill to the same level as with hay.

In conclusion, organoleptic factors are not involved in the low intake of our silages. In the same way, the digestive capacity of the animals, their ability to reduce particles, the rate of digestion of the silages and their flow out of the rumen do not limit intake. The observation of the feeding activities of sheep indicates a strong action of the fermentation products leading to rapid satiety. This behavioral approach is very original and must be used in a more systematic way in the future to obtain a better understanding of the mechanisms modifying intake of the conserved forages.

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