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# Effect of severe underfeeding on digestion in sheep

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**SUMMARY** – The effects of severe underfeeding on digestion were analysed in sheep in 2 trials carried out in France (trial 1) and in Tunisia (trial 2). Trial 1 was a replicated Latin square design with 6 wethers receiving a natural grassland hay at 3 intake levels: 100, 60 and 20% of energy maintenance requirements. Trial 2 was carried out on 4 dry ewes receiving a vetch and oat hay for 10 weeks at 100% of energy requirements, then 12 weeks at 20% of these requirements, then 4 weeks at the initial level. Five periods of measurements were reported, at the end of each period at 100% of requirements, and after 4, 8 and 12 weeks of underfeeding. In trial 1, neutral detergent fibre (NDF) digestibility was higher at 20% than at 60 and 100% of maintenance requirements (66.0, 60.8 and 59.4%, respectively). The same trend was observed for NDF retention time in the rumen whereas *in situ* degradability and activity of fibrolytic enzymes were not modified by intake. In trial 2, underfeeding resulted in a large decrease in NDF digestibility with means of 49.5 and 61.5% for low and high level, respectively, despite a very long retention time of particles in the rumen. It was not explained by variations in *in situ* degradability, which was not sensitive enough to indicate differences in microbial activity. These trials show potential differences in response to a same decrease in intake. The causes of the drop in digestibility at low intake in trial 2 remain to be explained.

**Key words:** Digestibility, sheep, underfeeding, rumen, retention time, microbial activity.

**RESUME** – "Effet de la sous-nutrition sévère sur la digestion chez le mouton". Afin d'analyser l'effet d'une forte sous-alimentation sur la digestion, deux essais ont été menés sur des moutons, l'un en France (essai 1) et l'autre en Tunisie (essai 2). L'essai 1 était un double carré latin 3 × 3 sur 6 moutons recevant un foin de prairie naturelle à trois niveaux d'ingestion correspondant aux besoins énergétiques d'entretien, à 60 et à 20% de ces besoins. L'essai 2 était mené sur 4 brebis tarées recevant un foin de vesce-avoine pendant 10 semaines au niveau énergétique d'entretien, puis pendant 12 semaines à 20% de ces besoins, puis pendant 4 semaines au premier niveau. Cinq périodes de mesure ont été effectuées, en fin de chaque période au niveau de l'entretien, et après 4, 8 et 12 semaines de sous-alimentation. Dans l'essai 1, la digestibilité du fibre neutre détergente (NDF) a été plus élevée à 20% qu'à 60 et 100% des besoins (66,0, 60,8 et 59,4%), le temps de rétention du NDF dans le rumen avait la même tendance. La dégradabilité du foin *in situ* et les activités des enzymes cellulolytiques n'ont pas été modifiées par le niveau d'ingestion. Dans l'essai 2, la sous-alimentation s'est traduite par une très forte chute de digestibilité (49,5 et 61,5% pour le NDF en moyenne aux niveaux bas et haut), malgré un temps de rétention des particules dans le rumen très prolongé, mais sans modification de la dégradabilité *in situ*, insuffisamment sensible pour mettre en évidence une variation d'activité microbienne. Ces deux essais montrent des différences potentielles de réponse à une sous-alimentation d'amplitude comparable. La forte chute de digestibilité à bas niveau d'ingestion dans l'essai 2 reste à expliquer.

**Mots-clés :** Digestibilité, mouton, sous-alimentation, rumen, temps de séjour, activité microbienne.

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## Introduction

In ruminants, a negative effect of level of intake on digestibility is generally observed (Chilliard *et al.*, 1995). For a given diet, when intake increases, the retention time of particles in the rumen decreases whereas the activity of rumen microbes is not modified, so that ruminal digestion is impaired. However, most experiments have been carried out at levels of intake higher than maintenance requirements. In the limited number of experiments examining levels lower than maintenance, the relationship between intake and digestibility was unclear. A decrease in intake to half maintenance level in different experiments has resulted in an increase, no variation or a decrease in digestibility (Doreau *et al.*, 2000). This variability of the response of digestion to underfeeding may be a consequence of the absence of effect of particle retention time in the rumen on digestion, and/or

of modifications of microbial ecosystem activity. Most data obtained on sheep only concern digestibility. Most trials in which underfeeding involved a decrease in intake have been obtained in cattle. In order to determine the effect of very extreme underfeeding on digestibility and digestive processes in sheep, two experiments were carried out, one in France and the second in Tunisia.

## Material and methods

### Experimental designs

#### *Trial 1 (France)*

Six Texel wethers (mean weight 70 kg) fitted with ruminal cannulae were used in a replicated 3 × 3 Latin square design. They received the same hay of natural grassland at three levels of intake corresponding to 100, 60 and 20% of energy maintenance (M) requirements. The hay contained, on dry matter (DM) basis, 8.8% crude protein (CP) and 67.5% neutral detergent fibre (NDF). Animals were fed in two equal meals, at 09:00 h and 16:00 h. Each period lasted 6 weeks.

#### *Trial 2 (Tunisia)*

Four Barbary ewes (mean weight 40 kg) fitted with ruminal cannulae were used. They received a vetch and oat hay at energy maintenance requirements (M) for 10 weeks, then at 20% of these requirements (L) for 12 weeks, then at M for a further 4 weeks. The hay contained, on DM basis, 7.5% CP and 80.9% NDF. Animals were fed once daily, at 08:00 h. Digestion measurements were made for 7 days at the end of each sequence at M level, and in the 4th, 8th and 12th weeks at L level.

### Measurements and analyses

#### *Trial 1 (France)*

Digestibility was measured by total collection of faeces for 6 days. Hay degradation rate was measured *in situ* by incubations in bags for 3, 6, 12, 15, 48 and 72 h and theoretical degradability (TD) was calculated assuming a 4%/h passage rate. The same passage rate was taken for the 2 intake levels, so that TD represents the intrinsic potential of degradation by rumen microbes, independently of variations in passage rate. Ruminal liquid dilution rate was measured using Cr-EDTA as marker; eight rumen liquid samples were then taken between 2 and 26 h after dosing. Ruminal liquid was collected on two successive days at 09:00 and 11:00 h for protozoa counting. Microorganisms adherent to particles were extracted by differential centrifugations on rumen contents sampled at 09:00 and 11:00 h. Their fibrolytic activities were then determined (Martin *et al.*, 1993). Another bacterial sample and a sample of solid phase were analysed for purine and pyrimidine bases in order to estimate the pool of bacterial DM. An estimation of NDF rumen retention time (RRT) was made from the ratio between ruminal pool size and flux of 120-h indigestible NDF (Knowlton *et al.*, 1996). At the end of each period, the rumen was manually emptied, and solid and water contents were determined. Statistical analysis was performed by analysis of variance followed by t-tests.

#### *Trial 2 (Tunisia)*

Digestibility was measured by total collection of faeces for 7 days. Hay degradation rate was measured *in situ* by incubations in bags for 3, 6, 12, 24, 48 and 96 h; TD was calculated assuming a 2%/h passage rate. Ruminal liquid dilution rate was measured using polyethylene glycol as marker; eleven rumen liquid samples were then taken between 1 and 31 h after dosing. Ruminal fluid was collected on two successive days at 08:00, 10:00, 13:00 and 16:00 h for protozoa counting. Chromium-mordanted hay was used as particle marker. Eighteen rectal samples were taken between 2 and 169 h after dosing, for RRT determination. At the end of each period, the rumen was manually emptied, and solid and water contents were determined. Statistical analysis was performed by analysis of variance followed by orthogonal contrasts (low vs high intake, before vs after underfeeding), and linear and quadratic contrasts (variations during underfeeding).

## Results

In trial 1, DM digestibility did not vary with level of intake, but NDF digestibility was higher at 20% of M level than at the other 2 levels (Table 1). On the contrary, in trial 2, decreasing intake resulted in a large decrease in DM and NDF digestibility, this latter being higher after underfeeding than before (Table 2). Decrease in CP digestibility was especially important (56.7 vs 23.0%, on average).

Table 1. Effect of level of underfeeding on digestibility and ruminal digestion (trial 1)

Item	Intake level (% maintenance)			SEM
	100	60	20	
Dry matter intake (g/d)	1071	644	215	
Dry matter digestibility (%)	58.7 <sup>a</sup>	59.7 <sup>a</sup>	62.0 <sup>a</sup>	0.8
NDF digestibility (%)	59.4 <sup>a</sup>	60.8 <sup>a</sup>	66.0 <sup>b</sup>	0.8
NDF rumen retention time (h)	20.3 <sup>a</sup>	22.8 <sup>a</sup>	33.0 <sup>b</sup>	0.9
Rumen liquid dilution rate (%/h)	6.8 <sup>a</sup>	5.9 <sup>a</sup>	4.0 <sup>a</sup>	0.4
Rumen contents (kg)	11.35 <sup>a</sup>	8.92 <sup>b</sup>	6.95 <sup>c</sup>	0.29
Rumen dry matter (%)	9.62 <sup>a</sup>	9.00 <sup>a</sup>	5.81 <sup>b</sup>	0.24
<i>In situ</i> theoretical degradability (%)	58.4 <sup>a</sup>	55.2 <sup>a</sup>	56.5 <sup>a</sup>	1.5
Protozoa (10 <sup>3</sup> /ml)	76.7 <sup>a</sup>	72.2 <sup>a</sup>	34.1 <sup>b</sup>	5.9
Bacterial rumen pool size (g DM)	430 <sup>a</sup>	314 <sup>a</sup>	299 <sup>a</sup>	72

<sup>a,b,c</sup>Means on the same row with different superscripts differ (P < 0.05).

Table 2. Effect of underfeeding and refeeding on digestibility and ruminal digestion (trial 2)

Item <sup>†</sup>	Period					SEM	Contrast		
	M1	L1	L2	L3	M2		M/L	M1/M2	L1/L2/L3
DM intake (g/d)	776	180	178	178	828				
DM digestibility (%)	51.1	34.6	30.4	38.8	60.8	2.2	**	**	**q
NDF digestibility (%)	56.3	47.7	50.1	50.8	65.8	2.2	**	**	ns
Particle RRT (h)	55.2	178.8	82.5	134.7	52.7	20.1	**	ns	ns
Rumen LDR (%/h)	10.8	5.8	4.8	5.1	10.8	1.4	**	ns	ns
Rumen contents (kg)	5.80	4.58	2.85	3.93	5.57	0.52	**	ns	**q
Rumen DM (%)	10.18	6.29	6.00	5.93	7.66	0.49	**	**	ns
<i>In situ</i> TD (%)	51.3	50.2	48.9	50.1	49.3	1.0	ns	ns	ns
Protozoa (10 <sup>3</sup> /ml)	68.8	29.3	17.0	13.3	37.9	4.1	**	**	**l

<sup>†</sup>RRT = rumen retention time; LDR = liquid dilution rate; TD = theoretical degradability.

\*\*P < 0.01; ns = non significant (P > 0.05); l = linear contrast; q = quadratic contrast.

Decrease in intake in trial 1 resulted in an increase in RRT of NDF and a decrease in the proportion of DM in rumen contents between treatments 60 and 20% of M only. The decrease in rumen liquid dilution rate (LDR) with intake was not significant. In trial 2, decrease in intake significantly increased particle RRT, with particles remaining in the rumen for a mean of 135 h, decreased rumen LDR, total contents and proportion of DM. At maintenance, rumen DM proportion was lower after underfeeding than before. Total contents were the lowest after 8 weeks of underfeeding, then they increased.

In trial 1, *in situ* TD did not vary with intake. Neither polysaccharidase (xylanase, avicelase, carboxymethylcellulase) nor glycosidase activities ( $\beta$ -D xylosidase,  $\beta$ -D glucosidase) varied with intake. Protozoa concentration decreased between 60 and 20% of M requirements. Bacterial rumen

pool size did not vary with intake but bacterial DM per kg rumen DM was higher at 20% of M. In trial 2, *in situ* TD did not vary with intake. Protozoa concentration strongly decreased with intake, decreased throughout the underfeeding period and did not recover their initial value after refeeding.

## Discussion and conclusion

Severe underfeeding resulted in very different responses in the 2 trials. In trial 1, a trend to an increase in digestibility was observed, whereas trial 2 showed an impairment of digestion. This difference cannot be explained by animal species, climate or type of diet. Decreases in digestibility due to underfeeding have also been observed in cows, in tropical (Grimaud *et al.*, 1998, 1999) and temperate (Doreau *et al.*, unpublished data) climates, and in sheep fed a concentrate diet (Gingins *et al.*, 1980). All these decreases have been observed with diets containing barley, oats or rice straw, but it is not possible to relate the response to underfeeding to forage composition.

In trial 1, variations in digestibility between 100 and 60% as well as between 60 and 20% of M requirements are explained by modifications of particle RRT. In trial 2, on the contrary, a very long time of residence of feed particles in the rumen did not prevent a decrease in digestibility, probably because at maintenance level the RRT was long enough to optimise ruminal digestibility.

At intake levels lower than maintenance, RRT may not affect digestibility. Ruminal digestibility of a given diet depends on: (i) particle RRT; (ii) microbial activity; and (iii) accessibility of particles to microbes. This latter factor includes the total area of feed particles, i.e. the effect of mastication to reduce their size, and attachment of bacteria to particles. It has been shown that underfeeding does not modify ruminal or faecal particle size (Grimaud *et al.*, 1998), chewing activity, or soluble Ca, which is involved in the attachment of bacteria to particles (Grimaud *et al.*, 1999).

Thus variation in microbial activity is likely. In trial 2, *in situ* degradability was not, however, modified. In the same way, it was not modified in the trial of Grimaud *et al.* (1998), in which digestibility was impaired by underfeeding. This could be due to a limit of *in situ* method, which does not reproduce in the bag all phenomena occurring in the whole rumen (Michalet-Doreau and Nozière, 1999). Enzyme fibrolytic activity measurement is a more sensitive method, but in trial 1 as in a previous trial (Kabré *et al.*, 1994), digestibility was not reduced by underfeeding, so these measurements are not conclusive. It can be regretted that enzyme activities were not measured in trial 2. On the other hand, the present trials have shown that bacterial biomass was not modified, and even increased per kg ruminal DM and that protozoa population, which decreased with underfeeding, was not modified per kg ruminal DM. The causes of any putative decrease in microbial activity during underfeeding, if it was proven to exist, remain thus to be found.

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