Original article

Comparative study of forestomach digestion in llamas and sheep

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Summary — To compare digestion in the forestomach of llamas and sheep, the animals were fed four different diets: hay alone (H), low in nitrogen; the same hay with soyabean meal (HS), with barley (HB) and with both soyabean meal and barley (HSB). The sheep intakes were restricted to obtain about the same intake level in the two species. On average, the digestibilities of DM, OM and NDF were significantly higher in llamas: respectively, + 2.7, 3.6 and 5.3 for the four diets. Added barley impaired hay digestion in the sheep, but very little in the llamas. The llamas retained nitrogen better than the sheep owing to very low urine losses. For hay alone, the retention time of digesta in the forestomach was higher in the llamas than in the sheep. In contrast, there was no difference between species for the other diets. The pH and ammonia levels were higher in llamas. In contrast, the SCFA levels were lower. In all cases the in-situ rate of digestion was greater in llamas. The low intake of llamas generally observed in the literature does not account for their better digestion. The stability of the two first compartment pH levels and an excellent cellulolytic activity are determining factors in the better digestion efficiency of plant cell walls in the llamas. However, higher NH_3 levels were observed in llamas, although the urinary N excretion was lower.

llama / sheep / hay / forestomach / digestion

Résumé — **Étude comparée de la digestion dans les pré-estomacs du lama et du mouton.** Pour comparer la digestion gastrique des lamas et des moutons quatre régimes ont été distribués : un foin pauvre en azote (H) ; le même foin avec du tourteau de soja (HS), de l'orge (HB), et du tourteau de soja et de l'orge (HSB). Les quantités ingérées par les moutons ont été limitées pour obtenir des niveaux d'ingestion comparables chez les deux espèces. En moyenne, les digestibilités de la MS, de la MO, et des parois (NDF) ont été significativement plus élevées chez les lamas : respectivement + 2,7, + 3,6 et + 5,3 pour les quatre régimes. L'apport d'orge a nettement perturbé la digestion du foin chez les moutons mais peu chez les lamas. Ces derniers ont eu une meilleure rétention azotée que les

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moutons, grâce à des pertes urinaires très faibles. Pour le foin seul, le temps de rétention dans les préestomacs a été plus élevé chez les lamas que les moutons ; il n'y a pas eu de différence entre les deux espèces pour les autres régimes. Le pH et les teneurs en NH_3 des contenus des deux premiers compartiments stomacaux ont été plus élevés chez les lamas. À l'inverse, les teneurs en AGV ont été plus faibles. Dans tous les cas, la vitesse de dégradation in situ du foin a été plus élevée chez les lamas. Le faible niveau d'ingestion volontaire des lamas généralement observé dans la littérature n'est donc ici pas la cause de leur digestion plus efficace. Une bonne stabilité du pH des préestomacs et une excellente activité cellulolytique sont en définitive des éléments déterminants pour expliquer une digestion plus efficace des parois végétales chez les lamas par rapport aux moutons. Une plus forte concentration en NH_3 a toutefois été notée dans les préestomacs des lamas, bien que l'excrétion d'azote urinaire ait été plus faible chez ces mêmes animaux.

lama / mouton / foin / préestomacs / digestion

INTRODUCTION

Llamas are known to digest plant cell walls more efficiently than sheep (Jouany et al, 1995; Lemosquet et al, 1996). This efficiency is apparently due to both a higher ruminal digestion rate (Kayouli et al, 1993; Dardillat et al, 1994), and a lower digestive outflow rate (Dulphy et al, 1994; Lemosquet et al, 1996). The microbial flora in llamas may also be more efficient due to the excellent stability of the physical and chemical conditions in the forestomachs and the greater nitrogen-recycling aptitude of llamas (Lemosquet et al, 1996). The slower flow may be accounted for by the almost entirely nocturnal rumination of llamas (Dulphy et al, 1997), and by a generally lower intake level than that found in sheep.

The purpose of this trial was to measure the respective impacts of two factors that might be implicated in the digestive superiority of llamas over sheep, namely i) their lower intake, which may increase the retention time of food in the forestomach, and ii) their higher ammoniacal nitrogen levels in the contents of this forestomach. Intake in sheep was restricted to make it comparable to that in llamas, and the nitrogen levels in the feed were adjusted to vary the nitrogen supply to the rumen microorganisms. In addition, to amplify the differences between the two species, an energy-rich concentrated feed was used (Dulphy et al, 1994; Lemosquet et al, 1996).

MATERIALS AND METHODS

Animals

Four llamas and four sheep were used, all fitted with rumen cannulas for manual emptying of the forestomach (forestomach refers to the reticulorumen for sheep, and compartments 1 and 2 for llamas), and introduction of nylon bags. All the animals were castrated males weighing 118 ($\pm$ 4) and 72 ($\pm$ 3) kg for the llamas and sheep, respectively.

Feeds and diets

A single forage was used, a tall fescue crop hay, harvested late, and low in nitrogen. Four diets were offered:

  hay alone (H);
  hay + 11.5% soyabean meal (HS) (hay supplemented to have 12% crude protein in the diet);
  hay (70%) + barley (30%) (HB);
  hay (60%) + soyabean meal (10%) + barley (30%) (HSB).

  The hay was chopped to 3–4 cm in length and fed once a day at 0900 hours. The concentrates were given 30 min beforehand. The chemical characteristics of the three feeds used are presented in table I.

Table I. Characteristics of feeds used (g/kg DM).

	Hay (H)	Soyabean meal	Barley (B)
Ashes[a]	89	60	34
Crude protein[b]	68	520	110
NDF[c]	667	142	177
AD lignin[c]	50	3	8

[a] After 6 h at 550 °C; [b] by Kjeldahl method; [c] by Goering and Van Soest method (1970).

Experimental design

The four diets were fed over four successive experimental periods, to both the llamas and the sheep simultaneously.

Before the trial, the hay had been fed ad libitum to all the animals. During this pretrial period, the llamas ingested 14.7 and the sheep 21.8 g DM/kg LW. During the trial, this hay was offered at 16 g DM/kg LW to both the sheep and the llamas, ie, 10% more than the lowest intake, to obtain ad libitum feeding in the llamas and restricted intake in the sheep. Each experimental period included 2 weeks adaptation to the diet, and then 4 weeks of measurements. The animals were grouped by species in two naturally lit, temperature-controlled rooms (18 °C) (the trial took place from November 1995 to April 1996).

Measurements

Refusals were weighed daily to calculate the exact DM intake of the animals. At the end of week 2 the animals were placed in digestibility crates. During week 3, feces and urine were collected and sampled daily for 5 days to calculate retained nitrogen values and digestibility of the offered feed for each animal.

During week 4, in-situ degradation was measured by means of nylon bags (mesh 50 microns) placed in the first digestive compartment of each animal and withdrawn after 2, 4, 8, 16, 24, 48 and 72 h (two bags per time). These bags contained the hay fed to the animals, ground and screened to 0.8 mm.

During week 5, for 2 whole days, forestomach juice was sampled at 0900, 1100, 1300, 1500, 1700, 2100 and 2400 hours, and then at 0500 and 0900 hours the following day to obtain the pH, ammonia and short chain fatty acid (SCFA) time course kinetics.

Finally, during week 6, the forestomach contents were manually removed twice from each animal, weighed, and returned after adding a boiling solution to bring them back to body temperature. These operations were made once before feeding, at about 0830 hours, and once afterwards, at about 1530 hours. The two removals were made more than 48 h apart. Values of pH, ammoniacal nitrogen, DM (48 h at 80 °C) and plant cell wall contents (Goering and Van Soest, 1970) were measured. These measurements made it possible to calculate the DM, NDF and AD lignin retention times, by comparing the forestomach contents with the intake values.

The solution used to warm the forestomach contents contained chromium EDTA to measure the water turnover rate, and therefore the retention time of water in the rumen. The concentration of chromium in the rumen juice was measured after 2, 4, 6, 11 and 24 h for the morning operation, and after 5, 18 and 21 h for the afternoon one.

These measurement and analysis methods have already been described by Lemosquet et al (1996).

Statistical analysis

The average results for each species (with their standard deviations), together with the effects of intra-species treatments and individual effects, were compared using SAS software (1985). The species effect was tested using the intra-species

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Table II. DM intake of diets and hay.

Diets	Llamas						Sheep						Effect of species
	H	HS	HB	HSB	Mean	SD	H	HS	HB	HSB	Mean	SD	
Live weight kg	116[a]	116[a]	118[a]	122[b]	118	4.5	72[a]	72[a]	72[a]	72[a]	72	1.5	$P < 0.01$
DM intake g/day													
hay	1669[a]	1646[a]	1412[b]	1330[b]	1514	126	1148[a]	1160[a]	1122[a]	1068[a]	1125	58	$P < 0.01$
soyabean meal	0	282	0	218	—	—	0	189	0	157	—	—	—
barley	0	0	641	605	—	—	0	0	490	441	—	—	—
g/kg LW													
hay	14.5[a]	14.2[a]	12.1[b]	10.9[b]	12.9	0.98	15.9[a]	16.1[a]	15.5[a]	14.9[a]	15.6	0.86	$P < 0.01$
g/kg LW$^{0.75}$													
hay	47.4[a]	46.6[a]	39.7[b]	36.2[b]	42.5	3.2	46.3[a]	46.9[a]	45.2[a]	43.4[a]	45.5	2.4	$P < 0.01$
NDF intake g/day	1131	1130	1044	1028	—	—	779	795	826	815	—	—	—
Proportion of CP in ingested DM (g/kgMS)	68	134	81	126	—	—	68	131	81	122	—	—	—

NB: Data with the same letter are not different for the same species, on the same line (idem for all tables). For all the tables: H = hay alone; HS = hay + soyabean meal; HB = hay + barley; HSB = hay + soyabean meal + barley.

residual standard deviation. A total of 32 observations were used in most cases.

RESULTS

Intake of hay (table II)

The hay intake of the llamas, expressed per kg liveweight, was lower than that of the sheep (–9% for H; –12% for HS; –22% for HB; –27% for HSB).

The added soyabean meal did not cause a decrease in intake between H and HS. In contrast, there was a non-significant decrease in hay intake between HB and HSB (–0.38 g/g for the llamas and –0.34 for the sheep).

The added barley produced a significant decrease in the hay intake in the llamas (–0.40 and –0.52 g/g) but not in the sheep (–0.05 and –0.18 g/g). This was probably because the llamas were fed ad libitum, whereas the sheep were restricted.

Digestibilities (table III)

On average, the digestibilities of DM, OM and NDF were significantly higher in the llamas than in the sheep (respectively, + 2.7, + 3.6 and + 5.3 points for the four diets). This was also the case for the digestibility of hay alone (+ 3.8 points) and for the digestibilities of the hay fed with added barley (+ 5.8 points). These digestibilities were estimated assuming the digestibility of the concentrate to be equal to the values published in the Inra tables (1989), for both species.

The addition of soyabean meal alone had a non-significant negative effect (–2.5 points) on OM digestibility of hay in the llamas, and practically no effect in the sheep. Effects on cell wall digestibility were never significant.

The addition of barley alone had a non-significant negative effect in the llamas on OM digestibility of hay (–3.0 points) and cell walls (–3.4 points). This effect was greater and significant in the sheep (respectively, –5.5 and –5.9 points).

Finally, the effect of adding both soyabean meal and barley was comparable in the llamas to that of adding each of the concentrates alone (–4.2 points for hay OM, significant, but –2.1 points for cell walls, non-significant). In the sheep the effect of adding the mixture of concentrates was also comparable to that of adding each concentrate separately (–4.8 points for hay OM, significant, but –1.1 points for cell walls, non-significant).

The quantities of undigestible crude protein per kg of hay or ingested feed were higher in the llamas (+ 3 g/kg ingested DM).

Nitrogen retention (table III)

However, the retained nitrogen was expressed (% of ingested N, or g per kg LW), the llamas retained significantly more nitrogen than the sheep. This higher retention was mostly due to a lower loss in urine.

The added soyabean meal appreciably increased nitrogen retention except, unexpectedly, for the sheep given barley, in which the added soyabean meal had no significant effect.

On average, the added barley had almost no effect on either the sheep or the llamas. However, it showed a tendency to increase the amount of nitrogen retained when added without soyabean meal and decrease it with soyabean meal, in both species.

Forestomach contents and retention times (table IV)

The quantities of fresh matter present in the morning in the forestomach (two first com-

Table III. Digestibility of diets and hay, undigestible crude protein (UNCP) and N balance.

Diets	Llamas						Sheep						Effect of species
	H	HS	HB	HSB	Mean	SD	H	HS	HB	HSB	Mean	SD	
Diet digestibility (%)													
DM	53.6^a	56.3^b	61.1^c	62.8^c	58.5	1.5	50.8^a	55.4^b	56.8^b	60.3^c	55.8	2.1	$P < 0.01$
OM	56.3^a	59.2^b	64.0^c	65.7^c	61.3	1.4	52.5^a	57.5^b	58.6^b	62.3^c	57.7	2.1	$P < 0.01$
NDF	52.0^a	49.5^a	48.6^a	49.9^a	50.0	2.3	46.5^a	46.4^a	40.6^b	45.4^{ab}	44.7	3.3	$P < 0.01$
Hay digestibility (%)													
OM	56.3^a	53.8^{ab}	53.3^{ab}	52.1^b	53.9	2.1	52.5^a	52.0^{ab}	46.0^b	47.7^b	49.5	2.8	$P < 0.01$
UNCP (g/kg DMI)													
Diet	39^a	44^b	43^b	48^c	44	1.6	37^a	40^b	41^b	46^c	41	1.8	$P < 0.01$
Hay	39^a	43^b	47^c	55^d	46	2.1	37^a	38^a	45^b	51^c	43	2.8	$P < 0.01$
N balance (g/day)													
N ingested	18.1^a	42.5^b	26.3^c	42.8^b	32.4	2.8	12.7^a	29.2^b	20.5^c	32.1^d	23.6	1.5	$P < 0.01$
N in feces	10.5^a	13.6^b	14.1^b	16.7^c	13.7	1.3	6.8^a	8.6^b	10.7^c	12.6^d	9.7	0.9	$P < 0.01$
N in urine	4.4^a	11.7^b	5.5^a	11.1^b	8.2	1.9	5.9^a	15.8^b	7.7^c	16.5^d	11.5	0.7	$P = 0.02$
N retained	3.2^a	17.2^b	6.7^a	15.0^b	10.5	2.5	0.0^a	4.8^c	2.1^b	3.0^d	2.5	0.7	$P < 0.01$
% ingested	18	40	25	35			0	16	10	9			

Table IV. Contents of forestomachs, their characteristics (DM, NDF, ADL) and retention times.

Diets	Llamas						Sheep						Effect of species
	H	HS	HB	HSB	Mean	SD	H	HS	HB	HSB	Mean	SD	
Total fresh content g/kg LW													
8 h	157[a]	132[b]	141[b]	107[c]	134	9	135[a]	124[a]	128[a]	137[a]	131	19	NS
15 h	194[a]	175[a]	141[b]	115[b]	156	17	184[a]	184[a]	171[ab]	152[b]	172	13	$P < 0.01$
DM content of digesta g/kg													
8 h	110[a]	105[a]	103[a]	98[a]	104	7	112[a]	123[ab]	120[ab]	125[b]	120	7	$P = 0.01$
15 h	130[a]	130[a]	135[b]	135[b]	133	3	138[a]	138[a]	140[a]	142[a]	140	8	$P = 0.03$
NDF g /kg DM													
8 h	738[a]	682[b]	694[c]	714[d]	707	7.6	749[a]	685[b]	730[a]	730[a]	724	16.2	$P < 0.05$
15 h	733[a]	704[b]	667[c]	609[d]	678	10.8	735[a]	699[b]	699[b]	664[c]	699	13.5	$P = 0.01$
ADL g/kg DM													
8 h	99[a]	71[b]	78[b]	89[c]	84	5.4	94[a]	74[b]	75[b]	78[b]	80	7.6	NS
15 h	84[a]	67[b]	62[c]	52[d]	66	2.6	75[a]	71[a]	61[b]	55[b]	65	5.3	NS
Retention times (h) in forestomach													
DM	36.9[a]	26.4[b]	23.0[bc]	19.0[c]	26.3	2.7	29.4[a]	26.6[a]	21.3[b]	20.8[b]	24.5	3.1	NS
NDF	40.0[a]	31.3[b]	30.7[b]	26.8[b]	32.2	3.0	32.1[a]	31.4[a]	29.7[a]	30.0[a]	30.8	3.9	NS
ADL	67.8[a]	45.6[b]	38.2[b]	40.7[b]	48.1	5.6	50.4[a]	48.6[a]	33.6[b]	40.9[ab]	43.4	8.9	NS
Water	15.5[a]	12.4[b]	11.3[b]	10.2[b]	12.4	1.4	16.4[a]	16.5[a]	11.4[b]	12.8[b]	14.3	1.2	$P = 0.03$

partments) of the animals and expressed per unit of liveweight were on average 11% higher in the llamas for diets H, HS and HB, but appreciably lower for diet HSB (–22%). In the afternoon these contents were on average 15% lower in the llamas for H, HB and HSB, but 5% higher for H. Added soyabean meal or barley thus reduced these contents in the llamas. This decrease was linked to a reduced hay intake, but this was not observed in the sheep except in the afternoon with the barley-supplemented diet.

The retention times of DM, cell walls (NDF) and lignin (ADL) in the forestomach were greater in the llamas, but only for hay alone. For diets HS, HB and HSB these retention times were similar in the two species. Added soyabean meal produced an appreciable decrease in the retention time of DM and cell walls in the llamas (–7.2 and –6.3 h), but had almost no effect on the sheep (–1.6 and –0.2 h). Added barley also caused an appreciable decrease in the llamas (–10.6 and –6.9 h, respectively, for DM and cell walls), and a decrease for DM in the sheep (–7 h).

Finally, the water retention time in the reticulo-rumen was significantly shorter in the llamas (–2 h). In these animals, soyabean meal and barley caused a reduction in the liquid retention time compared with hay alone. In the sheep, only the added barley had this effect.

Characteristics of forestomach contents

When emptying (table IV)

The DM values, in terms of the proportion of fresh material, for the forestomach contents before feeding were similar in the two species fed hay alone. In contrast, for all the other diets, and after feeding on hay alone, DM values were higher in the sheep. Added soyabean meal or barley lowered the DM

content in the llamas, but raised it in the sheep.

NDF values, in proportion to dry matter, were higher in the sheep (+ 17 g/kg in the morning and + 21 g/kg in the evening). In contrast, lignin values were the same for the two species. Overall, the added concentrate reduced the amount of cell wall and lignin in the forestomach contents.

In kinetic studies (table V)

pH (fig 1)

The time course of the pH during the day always displayed a decrease after feeding, followed by a subsequent increase.

Overall, the pH in the llamas was significantly greater than in the sheep (+ 0.37 points). The difference varied but it was systematic. Only the differences for diet H were non-significant (+ 0.14 points). With added concentrate, the differences reached + 0.46 points.

The added concentrate had little effect on the llamas, and only diet HSB produced a slightly lower pH than the others. Conversely, the effect was more pronounced in the sheep, especially between 1300 and 1500 hours and for the barley-supplemeted diets.

A slight difference was observed between the pH of contents sampled on emptying (total mixed contents) and in the kinetic studies (in-situ bag samples); + 0.15 points for the total mixed contents in the llamas and + 0.10 points in the sheep.

Ammonia (fig 2)

On average, there was more ammonia nitrogen in the forestomach contents of the llamas than in the sheep: + 35 mg/L for diets H and HB, which were nitrogen-deficient, and + 20 mg/L for diets HS and HSB. The difference was especially marked for the night samples (2400, 0500, 0900 hours). For the day samples (1300 to 2100 hours) the inter-species differences were non-significant.

Table V. Characteristics of contents in the forestomach (means calculated from kinetics values).

Diets	Llamas						Sheep						Effect of species
	H	HS	HB	HSB	Mean	SD	H	HS	HB	HSB	Mean	SD	
pH	6.83^{ab}	6.87^{ab}	6.88^{a}	6.67^{b}	6.81	0.12	6.69^{a}	6.49^{b}	6.38^{bc}	6.19^{c}	6.44	0.12	$P < 0.01$
N-NH$_3$ mg/L	64^{a}	154^{b}	76^{a}	167^{b}	115	16	35^{a}	138^{b}	35^{a}	142^{b}	88	15	$P < 0.01$
SCFA mmol/L	61^{a}	61^{a}	67^{a}	86^{b}	69	11	67^{a}	72^{ab}	78^{bc}	86^{c}	76	9	NS
Acid - % SCFA													
acetic	71^{a}	66^{b}	65^{b}	63^{c}	66	2.0	69^{a}	68^{a}	63^{b}	64^{b}	66	1.5	NS
propionic	19.2^{a}	19.7^{a}	21.6^{b}	19.9^{a}	20.1	1.7	20.8^{a}	19.8^{a}	23.8^{b}	18.7^{c}	20.8	1.2	NS
butyric	6.6^{a}	8.4^{b}	9.3^{b}	11.5^{c}	9.0	0.9	7.7^{a}	8.4^{a}	10.3^{b}	12.4^{c}	9.7	1.1	$P < 0.05$

Table VI. Characteristics of the kinetics of hay degradation in situ (DM) g/kg.

Diets	Llamas						Sheep						Effect of species
	H	HS	HB	HSB	Mean	SD	H	HS	HB	HSB	Mean	SD	
DM degraded													
0 h	379	379	379	379	—	—	379	379	379	379	—	—	—
16 h	472^{a}	505^{b}	495^{ab}	515^{b}	497	17	468^{a}	464^{a}	457^{a}	455^{a}	461	11	$P < 0.01$
24 h	579^{a}	570^{ab}	542^{bc}	555^{ab}	561	21	531^{a}	544^{a}	477^{b}	481^{b}	508	20	$P < 0.01$
48 h	695^{a}	664^{b}	678^{ab}	670^{ab}	677	18	653^{a}	664^{a}	585^{b}	582^{b}	621	31	$P < 0.01$
72 h	744^{a}	739^{a}	742^{a}	741^{a}	742	13	718^{a}	724^{a}	660^{b}	658^{b}	690	29	$P = 0.01$
a*	33.9	34.1	32.1	32.3	33.1	—	36.4	35.9	34.6	35.4	35.6	—	—
b*	49.9	45.0	53.0	47.1	48.8	—	53.1	51.8	51.7	48.5	51.3	—	—
c* × 100	2.44	2.89	2.24	2.92	2.62	—	1.56	1.75	1.29	1.33	1.48	—	—

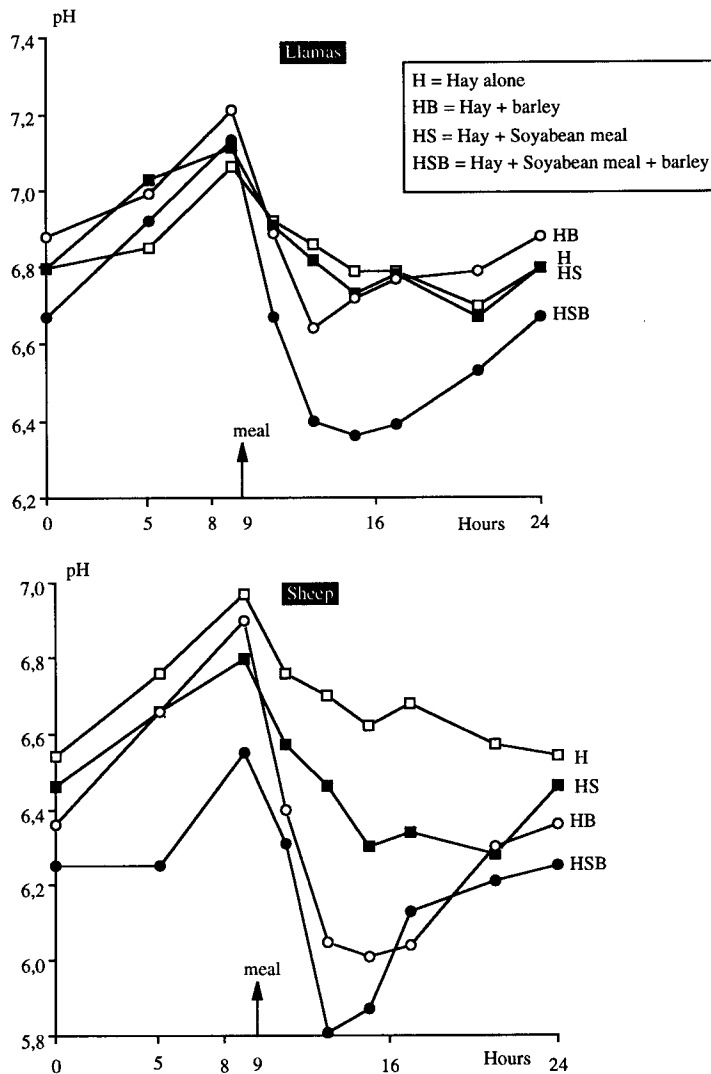* Parameters of the curve $y = a + b(1 - e^{-ct})$

Fig 1. Evolution of pH in the forestomach juice during the day.

The added soyabean meal had a marked effect in both species (+ 105 mg/L in the llamas and + 90 in the sheep). Conversely, the barley had almost no effect.

The differences between the concentrations in the total contents obtained by emptying and the sample of in-situ bag content were small: −9 mg/L for the total mixed contents in the llamas, but no difference in the sheep.

Finally, minimum values were low, especially in the sheep, during a long period with diet H, which was poor in nitrogen.
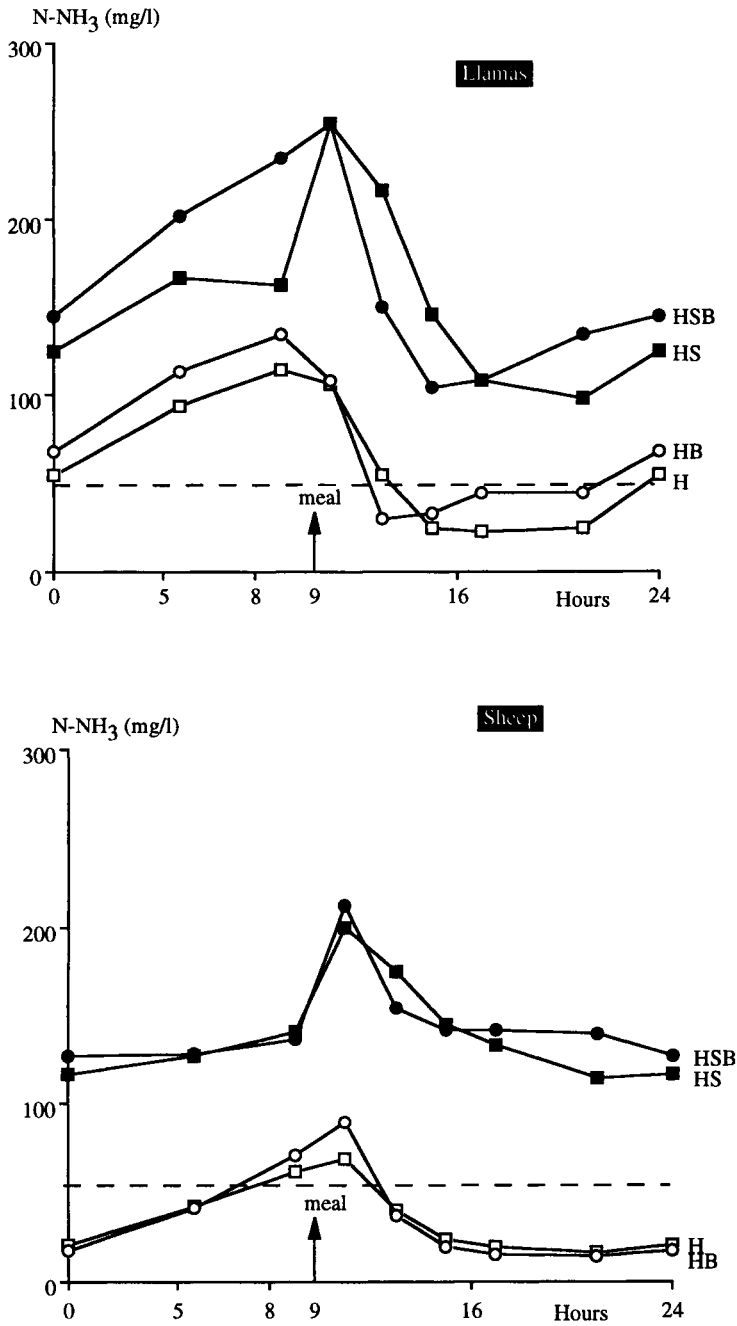
Fig 2. Evolution of N-NH3 level in forestomach juice during the day.

Short chain fatty acids (fig 3)

The SCFA contents of the forestomach contents were 9% lower in the llamas than in the sheep, but the average difference was non-significant, except at certain times and for certain diets: at 1500 and 2400 hours for diets HS and HB.

The proportion of acetic acid was not different on average between the two species. There was a higher proportion in the llamas without soyabean meal (+ 1.9) and a lower proportion in the llamas with soyabean meal (−1.7). The effect of soyabean meal was nil in the sheep and positive (+ 3.8) in the llamas. The effect of barley was always negative (−4.6 in the llamas, −5.2 in the sheep).

Likewise, the proportion of propionic acid was not significantly different between the llamas and the sheep. Without soyabean meal, the proportion was slightly lower in the llamas (−0.9). Added barley without soyabean meal raised the proportion of propionic acid in both species.

The proportion of butyric acid was almost systematically significantly lower (−0.7, ie, −8%) in the llamas. Added soyabean meal and barley increased the proportion of this acid in both species. The effects of the concentrates were additive in diet HSB.

Degradation rate in the rumen (table VI, fig 4)

The degradation of milled hay in bags to evaluate the cellulolytic activity of the forestomach contents was significantly higher in the llamas than sheep. The differences in degradation rates were as follows: + 3.6% at 16 h, + 5.3% at 24 h, + 5.6% at 48 h, + 5.2% at 72 h. The difference obtained at 24 h then persisted thereafter.

Added soyabean meal had only a weak effect. Added barley only slightly diminished hay degradation in the llamas, between 4 and 48 h, whereas it had a strongly marked negative effect in the sheep. Consequently, the differences in favour of the llamas, which occurred with diet H and tended to diminish with diet HS, widened appreciably with added barley.

DISCUSSION

The initial objective to equalize the intakes of the llamas and sheep was not fully reached. By appreciably restricting the intake of the sheep, the difference in the prestudy ad libitum intakes was strongly reduced, however. Even so, the digestiblity of the hay remained appreciably greater in the llamas, consistent with results obtained previously (Dulphy et al, 1998). In addition, the llamas minimized the negative effect of barley on the forage digestibility as has been shown before (Dulphy et al, 1994; Lemosquet et al, 1996). Added soyabean meal had almost no effect.

A slight advantage for llamas would be due to differences in selection of more digestible particles during ingestion. However, Lemosquet et al (1996) did not observe such a selection in favour of llamas and in the trials of Dulphy et al (1997) only the straw was concerned. Elsewhere for diets H and HS, the proportion of refusals were low: 6% for sheep, 8% for llamas.

The llamas displayed a higher nitrogen retention level than the sheep, also consistent with the results of Engelhardt and Schneider (1977) and Lemosquet et al (1996). This observation and the fact that their maintenance requirement of energy is lower in comparison with sheep (Engelhardt and Schneider, 1977; Vernet et al, 1997) probably explain why their weight increased (about + 1 kg per month), unlike the sheep whose weight remained stable. Elsewhere our results indicate that llamas are able to recycle ammonia nitrogen in the forestomach more efficiently during the night and the morning. The main cause of this good
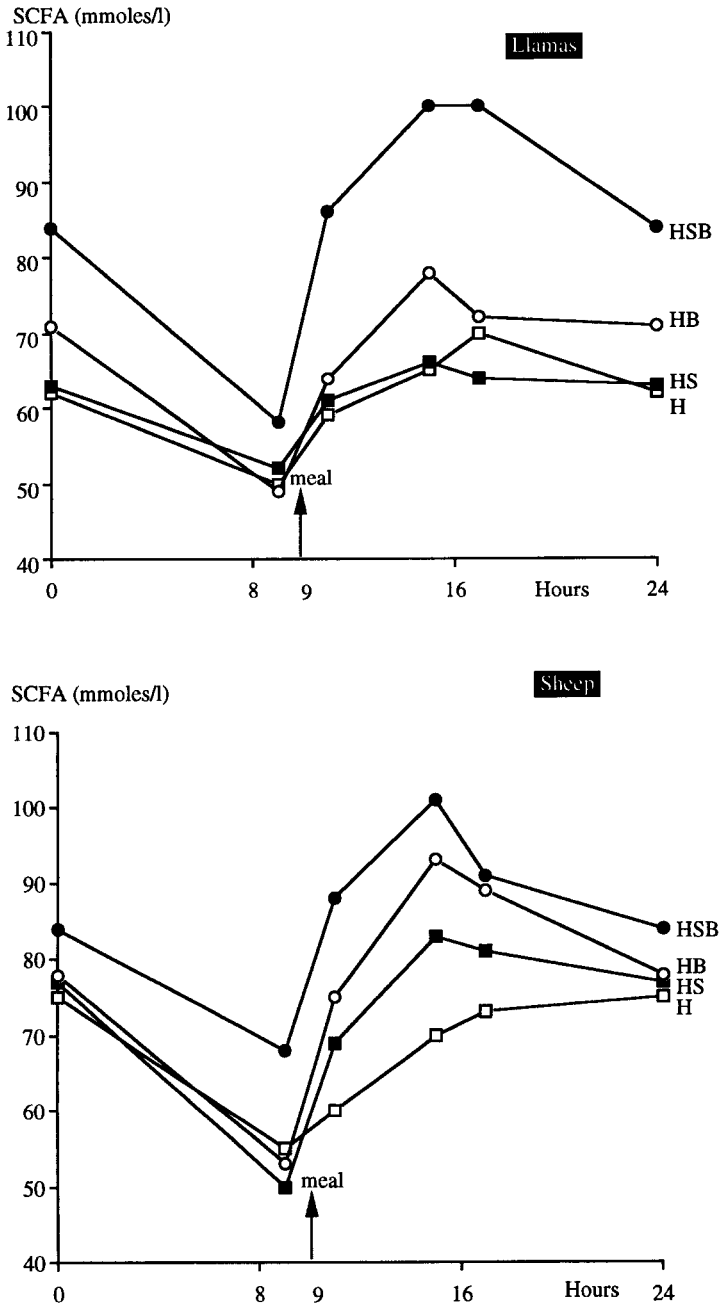
Fig 3. Evolution of SCFA level in forestomach juice during the day.

nitrogen retention is a low loss in urine, which is a characteristic of camelids (Engelhardt and Höller, 1982). This is an interesting feature, but could be a hazard if the feed is too rich in nitrogen, especially soluble nitrogen (Kayouli et al, 1993).
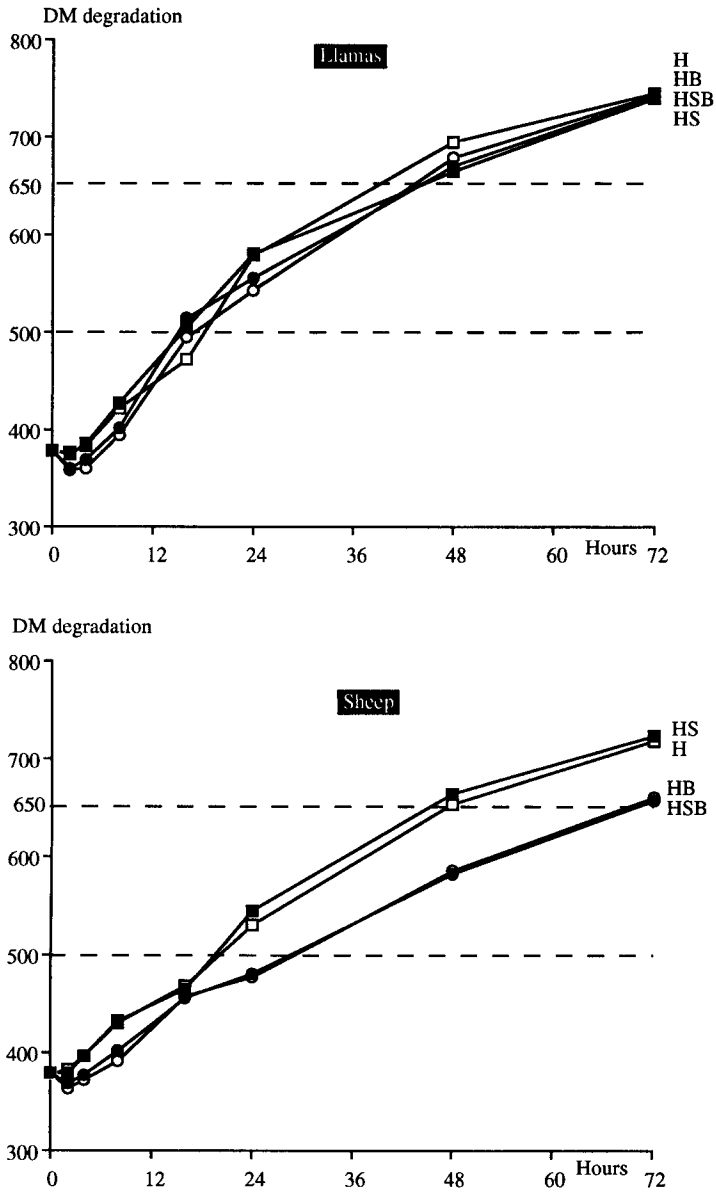

Fig 4. Evolution of in-situ degradation of ground hay over 3 days (g/kg).

The quantities of forestomach contents were comparable, for the basic hay-only diet, to the quantities found by Dulphy et al (1994). The addition of concentrate also had a classical negative effect (Rémond et al, 1995) on these quantities. However, in contrast to the results of Dulphy et al (1994) and Lemosquet et al (1996) the retention times of dry matter in the forestomach were close in the two species. To be precise, this was so in the presence of added concentrate; with hay alone, the differences observed previously were found. In this case, the higher hay digestibility in the llamas can be ascribed to slower transit and higher cellulolytic activity. Conversely, the differences in digestibility of the three diets containing concentrate cannot apparently be attributed to different retention times in the forestomach, and so are globally probably due to more favourable pregastric conditions in the llamas. Hay digestibility in the llamas was barely lowered by barley, but was markedly reduced in the sheep. In addition, with diet HSB the hay digestibility increased more in the llamas than in the sheep, despite a slightly lower residence time of the digesta in the forestomach.

For the DM content of the forestomach contents, there was almost no difference between species with hay alone, as reported by Dulphy et al (1994) and Lemosquet et al (1996). However, added concentrate caused an increase in this level in the sheep, especially in the morning, whereas the opposite effect was observed in the llamas. The different intakes in llamas and sheep may account for part of the differences observed. With diet HSB, the llamas ingested 9% less cell wall material than with diet H, whereas the sheep ingested 4.6% more. Even so, the differences were not sufficient to explain the 39% decrease in forestomach rumen DM in the llamas and the 12% increase in sheep, between diets H and HSB. This decrease in the forestomach filling rate in the llamas with diet HSB results essentially from a reduction of cell wall retention compared

with diet H. In sheep, the increase in transit rate with the diets containing concentrate was much smaller, about 6%.

Much higher pH values were systematically observed in the llamas, who were well able to dampen the effect of the added barley. This probably allowed a much higher cellulolytic activity. The presence of large amounts of ammonia during the night may also help maintain normal cellulolytic activity during the time when rumination is most active (Dulphy et al, 1997).

In the sheep supplemented with nitrogen, however, the marked increase in ruminal ammonia was accompanied by only a tiny increase in in-situ degradation, which remained well below that observed in the llamas. Ammonia alone is, therefore, not a limiting factor that would explain the lower digestibility of the cell walls in sheep.

Lower SCFA levels were found in the llamas than in the sheep, as already reported by Lemosquet et al (1996). This is probably linked to a more rapid absorption (Rübsamen and Engelhardt, 1978) and a higher water turnover, which would also mask the differences in forestomach ammonia that are higher for a given water turnover rate in llamas, confirming their greater capacity to recycle nitrogen.

The higher pH stability in llamas was well illustrated after feeding with diet HSB, which produced a SCFA level equal on average to that observed in sheep. The resultant pH was lowered by only 0.65 points; the presence of large amounts of buffering substances evidently prevents a further decrease. This buffer presence is related to a fast turnover of the liquid phase, which is not connected to a water intake different from that of the sheep (Lemosquet et al, 1996), but which corresponds to abundant gastric and salivary secretions known to be rich in bicarbonate (Rübsamen and Engelhardt, 1979). The high bicarbonate contents could explain the numerous bubbles observed in the sampling tube when llama forestomach

contents were mixed with the acid of the conservator.

In addition to the favourable characteristics of the forestomach contents, it is also probable that the higher water turnover rate in the llama forestomach helps to increase the cellulolytic activity, in particular through faster elimination of fermentation products and substances detrimental to microbial growth.

The fermentation pathways were similar in the two species, with a little more butyric acid being produced in the sheep, but fewer minor SCFAs. Jouany et al (1995) report a higher proportion of butyric acid in the forestomach of llamas.

The choice of diets and levels of intake gave retention times and levels of ammonia in the forestomach which were often identical in the llamas and sheep. This made it possible to measure the effect of these two factors on the digestive superiority of llamas. In the only case (hay alone) for which retention time was clearly increased (+ 50%), the digestibility of NDF was only increased by 5% (NS) in comparison with the diet hay + soyabean meal. The increase in the ammonia level following soyabean meal distribution has a variable effect on digestibility. These two factors then only partially explain the digestive superiority of llamas.

In-vivo digestibilities of hay and 24 h in-situ degradations were very similar, and above all very well related ($R = 0.956$ for eight pairs of results, llamas and sheep together). This confirmed that the observed differences between diets or between species were mainly related to microbial activity levels. The microbial activity levels depended on the stability of forestomach pH, especially when cereals are given to the animals.

In conclusion the greater digestive efficiency of llamas is explained by higher levels of microbial activity. These differences in activity levels seem to begin as early as the

beginning of the fermentation (Dardillat et al, 1994). Are they encouraged by better buffered forestomach contents? There may be other characteristics that are as yet undetermined. The greater digestive efficiency of llamas does not seem to be due to a low intake. Interestingly, this intake is not increased by cereal supplementation. Llamas regulate their intake to fit their metabolic requirements more closely than sheep.

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