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Microbial cell wall digestion in camelids

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SUMMARY - Digestion of cell walls is higher in camelids than in ruminants when animals are fed poor-roughage diets. The greatest differences between animals occur with the poorest diets. This could be due to differences in the microbial ecosystem between the two animal species. The only difference observed in forestomach microbes was that protozoa are B-type in camelids, while they are mainly A-type in ruminants. However, more experiments need to be carried out to confirm this observation. The higher cellulolytic activity in the forestomachs of camelids, is probably explained by the buffering capacity of digesta against acid conditions. pH remains stable even after the addition of cereals to the diet. In ruminants, the decrease in pH after feed intake results in a negative effect of starch on cellulose digestion. The mechanisms involved in this high buffering capacity are not yet known. However, the buffering capacity of digesta against alkaline conditions is very low. This means that camelids are very vulnerable to ammonia toxicity. The higher retention time of solid particles in the forestomachs also contributes to improve cell wall digestion by camelids, since the degradation of cellulose is a slow process.

Key words: Camelids, microbial digestion, cell wall degradation, ruminants.

RESUME - "Digestion microbienne des parois cellulaires chez les camélidés". La digestion des parois végétales est supérieure chez les camélidés, par rapport aux ruminants, lorsque les animaux reçoivent des régimes à base de fourrages de médiocre qualité. Les différences entre animaux sont d'autant plus importantes que les fourrages sont pauvres. Ce résultat peut s'expliquer par des différences au niveau de la composition de l'écosystème microbien. Nous avons montré que la population de protozoaires est de type B, alors qu'elle est fréquemment de type A chez les ruminants. Cette observation doit, toutefois, être confirmée sur un nombre plus important d'animaux. La plus grande activité cellulolytique peut, également, être due au pouvoir tampon supérieur des digesta en milieu acide. Le pH reste stable avec des régimes mixtes enrichis en céréales, ce qui limite les effets négatifs de l'amidon sur la cellulolyse qui est couramment observée chez les ruminants. Les mécanismes mis en jeu pour réguler le pH ne sont pas connus. En revanche, nous avons observé que le pouvoir tampon des digesta de camélidés est faible en milieu basique. Cela implique que les animaux soient sensibles aux intoxications par NH_3. Enfin, le temps de rétention des particules solides, qui est supérieur dans les préestomacs de camélidés, contribue vraisemblablement à accroître la digestion des parois végétales, qui est un processus lent.

Mots-clés : *Camélidés, digestion microbienne, parois cellular, dégradation, ruminantes.*

Introduction

All published reports on digestion in camelids, show that they have a particular ability to use low-quality forages from desert areas. Recent experiments, carried out on dromedaries in Tunisia and on llamas in France, have confirmed these findings. In this paper, we will discuss the results of studies made in France, Tunisia and Germany on differences in the environment of microbes in the forestomachs of camelids and ruminants and the subsequent changes in the microbial populations, in order to explain why cellulolytic activity in camelids is more efficient.

Comparative cell wall degradation in the forestomachs of camelids and ruminants

Kayouli *et al.* (1991) observed that dromedaries were able to digest low-quality roughages more efficiently than sheep (Fig. 1). With low-digestible wheat straw, the cellulolytic activity of microbes in camelids was 20% higher than that in ruminants. Kinetic studies showed that these differences in digestive ability do not appear until after a 24 h period in the main forestomach (Table 1). The rate of degradation was not significantly different between the animals.

The same experiments made with llamas and sheep in France showed that the degradation of wheat straw ADF was greater in llamas. The differences between the two animal species were greatest when they were fed a roughage diet supplemented with starch. This indicates, as will be discussed later, that camelids are able to limit the negative effect of starch on cellulose digestion.

The degradation of wheat straw placed in nylon bags and introduced into the main forestomach was greater in llamas than in sheep after 72 h of incubation. Subsequent cross-incubations between the animals showed that while the 72 h ingested residue from llamas remained practically unaltered after a further 48 h in the sheep rumen, the camelids, over the same period, were able to continue digesting comparable samples from the ruminants.

A similar study carried out on dromedaries, goats and sheep in Tunisia, showed that the greatest degradation of oat vesce hay occurred in dromedaries and goats. When animals were fed a hay diet, the dromedaries had the most efficient cell wall digestion, but differences between dromedaries and goat were no longer significant when the animals were fed a mixed diet (Table 2).

Comparisons of digestibility along the whole digestive tract by measuring total faeces collection and feed intake, showed that dromedaries digested more (+15%) oat-vesce dry matter than Tunisian sheep (Table 3).

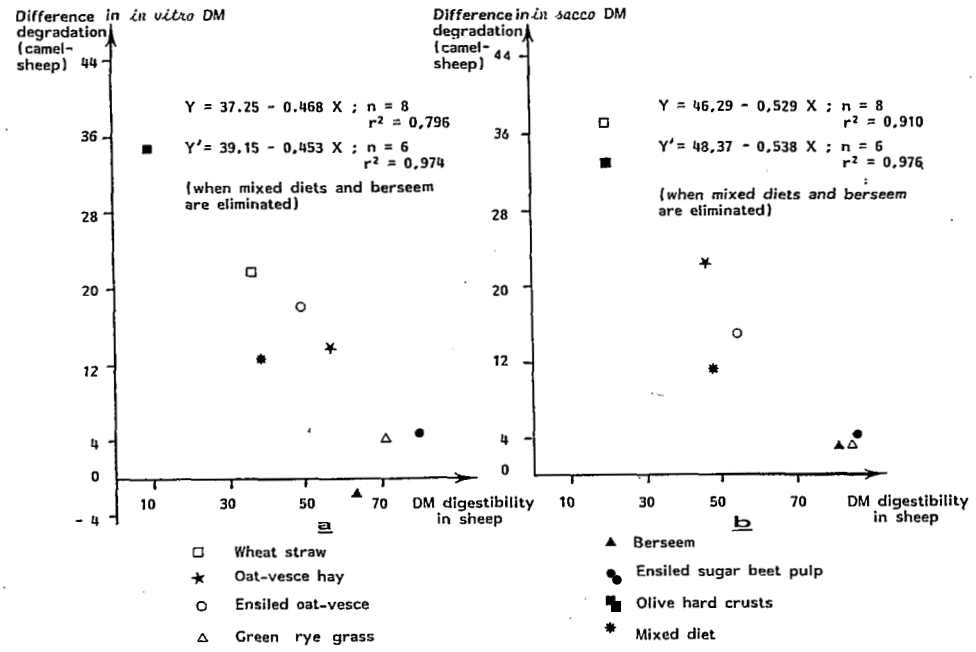

Fig. 1. Correlation between the digestibilities of different feeds measured in sheep (X) and differences of rumen microbial activity between dromedaries and sheep (Y) estimated *in vitro* (a) or estimated *in sacco* (b) (from Kayouli *et al.*, 1991).

Comparisons of cellulolytic microbial ecosystem from the forestomachs of camelids and ruminants

Little is known about the microbial ecosystem of the main forestomach of camelids (Jouany and Kayouli, 1989). The concentrations of bacteria and protozoa, are close to those in ruminants. Recent experiments carried out at INRA, in France, have shown that camelids harbour anaerobic fungi. Some genera are similar to those observed in ruminants (Fonty, personal communication). However, no complete inventory has been made, either in camelids or in ruminants.

The results from comparative studies on dromedaries and sheep (in Tunisia) and on llamas and sheep (in France) showed that protozoa concentrations are lower in camelids and that protozoa populations are all of the B-type (Table 4). Similar results were recently obtained in Australia (T. Day, personal communication). These differences could partly explain the higher cellulolytic activity in camelids since we know that both *Eudiplodinium* and *Epidinium* have efficient enzymatic equipment able to hydrolyse cell wall carbohydrates and ferment the oligosaccharides obtained after hydrolysis (Williams *et al.*, 1986).

Although the amount of recycled nitrogen is higher in camelids and there is no differences between the two animal species in the degradation of feed proteins into

NH_3-N, there is a lower ammonia concentration in the forestomachs of camelids (Table 5). This could be a consequence of the lower protozoa concentration in camelids, as discussed by Jouany (1991). As a result of the lower protozoa biomass, the decrease in microbial and dietary protein degradation in the forestomachs of camelids and the increase in microbial protein yield, would be good for the animals since the supply in intestinal amino acids is improved. To our knowledge, no direct evaluation of these parameters has been done.

Table 1. Kinetics of *in sacco* degradation of different substrates in the sheep and dromedary rumen (n = 4)

	Time (h)					SD
	6	12	24	48	72	
Wheat straw						
Sheep	9.9	12.6	17.7	22.6	27.0	2.4
Dromedary	9.4	12.4	17.4	29.4**	34.3**	2.3
Oat-vesce hay						
Sheep	21.5	27.9	35.9	43.7	49.3	2.8
Dromedary	22.4	28.2	41.2*	56.7**	61.8**	2.4
Lucerne						
Sheep	21.8	36.4	45.3	49.3	49.4	2.4
Dromedary	19.9	40.8*	51.0*	53.3*	53.7*	2.5

SD: Standard deviation of the mean
* $P < 0.05$; ** $P < 0.01$

Characterisation of digesta in relation to cellulolytic activity

The buffering capacity of digesta against acid conditions is higher in camelids than in ruminants (Table 6). This is clear when determinations on rumen contents are made immediately after sampling. It is interesting to note that this ability disappears completely when digesta are incubated *in vitro* for long-term fermentations (longer than two hours). This means that the buffering capacity is due to the ability of forestomach wall absorbing VFA and perhaps secreting bicarbonate. *In vivo*, we observed that pH in different places of the camelids (llamas) forestomach was always higher than in sheep rumen (Table 7). pH was alkaline in the total contents of compartment 1 in starved llamas. Values of pH = 7.4 were observed in glandular sacs, and did not decrease after feeding. The buffering capacity of digesta against alkaline conditions is very low in camelids (Table 6). This means that camelids are very sensitive to urea supplementations. High levels of soluble nitrogen in the diet, which are commonly tolerated by ruminants, are fatal for camelids.

Table 2. *In sacco* degradation of oat-vesce hay

		N	Incubation time (h)	
			72	120
Hay diet	Dromedaries (D)	12	53.7^{aA}	57.4^{a}
	Goats (G)	6	48.0^{b}	52.0^{b}
	Sheep (S)	10	44.2^{cA}	48.3^{c}
	G + D	24	48.0^{b}	56.9^{aA}
	S + D	46	44.2^{cA}	54.9^{dA}
Mixed diet	Dromedaries	12	49.3^{aB}	55.8^{a}
	Goats	6	46.6^{a}	53.5^{ac}
	Sheep	10	39.6^{bB}	46.0^{b}
	G + D	22	46.6^{a}	54.7^{aB}
	S + D	40	39.6^{bB}	51.3^{cB}
RSD			3.3	3.0
"Animal" effect			S	S
"Diet" effect			S	S

^{a,b,c} Comparisons between animals fed the same diet. Means on a row with different superscripts are significantly different ($P < 0.05$)
^{A,B} Comparisons between diets for the same animal species. Means on a row with different superscripts are significantly different ($P < 0.05$)
S: significant effect ($P < 0.05$) from variance analysis
N: number of determinations

The turnover of liquid phase is higher in camelids (Table 8). This is due to a higher rate of salivation, to water recycling in the forestomachs, and to bicarbonate secretion which is associated with VFA absorption. Glandular sacs are probably involved in these processes. All these factors contribute to make pH more stable in the forestomachs. In addition, the higher rate of dilution could have a positive effect on microbial protein synthesis (Harrisson *et al.*, 1975).

Also, we observed that the temperature of the rumen contents is different between camelids and ruminants (37°C *vs* 39°C). Perhaps this could have an effect on the balance between microbes or/and on their cellulolytic activity.

The dry matter content of rumen digesta, tends to be higher in camelids (Table 9). This could be related to the longer retention time of solid digesta in camelids forestomachs, as reported by Lechner-Doll *et al.* (1991) and Kayouli *et al.* (1993). The higher cell wall digestion in camelids could be a consequence of their longer retention time in the forestomachs. This last factor could limit feed intake in camelids.

Table 3. Digestibility of feed in dromedaries and sheep

Trials	Animals	Feed or substrates	Digestibility (%)	Method
(1)	Dromedary	Wheat straw	29*	*in sacco*
	Sheep		21	
	Dromedary	Oat-vesce hay	56*	
	Sheep		47	
	Dromedary	Olive hard crusts + Wheat bean	54*	
	Sheep		47	
	Dromedary	Berseem	84	
	Sheep		82	
(2)	Dromedary	Oat-vesce hay	61*	*in vivo*
	Sheep		53	
(3)	Dromedary	Oat-vesce hay	54*	*in sacco* (72 h)
	Sheep		44	
(4)	Dromedary	Oat-vesce hay	49*	*in sacco* (72 h)
	Sheep		40	

* Values are significantly different ($P < 0.05$)
(1) Animals were fed a diet based on olive hard crusts + wheat bran (60/40) (Kayouli *et al.*, 1991)
(2) Animals were fed a diet based on oat-vesce hay *ad libitum* supplemented with a concentrate (500 g and 100 g respectively to dromedaries and sheep) (Kayouli *et al.*, 1993)
(3) Animal were fed oat - vetch hay
(4) Animals were fed oat - vetch hay + concentrate (50/50)

Table 4. Protozoa in "rumen" digesta

		N	Total Protozoa (x $10^5 ml^{-1}$)	Ento.	Epid.	Eudipl.	Polypl.	Ophryos.	Isotr.
Hay diet	Drom.	16	2.7^{a}	59.6^{a}	22.0^{aA}	10.1^{a}	0	0	-
	Goats	8	4.6^{b}	63.6^{bA}	12.1^{b}	2.9^{b}	0	7.6^{aA}	13.8^{A}
	Sheep	16	4.1^{bA}	81.8^{bA}	0	0	1.6^{A}	5.6^{bA}	11.6
Mixed diet	Drom.	20	3.3^{a}	62.9^{a}	17.5^{aB}	10.0^{a}	0	-	-
	Goats	10	5.3^{b}	76.9^{bB}	7.9^{b}	1.6^{b}	0	4.2^{B}	9.3^{B}
	Sheep	19	5.0^{bB}	83.7^{cB}	0	0	2.1^{B}	4.0^{B}	9.4
RSD			1.2	7.2	5.5	3.0	0.5	2.2	3.9
"Animal" effect			S	S	S	S	-	S	NS
"Diet"effect			S	S	S	NS	S	S	6S

^{a,b,c} Comparisons between animals fed the same diet. Means on a row with different superscripts are significantly different ($P < 0.05$)
^{A,B} Comparisons between diets for the same animals species. Means on a row with different superscripts are significantly different ($P < 0.05$)
Ento.: *Entodinium* spp.; Epid.: *Epidinium* spp.; Eudipl.: *Eudiplodinium* spp.; Polypl.: *Polyplastron multivesiculatum*; Ophryos.: *Ophryoscolex* spp.; Isotr.: *Isotricha* spp.

Conclusion

A more efficient microbial population associated with a longer retention of feed in the forestomachs are means by which camelids make a better use of low-digestible roughages. Low feed intake and high feed efficiency are the necessary conditions to maintain large numbers of animals in a desert area. The more rapid turnover of liquid phase and the lower number of protozoa could be the reason why the flow of amino acids in the duodenum of camelids is higher than in ruminants fed the same diet.

As dromedaries can survive for several days without water and are able to graze plants with low nitrogen content, it is clear that they favourably compete with other herbivores in the desert.

Table 5. Ammonia concentration in "rumen" digesta (mg l^{-1})

		N	Time after feeding (h)			
			0	2	5	8
Hay diet	Drom.	8	23.5^{aA}	43.7^{aA}	41.1^{A}	25.4^{bA}
	Goats	6	52.4^{bA}	78.2^{bA}	45.0^{A}	35.0^{aA}
	Sheep	12	43.7^{bA}	73.1^{bA}	41.1^{A}	20.6^{bA}
Mixed diet	Drom.	16	104.3^{aB}	119.3^{aB}	109.9^{aB}	95.4^{aB}
	Goats	7	154.0^{bB}	183.7^{bB}	131.0^{bB}	124.6^{bB}
	Sheep	14	118.9^{cB}	150.8^{cB}	124.6^{bB}	112.8^{cB}
RSD			14.9	17.1	13.3	10.2
"Animal" effect			S	S	S	S
"Diet" effect			S	S	S	S

^{a,b,c} Comparisons between animals fed the same diet. Means on a row with different superscripts are significantly different ($P < 0.05$)
^{A,B} Comparisons between diets for the same animals species. Means on a row with different superscripts are significantly different ($P < 0.05$)
S: significant effect from variance analysis ($P < 0.05$)
N: Number of determinations

Table 6. Buffering capacities of "rumen" digesta (2 hours after feeding)

		N	Against acid conditions (meq HCl to get pH = 4)	Against alkaline conditions (meq NaOH to get pH = 9)
Hay diet	Drom.	16	11.1	2.0^{aA}
	Goats	8	10.4^{A}	2.8^{bA}
	Sheep	16	10.6^{A}	2.8^{aA}
Mixed diet	Drom.	8	11.0^{a}	2.6^{aB}
	Goats	4	8.8^{bB}	7.0^{bB}
	Sheep	8	8.6^{bB}	4.8^{cB}
RSD			0.97	0.37
"Animal" effect			S	S
"Diet" effect			S	S

^{a,b,c} Comparisons between animals fed the same diet. Means on a row with different superscripts are significantly different ($P < 0.05$)
^{A,B} Comparisons between diets for the same animal species. Means on a row with different superscripts are significantly different ($P < 0.05$)
S: significant effect ($P < 0.05$) from variance analysis
N: Number of determinations

Table 7. pH in the forestomachs of llama and sheep

Animal	N	Place of sampling						
		1	2	3	4	5	6	7
Llamas								
Starved	5	7.0[a]	7.1[a]	7.2[a]	7.4[a]	7.4	6.8	7.9
Fed	10	6.5[b]	6.9[a]	6.9[b]	7.3[b]	7.4	6.7	7.7
Sheep								
Starved	5	6.6[b]	6.6[b]	6.8[c]	ND	ND	6.9	7.8
Feed	10	6.4[b]	6.4[b]	6.6[d]	ND	ND	6.7	ND
RSD		0.3	0.25	0.10	0.07	0.21	0.22	
Effect		S	S	S	-	-	NS	NS

Values on a row with different superscripts are significantly different ($P < 0.05$)
1: dorsal sac; 2: ventral sac; 3: reticulum or compartment 2; 4: glandular sac in reticulum; S: glandular sac in ventral sac; 6: omasum or compartment 3; 7: oesophagus
S: significant effect ($P < 0.05$); NS: non significant effect ($P < 0.05$) from variance analysis
ND: not determined
N: number of determinations

Table 8. Retention time of solid particles and liquid phase in the forestomachs of camelids and sheep

	N	Turnover of liquid phase (% h^{-1})		Retention time of solid particles (hrs)	
		Trial 1	Trial	Trial 1	Trial 2
Dromedary	2	17	19	55*	32
Sheep	3	12	11	30	22

* Values on a row are significantly different ($P < 0.05$)
Trial 1: animals were fed a diet based on oat-vetch hay *ad libitum* supplemented with 500 and 100 g respectively for dromedaries and sheep (Kayouli *et al.*, 1993)
Trial 2 : animals were fed a diet of oat-vetch hay
N: number of determinations

Table 9. Characteristics of digesta

	N	Llamas		Sheep		RS
		T (0 h)	T (2 h)	T (0 h)	T (2 h)	
Rumen volume (kg)	2	13.1	15.3	10.3	11.1	1.4
Dry matter content (%)	2	12.2^{ab}	13.0^{a}	10.5^{b}	11.9^{ab}	0.9
Volume kg^{-1} DM intake	2	8.1	9.3	7.7	9.0	1.4

T: Time after feeding
Values with different superscripts are significantly different ($P < 0.05$)
N: number of determinations

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