Further studies on the changing composition of the digesta along the alimentary tract of the sheep

2. Volatile fatty acids and energy relative to lignin

By A. M. BADAWY,* ROSA M. CAMPBELL, D. P. CUTHBERTSON AND W. S. MACKIE

Rowett Research Institute, Bucksburn, Aberdeenshire

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The object of this part of our study was to extend our earlier investigations on the changes in dry matter, ash, energy, and steam-volatile fatty acids (V.F.A.) along the alimentary tract of sheep as previously reported by Boyne, Campbell, Davidson & Cuthbertson (1956) but with lignin as a marker. The behaviour of nitrogen has been described separately in the preceding paper, where references to the value of lignin as a marker have already been given (Badawy, Campbell, Cuthbertson, Fell & Mackie, 1958).

EXPERIMENTAL

The alimentary-tract contents were collected from the six 1-year-old Greyface wethers described by Badawy, Campbell, Cuthbertson, Fell & Mackie (1958, Exp. 1). The parts of the tract dealt with were: (1) reticulo-rumen sac as one part, (2) omasum, (3) abomasum, (4) proximal half of the small intestine, (5) distal half of the small intestine, (6) caecum and (7) colon.

Analyses of the wet material were begun immediately after emptying of the portion of the tract concerned. Dry matter, total nitrogen and V.F.A. were estimated on the wet material, and ash, lignin and energy on the dried material.

The chemical methods were as described by Boyne *et al.* (1956) and by Badawy, Campbell, Cuthbertson, Fell & Mackie (1958).

RESULTS

The effect of the character of the diet on the total contents of various parts of the tract is shown in Table 1. The contents of group 1 which had the highest dry-matter and crude-fibre intakes, were higher than those of either group 2 or group 3 in respect of the reticulo-rumen, omasum, caecum and colon. Dry-matter, ash and V.F.A. percentages are shown in Tables 1 and 2. The rises in the percentage of dry matter in the omasum and subsequently in the caecum and colon can be accounted for by dehydration. The sharp rise in the percentage of ash in the dry matter of the abomasum was presumably due largely to the chloride of the gastric juice.

* Present address: Faculty of Agriculture, University of Alexandria, Alexandria, Egypt.

Volatile fatty acids

The V.F.A. changes in terms of wet contents (Table 2) followed parallel lines in the three dietary groups. In the caecum and colon there was the characteristic rise previously reported by Elsden, Hitchcock, Marshall & Phillipson (1946) and Boyne *et al.* (1956).

As was to be expected, ratios of V.F.A. to lignin (Table 2) showed that a considerable loss of V.F.A. took place from the reticulo-rumen sac to the abomasum due to absorption

Table 1. *Mean weight of contents (g) and percentages of dry matter and of ash on a dry-matter basis along the alimentary tract of sheep (see also Table 1 of Badawy, Campbell, Cuthbertson, Fell & Mackie, 1958)*

(Two sheep/group)

Group no.	Site: Reticulo-rumen sac	Omasum	Abomasum	Proximal small intestine	Distal small intestine	Caecum	Colon
				Contents			
1	6579	154·5	185·1	189·1	424·5	491·7	495·3
2	4623	101·1	250·1	137·7	519·9	373·6	345·8
3	4123	83·3	384·7	217·4	305·7	337·3	325·1
Mean	5108	113·0	273·3	181·4	416·7	400·9	388·7
				Dry matter			
1	11·39	20·45	10·18	9·82	8·25	11·37	13·76
2	12·80	29·21	10·95	7·80	7·14	12·99	17·05
3	14·59	23·83	9·75	10·75	8·57	13·13	17·87
Mean	12·93	24·50	10·29	9·46	7·99	12·50	16·23
				Ash			
1	9·86	13·18	50·42*	14·09	17·47	15·88	14·78
2	8·03	5·56	19·08	14·72	16·06	12·52	12·19
3	8·07	9·62	26·65	12·82	17·58	13·16	12·74
Mean	8·65	9·45	32·05	13·88	17·04	13·85	13·24

* An abnormally high ash concentration (over 70 %) was found for one sheep.

Table 2. *Mean concentrations of steam-volatile fatty acids (m-equiv./100 g contents) and ratios to lignin (m-equiv./g) along the alimentary tract of sheep*

(Two sheep/group)

	Group no. 1		2		3		Mean	
Site	Concentration	Ratio to lignin	Concentration	Ratio to lignin	Concentration	Ratio to lignin	Concentration	Ratio to lignin
Reticulo-rumen sac	8·52	3·89	10·65	5·03	23·15	4·60	10·44	4·51
Omasum	3·78	0·83	4·20	1·22	5·81	1·25	4·66	1·10
Abomasum	0·26	0·30	0·30	0·40	0·51	0·35	0·36	0·35
Proximal small intestine	0·30	0·42	0·26*	0·32*	0·36	0·41	0·34	0·38
Distal small intestine	0·31	0·27	1·86	2·33	0·63	0·46	0·93	1·02
Caecum	5·12	1·91	9·95	3·37	7·60	2·25	7·56	2·51
Colon	4·61	1·35	8·22	2·04	6·48	1·36	6·44	1·58

* Insufficient material for analysis of lignin, values for one sheep only.

from the former and possibly also from the omasum (see Badawy, Campbell, Cuthbertson & Mackie, 1958). There was a rise in the concentration of V.F.A. in the second half of the small intestine and a pronounced rise of V.F.A. in the caecum followed by some loss in the colon. These changes would appear to indicate some degree of microbial activity in the distal half of the small intestine probably reaching a maximum in the caecum. The nature of the diet seems to have some effect on the V.F.A. concentration particularly in the reticulo-rumen sac, in which organ the concentration was highest in group 3 and lowest in group 1.

From the ratios V.F.A.: lignin (Table 2) and the values given in Table 4 for lignin in the food, and on the assumption that the lignin consumed daily passed intact through the tract at least as far as the duodenum, it was possible to calculate the amount of V.F.A. (expressed as g acetic acid) absorbed from the digesta in the omasum and the abomasum. In the three groups the amounts absorbed in the omasum were 22·6, 13·3 and 17·7 g (mean 17·9 g). In the abomasum the amounts absorbed were 3·9, 2·9 and 4·8 g (mean 3·9 g).

Energy value

In the omasum, owing to dehydration, the gross-energy values of the contents in the three groups (Table 3) in terms of the wet contents were found to be almost double the values in the reticulo-rumen sac, which also held to some extent in terms of percentage dry matter (Table 1). A sharp decrease in the energy value was noted in the abomasum with the inflow of gastric juice, followed by an increase in the proximal half of the small intestine due to the addition of protein from secretion, mucin and from shed epithelium. This decrease was followed by a decrease in the distal half, after which part the values tended to increase again considerably. In terms of dry matter and lignin the mean energy values of the three groups decreased slightly from the reticulo-rumen sac to the abomasum with a pronounced increase in the proximal half of the small intestine. This finding confirmed earlier work (Boyne *et al.* 1956) and must at least in part be due to the nature of the nitrogenous matter shed as the result of the mode of killing the animal (see Badawy, Campbell, Cuthbertson, Fell & Mackie, 1958). The fat content of the shed mucosa might also be a factor in raising the level.

The increase in nitrogen in the first half of the small intestine was followed by a considerable decrease in the distal half and in the caecum, and there was almost no change from the caecum to the colon. Ratios of energy to lignin in group 1 showed a slight loss of energy from the reticulo-rumen to the omasum, in group 3 there was no change, but in group 2 a definite increase. Energy values along the whole tract in groups 2 and 3 were higher than in group 1. This difference was more pronounced in the abomasum than in the other parts studied.

Table 4 shows that the mean total-digestion coefficient of lignin of the six sheep was 22·1% and the range from 6·8 to 28·8%. Such high values are unusual though there are parallel experiences in the literature (Badawy, Campbell, Cuthbertson, Fell & Mackie, 1958). It is considered unlikely that these apparently high total-digestibility figures will seriously affect the interpretation of the results as far as digestion up to the ileo-caecal valve is concerned.

Table 3. *Mean energy values of the contents in the alimentary tract of sheep in terms of Cal./100 g wet material, Cal./g dry matter and ratios to lignin (Cal./g lignin)*

(Two sheep/group)

	Group no. 1			Group no. 2			Group no. 3			Mean		
Site	Cal./100 g wet material	Cal./g dry matter	Cal./g lignin	Cal./100 g wet material	Cal./g dry matter	Cal./g lignin	Cal./100 g wet material	Cal./g dry matter	Cal./g lignin	Cal./100 g wet material	Cal./g dry matter	Cal./g lignin
Reticulo-rumen sac	51·1	4·49	23·3	58·5	4·57	27·6	69·2	4·74	26·2	59·6	4·60	25·7
Omasum	93·1	4·55	20·6	133·4	4·57	38·8	128·4	4·85	26·0	118·3	4·66	28·5
Abomasum	22·7	2·65	25·1	44·3	3·99	45·0	37·3	3·84	30·7	34·8	3·49	33·6
Proximal small intestine	49·7	5·06	71·9	49·9	5·09	62·1	52·8	4·89	59·0	50·8	5·01	64·4
Distal small intestine	37·6	4·55	33·0	33·0	4·63	38·0	37·2	4·35	27·3	36·0	4·51	32·8
Caecum	48·5	4·27	18·0	63·6	4·89	21·4	58·4	4·45	17·3	56·8	4·54	18·9
Colon	60·2	4·37	17·6	82·5	4·85	20·5	81·5	4·56	17·1	74·7	4·59	18·4

The total-digestion coefficient of the energy content of the feed (Table 4) was 68·1% and the range from 61·1 to 74·0%.

Table 4. *Total-digestion coefficients of lignin and energy in sheep*

		Lignin			Energy		
Group no.	Sheep no.	In food (g)	In faeces (g)	Digestion coefficient (%)	In food (Cal.)	In faeces (Cal.)	Digestion coefficient (%)
1	1	126·6	101·7	19·7	4413	1717	61·1
	2	118·7	84·5	28·8	4144	1429	65·5
2	3	58·3	54·3	6·8	3142	874	72·2
	4	58·3	43·2	26·0	3142	818	74·0
3	5	88·4	66·2	25·1	3240	1062	68·2
	6	88·4	65·5	25·9	3240	1031	67·7
Mean				22·1			68·1

DISCUSSION

That the reticulo-rumen contained 74% of the total dry matter found in the whole tract some 4 h after feeding is in agreement with the earlier findings (Boyne *et al.* 1956). The increase in the percentage of dry matter in the omasum, caecum and colon is considered to be due to the dehydration taking place in these parts. That the dry-matter percentages in the reticulo-rumen sac and the omasum in groups 2 and 3 were higher than in the first group, may possibly have been due to these groups having been fed on relatively larger amounts of finely ground concentrates (400 g daily) than the first group (225 g daily). Bearing to some extent on this point is the finding of Balch & Johnson (1950) that on feeding ground hay to cattle a higher dry-matter content of the digesta is produced in all parts of the reticulo-rumen than with longer material.

The most striking but not unexpected change in the ash concentration was the large rise in the abomasum. It was most noticeable in group 1. But one of the two sheep in this group had an ash concentration in the abomasum of over 70% on a dry-matter basis, which we presume must have been due to the ingestion of sand or earth before transference of the sheep to a concrete pen. This explanation is borne out by the fact that the insoluble fraction amounted to 60%, though it is conceivable that siliceous matter is sometimes retained in the abomasum.

The changes in V.F.A. concentration followed a general trend (Table 2). The highest values corresponded generally to those parts of the tract in which microbial activity is known to exist. These parts are the reticulo-rumen, caecum and colon. This finding is in agreement with those of Barcroft, McAnally & Phillipson (1944*a*), Elsden *et al.* (1946) and Boyne *et al.* (1956). Ratios of V.F.A. to lignin appear to indicate absorption of the V.F.A. in the omasum which is in agreement with work published by Barcroft *et al.* (1944*b*), Elsden *et al.* (1946) and Gray, Pilgrim & Weller (1954) and is further discussed by Badawy, Campbell, Cuthbertson & Mackie (1958). The increase in V.F.A. concentration in the contents of the small intestine, which was more pronounced in the distal part than in the more proximal, is in agreement with the findings of Barcroft *et al.* (1944*a*) and Boyne *et al.* (1956). The latter workers attributed this increase to micro-organisms passing the ileo-caecal junction. The higher level of V.F.A. in the reticulo-rumen sac of the second and third groups might be held to be due to the meal which was given with the hay 4 h before killing. The meal given to the second group contained ground maize and decorticated groundnut meal and that to the third group consisted of linseed meal and crushed oats. These concentrates, particularly the maize with its high starch content, might be considered to promote a rapid production of V.F.A. The meal given to the first group 4 h before killing consisted only of hay which needs a longer period for its fermentation. This explanation is supported by the experiments of Hale, Duncan & Huffman (1947) who found that during the first 6 h after feeding the soluble nutrients disappeared rapidly from the rumen, but cellulose did not disappear to any appreciable extent.

The increase in the gross-energy value (Table 3) of the wet contents of the omasum, caecum and colon was due mainly to dehydration. The decrease in the abomasum is held to have been due to the addition of water to this organ and to the relatively higher content of ash. The increase in the proximal half of the small intestine was attributed mainly to the considerable addition of nitrogenous compounds in this part, probably due mainly to shedding of the epithelium as well as to secretion. These changes were discussed by Badawy, Campbell, Cuthbertson, Fell & Mackie (1958). The decrease in the distal half of the small intestine, however, might have been due to absorption. The changes in energy values along the tract of the three groups of sheep relative to lignin agreed in that the values increased considerably in the abomasum, but most markedly in the proximal half of the small intestine, and decreased thereafter. These increases, in the small intestine in particular, could be attributed to the addition of energy-yielding compounds in the secretion and through shedding of epithelium outweighing the effect of the absorption of the products of digestion, as discussed fully by Badawy, Campbell, Cuthbertson, Fell & Mackie (1958). In the omasum, the ratio energy:lignin in group 2 indicated a considerable increase of energy, whereas in groups 1 and 2 the ratios were not greatly affected when compared with the results for the reticulo-rumen. These differences might have been due to the character of the rations, for in group 2 the last meal consisted of equal amounts of hay and ground-maize mixture. The ground-maize mixture contained a low amount of lignin and, since it was finely ground, it presumably passed to the omasum at a faster rate than the hay, therefore decreasing the lignin content of the omasum in the earlier stages of digestion and consequently increasing the energy:lignin ratios in this organ. In group 1 the last meal was hay only. In group 3 the last meal consisted of equal amounts of hay and linseed mixture, but the finely ground concentrate mixture seemed not to have affected the energy:lignin ratio in the omasum since its lignin content was almost that of hay. There is ample evidence that some energy-yielding substances, e.g. V.F.A., are absorbed from the digesta on passing from the reticulo-rumen through the omasum (as described by Badawy, Campbell, Cuthbertson & Mackie, 1958).

SUMMARY

1. Six 1-year-old Greyface wethers wer grouped into three groups of two animals each and fed on three different dietary regimes commonly used at this Institute. The animals were transferred to metabolic cages and after adaptation 24 h collections of faeces were made for 6 days. Dry matter, ash, nitrogen, lignin and energy were estimated in the food and the faeces. The sheep were killed by humane killer and bled 4 h after the last meal, and the digesta in the different parts of the tract were analysed for dry matter, steam-volatile fatty acids, ash, nitrogen, lignin and energy. The changes in nitrogen content have already been described by Badawy, Campbell, Cuthbertson, Fell & Mackie (1958).

2. The reticulo-rumen sac 4 h after feeding was found to contain 74% of the total dry matter of the whole digestive tract.

3. Owing to dehydration, dry-matter percentages were considerably higher in the omasum and the colon than in the other parts of the tract, the omasum having the highest value.

4. The highest concentration of ash on a dry-matter basis was found in the abomasum, then the distal half of the small intestine, then the proximal half of the small intestine, the caecum and the colon, and finally the omasum and the reticulo-rumen sac in that order.

5. The highest values for the lower V.F.A. as m-equiv./100 ml. contents or as a ratio to lignin corresponded to the main sites of microbial activity, namely, the reticulo-rumen sac, caecum and colon. The apparent absorption of these acids was of the order of 18 g (expressed as acetic acid) in the omasum and 4 g in the abomasum in 24 h.

6. The calorific values of the digesta were highest in those zones where dehydration was taking place, particularly in the omasum and, to a less extent, the caecum and colon; relative to lignin they were greatest in the proximal half of the small intestine, presumably owing to the protein of the digestive juices, mucin and shed epithelium that are added there. Possibly the fat content of the last might also play a significant part.

7. The apparent total-digestion coefficient of lignin in this series of experiments averaged 22·1%. It is considered unlikely that this would significantly affect the interpretation of the results down to the ileo-caecal valve.

8. The mean total-digestion coefficient of energy was 68%.

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