The digestion of foodstuffs in the stomach of the sheep and the passage of digesta through its compartments

1. Cellulose, pentosans and solids

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(*Received* 22 *April* 1958)

In any attempt to explore the overall changes which foodstuffs undergo while in the compartments of the compound stomach of ruminants, or to determine what happens there to the newly formed products and unchanged residues, certain difficulties have to be faced which are common to all investigations of the passage of digesta through these organs. Interpretation of the nature of the changes is complicated by the fact that food, water and saliva enter the rumen to mix in this diverticulum with a considerable bulk of residues from earlier feeds. Moreover, although digesta pass more or less continuously from the rumen to the omasum, through the reticulum, the contents of the reticulum may not be representative either of the contents of the reticulo-rumen as a whole, or, necessarily, of the material passing to the omasum. Absorption of some of the digestion products through the walls of the rumen and other compartments of the fore-stomachs further complicates the situation.

In view of these difficulties it is natural that attention should be given to ratio techniques which employ indigestible markers, since by these means it may be possible to determine precisely the extent to which the digesta in the reticulo-rumen or other compartments differ from the fodder originally eaten. It is important to realize, however, that a change in the ratio of a food component to a marker within the rumen contents could justifiably be used as a measure of the extent of digestion there only if the ratio of these two components of the material leaving the organ were identical with that of the material left behind, at any given time. In other words, the marker could not function as such in the contents of a diverticular organ such as the rumen if it were passed from this compartment at a different rate from that of the food component under consideration.

In order to obtain satisfactory data for calculating the extent of the digestion in the rumen it would be best to examine the digesta, throughout the day, as they leave the reticulo-omasal orifice. At present this procedure is impracticable without undesirable surgical intervention, and it is therefore essential (1) to examine the ratios in the omasum or abomasum as well as in the rumen itself and (2) to provide data that extend over, and are representative of, the whole period of the feeding cycle.

Mäkelä (1956) measured the extent of digestion of N-free organic matter in the stomach of cows by comparing lignin ratios in the fodder and in the abomasal contents, but did not attempt to differentiate between the separate compartments of the stomach. Recently Boyne, Campbell, Davidson & Cuthbertson (1956) have examined the digesta in the alimentary tract of sheep, and have reported changes in the concentrations of a number of food components at various levels of the tract. They did not, however, relate the concentrations of these components to any undigested marker, and interpretation of the changing ratios between them must necessarily be largely speculative.

On one or other of these grounds, previous work on the extent of digestion taking place in the rumen (Hale, Duncan & Huffman, 1947; Gray, 1947; Marshall, 1949; Balch, 1957) may be considered incomplete.

EXPERIMENTAL

Animals and their management. Merino sheep were slaughtered at various times after feeding so that the digesta in the compartments of the compound stomach could be collected and analysed for their content of lignin, solids, cellulose and pentosans. Four groups of sheep were studied. Individuals of each group were given a constant amount of one of four selected diets for at least 2 weeks before they were slaughtered. The reticulo-rumen, omasum, and abomasum were tied off with tape before the contents were collected.

Daily rations. The four rations were: (1) 500 g wheaten hay and 250 g wheat straw, (2) 800 g wheaten hay, (3) 400 g wheaten hay and 400 g lucerne hay, (4) 800 g lucerne hay.

Rations (3) and (4) were consumed rapidly, usually within 2 h, the others more slowly.

Sampling of the digesta. To ensure satisfactory samples from the reticulo-rumen, the whole of its contents was first separated into 'liquid' and 'moist solids' fractions by squeezing the mass through muslin. Suitable portions of each fraction were then taken to reconstitute accurate samples of the original material. The digesta in the omasum and abomasum were always of a consistency suitable for direct sampling, but often the whole contents were needed. The quantities of digesta taken as samples were, whenever possible, of the order of 200 g.

Treatment of samples. The samples were weighed, the solids were precipitated by the addition of absolute alcohol (not less than 70% of the final volume) and the mixture was filtered through a tared filter-paper. The residues on the papers were dried in the air at room temperature, weighed, ground, and stored in air-tight bottles to await analysis. The clear alcoholic filtrates were retained for the determination of their nitrogen contents which are discussed in paper 2 of this series (Gray, Pilgrim & Weller, 1958).

Analysis of the alcohol-precipitated solids. Wherever the term 'solids' is used here it will refer to the air-dried, alcohol-precipitated solids of the digesta. They were subjected to the following analytical procedures.

(1) Lignin was determined by the 72% H_2SO_4 method slightly modified from the procedure used by Norman & Jenkins (1934*a*, *b*). Preliminary extraction with alcohol–benzene was followed by extraction with 5% H_2SO_4 for 3 h. The residue was left in contact with 72% (w/w) H_2SO_4 for 16 h at 16–20°.

(2) Cellulose was determined by the method of Norman & Jenkins (1933).

(3) Pentosans were calculated from the yield of furfural obtained according to the standard A.O.A.C. procedure (Association of Official Agricultural Chemists, 1955).

RESULTS

The lignin, cellulose and pentosan contents of the rations are given in Table 1. It will be noticed that small differences were found between the rations of individual sheep on the same feeding regime. Some of these differences were due to use of batches of hay cut at different times.

Table 1. *Percentage composition of rations on an air-dry basis*

Ration	Sheep no.	Lignin	Cellulose	Pentosans
(1) Wheaten hay, 500 g; wheat straw, 250 g	1–4	9·30	34·6	21·4
(2) Wheaten hay, 800 g	5–10	8·95	33·6	20·4
	11	8·30	27·3	20·6
(3) Wheaten hay, 400 g;	12	8·12	27·4	17·6
lucerne hay, 400 g	13–16	7·54	28·4	16·4
(4) Lucerne hay, 800 g	17	7·22	17·9	12·2
	18	7·40	21·2	13·2
	19, 20, 26	7·66	24·5	13·3
	21–25	7·44	21·7	13·3

In Table 2 are shown the results for all the groups of sheep. They include the concentrations of solids in the digesta of the rumen (reticulo-rumen), the omasum and the abomasum, together with the concentrations of cellulose, pentosans, and lignin in these solids. From these values the digestion coefficients of cellulose, pentosans and solids in the digesta of the three compartments at various times of the day for each ration have been calculated and listed in Table 3. A summary of the coefficients in the omasum and abomasum is given in Table 4. The calculations were made in the usual way, e.g.

Digestion coefficient of cellulose

$$= 100 - \left[\frac{\text{cellulose in solids of digesta (\%)}}{\text{lignin in solids of digesta (\%)}} \times \frac{\text{lignin in fodder (\%)}}{\text{cellulose in fodder (\%)}} \times 100\right].$$

The weights of the total contents and of the solids in the reticulo-rumen of all animals are listed in Table 5.

The indigestibility of lignin in ruminants and its consequent use as a marker in digestibility studies have been discussed by a number of writers in the past (see e.g. Gray, 1947; Kane, Jacobson & Moore, 1950) and need little further consideration here.

Gray reported on the indigestibility of lignin in sheep fed on a mixture of lucerne hay and wheat straw. Similar results have been found for rations of lucerne hay alone and wheaten hay alone.

Table 2. *Percentage of solids, and the percentage of lignin, cellulose and pentosans in them, in the digesta in the stomach compartments of the sheep*

Ration	Sheep no.	Time after beginning of feeding (h)	Rumen				Omasum				Abomasum			
			Solids	Lignin	Cellulose	Pentosans	Solids	Lignin	Cellulose	Pentosans	Solids	Lignin	Cellulose	Pentosans
Wheaten hay and wheat straw	1	5	14·5	12·1	38·3	23·9	20·8	13·7	36·3	22·7	9·50	14·2	38·1	24·6
	2	10	13·5	12·2	35·4	24·3	21·3	13·8	33·2	22·2	11·6	13·6	36·2	23·3
	3	17	10·8	13·8	41·1	24·3	18·8	14·3	34·9	23·6	9·30	14·2	37·2	24·0
	4	24	9·72	14·0	42·1	24·1	18·9	14·8	38·0	24·9	9·05	14·3	38·4	24·4
Wheaten hay	5	2	13·3	12·5	38·5	23·4	20·1	15·7	35·1	23·7	8·35	15·6	36·1	23·6
	6	5	13·0	12·4	35·1	24·9	21·5	14·7	26·2	22·0	9·26	14·5	32·9	22·8
	7	7	11·5	13·3	38·4	24·8	19·6	14·5	32·4	22·8	9·61	14·5	34·2	22·9
	8	10	11·2	13·0	33·0	23·4	19·9	14·3	31·7	22·5	8·38	14·3	32·4	22·5
	9	16	11·4	15·1	34·8	23·6	18·5	15·3	28·2	22·2	7·46	15·1	28·1	21·8
	10	24	8·25	14·9	31·0	24·2	18·4	16·0	30·9	24·8	7·60	15·5	35·0	23·5
	11	24	5·92	15·1	34·3	23·7	16·8	16·7	31·2	24·3	6·76	14·9	29·8	23·1
Wheaten hay and lucerne hay	12	3	8·60	13·3	34·4	19·3	22·2	16·7	32·5	19·4	7·9	16·6	35·3	21·3
	13	5	13·0	13·2	37·0	20·7	19·6	13·9	30·3	18·0	7·3	14·8	32·2	20·9
	14	10	11·0	14·9	34·3	19·7	19·5	15·3	31·3	18·9	7·9	15·2	33·7	21·4
	15	16	8·78	14·5	35·3	20·6	19·0	15·6	30·9	20·8	8·1	16·3	34·7	20·8
	16	24	7·48	15·9	37·3	21·2	18·8	16·2	37·0	23·0	6·5	17·0	37·3	22·1
Lucerne hay	17	2	10·5	14·7	26·7	15·8	21·3	19·7	25·9	17·0	4·7	18·8	23·3	16·2
	18	2½	13·0	12·4	28·7	15·3	20·7	18·1	23·2	16·7	3·0	18·1	22·6	16·3
	19	5	14·3	14·5	28·9	16·5	15·8	17·0	24·8	15·7	5·98	15·5	28·5	15·5
	20	7	11·1	13·3	28·8	15·4	18·9	17·9	20·4	14·6	3·0	16·8	22·0	14·8
	21	10	10·6	18·4	25·1	16·9	17·5	18·4	23·7	14·5	8·7	19·5	26·1	16·9
	22	12	12·2	16·4	26·8	15·2	17·0	18·6	22·4	13·4	3·9	17·6	—	12·4
	23	16	8·6	18·6	27·0	16·2	18·1	19·9	26·8	15·9	4·81	18·1	—	13·0
	24	20	7·7	18·5	26·1	17·6	20·2	20·6	22·6	16·1	8·81	21·8	30·0	18·1
	25	24	8·5	19·1	28·2	18·3	20·6	20·3	24·8	17·5	6·3*	13·4*	18·3*	13·0*
	26	24	8·2	18·5	26·3	17·5	18·9	19·0	22·3	15·8	8·5	21·3	29·6	17·1

* Much sand present in this abomasum.

Table 3. *Digestion coefficients (%) of cellulose, pentosans and solids in the stomach compartments of the sheep*

Ration	Sheep no.	Time after beginning of feeding (h)	Cellulose			Pentosans			Solids		
			Rumen	Omasum	Abomasum	Rumen	Omasum	Abomasum	Rumen	Omasum	Abomasum
Wheaten hay and wheat straw	1	5	15	29	28	14	28	25	23	32	35
	2	10	22	35	28	13	30	26	24	33	32
	3	17	20	34	30	23	28	27	33	35	35
	4	24	19	31	28	25	27	26	34	37	35
Wheaten hay	5	2	18	40	38	18	34	34	28	43	43
	6	5	26	52	39	12	34	31	28	39	38
	7	7	23	40	37	18	31	31	33	38	38
	8	10	32	41	40	21	31	31	31	37	37
	9	16	38	51	50	31	36	37	41	42	41
	10	24	44	48	40	29	32	34	40	44	42
	11	24	31	43	39	37	41	37	45	50	44
Wheaten hay and lucerne hay	12	3	23	42	37	33	46	41	39	51	51
	13	5	26	42	42	28	40	35	43	46	49
	14	10	39	46	41	39	43	35	49	51	50
	15	16	35	47	44	35	39	41	48	52	54
	16	24	38	39	42	39	35	40	53	53	56
Lucerne hay	17	2	28	47	50	36	49	49	51	63	62
	18	2½	19	55	56	30	48	49	39	59	59
	19	5	32	50	37	36	48	44	47	55	51
	20	7	32	64	59	33	53	49	42	57	54
	21	10	57	60	58	47	55	50	60	60	62
	22	12	44	59	—	48	60	60	55	60	58
	23	16	50	54	—	51	55	60	60	63	59
	24	20	52	62	53	47	56	53	60	64	66
	25	24	49	58	53	46	52	46	59	63	45*
	26	24	55	63	56	46	52	54	59	60	64

* Much sand present in this abomasum.

Table 4. *Summary of the values for coefficients of digestion of cellulose, pentosans and solids found in the omasum and abomasum of the sheep*

Ration	Digestion coefficient (%) Cellulose	Pentosans	Solids
Wheaten hay and wheat straw	28–35	25–30	32–37
Wheaten hay	37–50	31–41	38–50
Wheaten hay and lucerne hay	37–47	35–46	46–56
Lucerne hay	47–64	44–60	51–66

Table 5. *Total contents and solids in the reticulo-rumen of the sheep*

Time after beginning of feeding	Total contents (g) (ration no.)				Solids (g) (ration no.)			
(h)	(1)	(2)	(3)	(4)	(1)	(2)	(3)	(4)
2	—	8990	—	8367	—	1200	—	880
3	—	—	7088	5909	—	—	610	770
5	6350	9600	6325	5388	920	1120	820	780
7	—	8030	—	6979	—	920	—	770
10	5466	8220	5779	6708	737	920	635	710
12	—	—	—	4690	—	—	—	570
16	—	7010	4180	4307	—	795	367	370
17	5985	—	—	—	645	—	—	—
20	—	—	4649	—	—	—	—	360
24	5063	4590	3751	3822	493	380	281	325
Solids given each day					750	800	800	800

Digestion of cellulose

Wheaten hay (*ration* 2). The values in Tables 2 and 3 show clearly that the coefficients of digestion of cellulose measured in the abomasal contents remained fairly constant throughout the day, and it is concluded that about 40% of the dietary cellulose was digested in the stomach as a whole. Immediately after feeding, in reflection of the influx of fresh fodder, the digestion coefficients of the rumen contents as indicated by the cellulose: lignin ratios fell to about one-half of their previous values. Subsequently, the breakdown of cellulose in the rumen was reflected by a gradual increase in the digestion coefficients until they reached values similar to those maintained in the abomasum throughout. In the first 7 h after feeding, a considerable quantity of digesta must have left the rumen; if this material had a cellulose: lignin ratio as high as that of the rumen contents, its passage to the omasum and abomasum during this period would have led to a decrease in the cellulose-digestion coefficients there, since it is unlikely that cellulose could be digested there more rapidly than in the rumen itself. The coefficients in the omasum, however, were as high as those in the abomasum and in neither organ did they fall in response to food intake. Thus, only material well digested in respect of cellulose reached the omasum, even during the period immediately after feeding; it may be concluded that the digesta in the omasum and abomasum, and not those in the rumen, were representative of the material leaving the reticulo-rumen throughout the feeding cycle. This view is supported by the results for all the rations examined—and in relation not only to cellulose but also to the pentosans and to the solids as a whole. It will be recalled that Schalk & Amadon (1928) investigated the composition of the bolus regurgitated by cattle soon after feeding and, finding that it consisted not of the recently eaten fodder, but rather of well-digested material from earlier feeds, they suggested that it was largely this material that passed to the omasum. Our findings provide striking evidence in favour of this suggestion.

It will be noticed that the coefficients in the omasum were nearly all a little higher than those in the abomasum, but it is not possible to say whether the differences were large enough to be significant. If they are real they may point to a more complete digestion of cellulose in a small part of the solids in the omasum.

Because of selection of material passing to the omasum, it becomes evident that examination throughout the day of digestion coefficients in the rumen material alone would not have been sufficient to establish the extent of digestion of cellulose in that organ. As judged by the coefficients in the two following compartments, it is concluded that about 40% of the cellulose of the fodder was digested in the reticulo-rumen.

Other rations. As it is clear from Tables 2 and 3 that the patterns of the cellulose: lignin ratios within the stomach compartments of the animals fed on the other rations were very similar to those already discussed, it must again be concluded that the breakdown of cellulose occurred largely, if not entirely, in the reticulo-rumen. The digestion coefficients of cellulose in the omasum and abomasum varied from less than 35% for wheaten hay with straw to over 50% for lucerne hay. The ranges of values for all four rations are summarized in Table 4. It is concluded that these values represent the extent of digestion of cellulose in these fodders while in the rumen.

Digestion of pentosans

The values in Table 3 show that the digestion of pentosans followed a remarkably similar course to that of cellulose; the results are summarized in Table 4.

Digestion of solids

The concentrations of lignin in the solids from the various compartments (Table 2) again suggest that only well-digested material reached the omasum and abomasum from the reticulum even in the period immediately after the ingestion of fresh fodder. The digestion coefficients for solids in the stomach (Tables 3 and 4) increased from about 35% for wheaten hay and straw to about 40% for wheaten hay, 50% for the mixture of wheaten hay and lucerne hay, and about 60% for lucerne hay. It must be realized, however, that the 'solids' measured here may contain some solids not present in the foodstuffs because of the secretion of substances into the stomach. The values are also uncorrected for the solids that passed into the alcoholic filtrates during their preparation, and for the small differences in moisture content of the solids and fodders. The abomasal values are also slightly affected by the tendency for sand to collect in this organ. In one instance the extent of this contamination was striking.

Passage of digesta out of the rumen

The values in Table 5 show that very considerable changes took place in the total content of the rumen as well as in the quantity of solids present at various times of the day. The weight of the whole contents fell by the end of the day, to as little as one-half of the amount present 2–4 h after the beginning of feeding. As the solids accounted for only 10–14 % of the total weight, it is evident that changes in the amount of fluid present in the rumen must have been considerable. The precise quantities involved cannot be estimated because the amount of fluid present merely represents a balance between that entering in the drinking water, the saliva, and possibly from the blood, and that leaving by absorption or by passage to the omasum.

The animals in these experiments were given constant rations, and it can be presumed that the weight of solids leaving the rumen each day was about the same as the weight taken in. It is apparent from Table 5 that between 60 and 70 % of the solids present in the rumen after feeding must have left the organ during the day, either by absorption as soluble products or as residues passing to the omasum.

DISCUSSION

Hale *et al.* (1947) have attempted to measure the rate and extent of digestion of various components of alfalfa hay in the rumen of the cow by analysing the whole contents at the middle and end of the feeding cycle. Their results were based on (1) the indigestibility of lignin in the rumen and (2) the assumption that only material that had been fully digested could pass from the reticulum to the omasum. Our findings give strong support to this assumption, although there is as yet insufficient evidence to show that the segregation of new and well-digested material is complete. It must be pointed out, however, that these authors used a different method for the determination of lignin—one which gave a much higher value for the lignin content of the fodder. Not all of this 'lignin' could be accounted for in the faeces. The extent of digestion of cellulose in the alfalfa (lucerne) hay implied in the values of Hale *et al.* is similar to that found in the present experiments. Their claim that little if any attack was made on cellulose during the first half of the feeding cycle cannot be supported by our results, although they may seem to suggest a slower attack in the early part of the day. It will be realized that the interpretation of changes in the cellulose: lignin ratios in the rumen is complicated by the fact that they must be considered in the light of the evidence that only well-digested material passes out of it to the omasum. The results, being drawn from a series of different animals, cannot be considered suitable for the sort of calculation applied by Hale *et al.* to determine the rates of attack on nutrients in the rumen.

Early work by one of us (Gray, 1947) indicated that the extent of digestion of cellulose in the rumen of sheep given a mixture of lucerne hay and wheat straw was about 40 %. This work included an examination of the cellulose: lignin ratios in the omasum and abomasum, but the results were limited in regard to the time after feeding. Similar limitations affect the findings of Marshall (1949) on the digestion of pentosans by sheep.

The work of Balch (1957) also deals with the problems of determining the extent of digestion of food components in the reticulo-rumen. Balch was aware that the material passing to the omasum might not be of the same composition as the material remaining in the rumen itself. Working with cattle, he was able to collect digesta from the reticulum of the living animal, and considered that he could thereby obtain a proper sample of the material passing through the reticulo-omasal orifice. It is by no means certain, however, that it would be so. The fact that the solids in the omasum of the sheep are almost all very finely divided may point to some form of physical separation or selection at the reticulo-omasal orifice itself. Only a comparison with omasal or abomasal material or both could decide the validity of his procedure.

Balch used the lignin-ratio technique to measure the extent of digestion of crude fibre but not of cellulose. Unfortunately, he reported only the analyses of the composite samples of digesta collected during the feeding cycle, so it is not possible to determine from them the extent of variations in the lignin ratios throughout the day, or to know to what extent the material assumed to be passing the omasum was different from that in the rumen itself.

It should be pointed out that the diets used in our experiments consisted of relatively uniform material, and it is not to be expected that the digesta of sheep fed on mixed diets containing materials of widely different densities would behave in the same way. Under such circumstances it would be more difficult to fulfil the requirement that the samples collected should be representative of the digesta during the whole period of the feeding cycle.

SUMMARY

1. Digestion coefficients for cellulose, pentosans, and solids have been measured by the lignin-ratio technique in the stomach compartments of twenty-six Merino sheep fed on four different roughage rations and slaughtered at different times after feeding.

2. The results provide evidence that only well-digested material reached the omasum and abomasum from the rumen even in the period immediately after feeding. For this reason the extent of digestion in the rumen could not be determined from the changing coefficients in the rumen itself, but was indicated by the more constant values in the omasum and abomasum.

3. The extent of digestion of cellulose in the rumen of sheep fed on wheaten hay and wheat straw was about 30%, on wheaten hay about 40%, and on lucerne hay more than 50%.

4. The extent of digestion of pentosans and solids in the rumen was very similar to that of cellulose.

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The digestion of foodstuffs in the stomach of the sheep and the passage of digesta through its compartments

2. Nitrogenous compounds

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(*Received* 22 *April* 1958)

In recent years important advances have been made in our understanding of the digestion of nitrogenous compounds by ruminants, and it is now known that very extensive changes take place in such compounds before the arrival of digesta in the abomasum and small intestine. Among these changes is the formation of ammonia in the rumen, to an extent which leads to its accumulation there in amounts that vary markedly according to the nature of the nitrogenous compounds eaten (McDonald, 1948, 1952). It has been demonstrated that ammonia can readily be absorbed from the rumen into the blood stream (McDonald, 1948) and it is therefore clearly important to establish the extent to which this phenomenon occurs under various feeding regimes. The formation and absorption of large quantities of ammonia might perhaps be indicative of a serious wastage of nitrogen in the animal's economy.

The mere concentration of ammonia in the rumen cannot indicate accurately the extent of its formation, and it would undoubtedly be difficult to measure directly the amount of nitrogen passing through the rumen wall. With the aid of a suitable marker in the fodder and digesta, however, it may be possible to calculate the quantity of nitrogen reaching the abomasum and small intestine during the feeding cycle. In the experiments described below lignin (L) has been used as such a marker.

EXPERIMENTAL

Nitrogen and lignin in the stomach compartments

In the first paper of this series (Gray, Pilgrim & Weller, 1958) details of the feeding and slaughtering of a number of Merino sheep have been described. The same animals provided values for the present work, but an additional number of sheep were included in the group fed on lucerne hay. The experimental rations, which were selected