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DIGESTION AND ABSORPTION IN THE LARGE INTESTINE OF THE SHEEP

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The food eaten by sheep is digested in three stages. It is first fermented by micro-organisms in the reticulo-rumen where about two-thirds of the organic matter is degraded and absorbed. Food residues, saliva and the micro-organisms themselves then pass on to the abomasum and small intestine where they are exposed to acid and enzymes secreted by the sheep. What remains finally flows into the large intestine where it is subjected to microbial attack a second time and where water and salts are absorbed. A considerable amount is known about ruminal digestion but much less about the changes that occur in the small and large intestines, and the experiments described in this paper were undertaken to measure the digestion of cellulose and nitrogenous substances and the absorption of water and electrolytes by the large intestine. A brief summary of the results has been published (Goodall & Kay, 1962).

Conscious sheep were used fitted with re-entrant cannulae in the terminal ileum. These diverted the flow of digesta to the large intestine through an external loop and by comparing the intake of food, the flow through the loop and the output of faeces over 24 hr periods, the extent of digestion and absorption of various components of the diet occurring before and after the point of cannulation were measured. This technique has previously been used by Hogan & Phillipson (1960) in sheep, by Smith (1962) in calves and by Cunningham, Friend & Nicholson (1963) in pigs. Sineshchekov and his colleagues (Sineshchekov, 1953, 1962) have also used this approach to a wide variety of problems in sheep, cattle, pigs and horses.

METHODS

Sheep. Two Scottish Blackface sheep were used: Alfred, a 2-year-old wether weighing about 32 kg, and Clara, a 2-year-old ewe weighing about 43 kg. They were housed in rooms at a constant temperature (18° C) and illumination (12 hr daily).

At operation for insertion of the ileal cannulae the sheep were anaesthetized with pentobarbitone sodium and the ileum was divided 5–10 cm from the ileo-caecal junction. The cut ends were closed and a moulded plastic cannula with an internal diameter of 11 mm (Ash, 1962) was sewn into the side of each stump. The cannulae were exteriorized through stab wounds in the abdominal wall and were joined by glass or Perspex tubing to re-establish the flow of digesta. Both sheep recovered rapidly from the operation and were eating their full rations within a week.

Three or 4 weeks after operation the sheep were put into metal metabolism cages (Duthie, 1959) and haltered loosely. The cages allowed faeces and urine to be collected separately.

In these sheep the cannulae were placed in the lower half of the flank with the proximal cannula ventral to the distal cannula. This was a poor arrangement since the animals lay on the proximal cannula if they rested on their right sides, and so had to be dissuaded from doing so during the collection of digesta. Another difficulty was that the cannulae occasionally became blocked with food particles when a hay diet was given. When this happened the sheep soon stopped eating altogether but after the blockage was removed, releasing a rapid stream of unusually fluid digesta, the sheep recovered their appetites within a few hours. No collection of digesta was started for at least 2 days afterwards.

Diets. Three diets were offered in turn:

(1) 700 g of good-quality dried grass;

(2) 450 g of poor stalky hay plus 150 g of mixed linseed meal (2 parts) and crushed oats (1 part) which contained 1 % of NaCl;

(3) 700 g of medium quality hay.

The analysis of these diets is shown in Table 1. The food was divided equally into two meals given at 9 a.m. and 4 p.m.

TABLE 1. Composition of the diets

	g/100 g fresh weight			m-equiv/100 g fresh weight		
	Dry matter	Cellulose	Total nitrogen	Na^+	K^+	Cl^-
Dried grass	84	19	1·8	11	45	21
Hay + meals	85	20	1·8	7	22	10
Hay	83	25	1·6	15	44	16

Collections. At least 10 days after being placed on each diet the flow of digesta through the terminal ileum was recorded and sampled for a 72 hr period. The procedure was as follows. The cannulae were disconnected and a glass U-piece was inserted into each. Polythene tubing was joined to the proximal U-piece to conduct the digesta down to a 100 ml. gradulated cylinder. When filled to the 100 ml. mark the cylinder was weighed, the contents were mixed in a beaker and 20 ml. of digesta were removed for analysis with a wide-mouthed pipette or syringe. This proved to be a representative sample since when both the sample and the remaining 80 ml. were analysed the concentrations of dry matter and total nitrogen were the same. Twenty millilitres of 'donor' digesta, collected during the previous week, were added to restore the volume of the remaining digesta to 100 ml. and this was then poured slowly into a funnel leading down to the U-piece in the distal cannula. The equipment attached to each cannula was supported by strings running over pulley wheels to counterweights and this allowed the sheep to lie down or stand up and move freely in the cage. A trial collection period and the 'donor' collections served to accustom the sheep to the experimental procedure, an important preliminary.

The samples were pooled to give three 24 hr samples. They were cooled by iced water during collection and subsequently were stored at 1° C until analysed. Faeces were collected for three 24 hr periods, lagging behind the digesta collections by 19 hr to allow roughly for the time taken by food residues to pass through the large intestine (Coombe & Kay, in preparation).

Analysis. Dry matter was measured by drying at 105° C for 48 hr, total nitrogen in fresh samples by the macro-Kjeldahl method, and cellulose in dried samples by the method of Crampton & Maynard (1938). Sodium and potassium were estimated by flame photometry on acid extracts of ashed samples (Duthie & McDonald, 1960), and the insoluble ash, retained on porosity 3 sintered crucibles, was weighed. When NaCl and KCl were added to twelve samples of digesta and faeces so as to triple their normal concentrations 99 % of the sodium (range 86–110 %) and 92 % of the potassium (range 81–100 %) were recovered. Chloride was estimated potentiometrically (Sanderson, 1952) on the supernatant fluid obtained by digestion of fresh samples with 0·1 N-nitric acid for 48 hr. The sample tubes were sealed with waxed paper so that an accurate estimate of the total water present could be used for calculation of the chloride present in the sample, and this method gave recoveries of 97–99 % of added chloride.

In ileal contents, at least, sodium and potassium seem to be confined to the aqueous phase and are distributed equally throughout it for it was found that analysis of the supernatant obtained by centrifuging samples, in which the supernatant was prepared for flame photometry simply by dilution, gave concentrations in m-equiv/kg water that did not differ significantly from those found for the ashed whole samples. It was assumed that this was true of faeces as well and so the concentrations of sodium, potassium and also chloride have been expressed as m-equiv/kg water to facilitate comparisons between samples differing in dry matter content. This was done by dividing total electrolyte by total water.

RESULTS

Flow. Table 2 records the flow of digesta through the terminal ileum. The flow varied with the diet, being only about 1½ kg/24 hr when the digestible dried grass diet was fed but nearly twice this amount when the less digestible hay and meals or hay only diets were fed. This difference between the grass diet and the two hay diets was highly significant ($P < 0{\cdot}01$).

TABLE 2. The flow of digesta through the terminal ileum in kg/24 hr

	Day 1	Day 2	Day 3	Mean
Dried grass				
Alfred, 698 g	1·30	1·60	1·57	1·49
Clara, 636 g	1·58	1·56	2·15	1·76
Hay + meals				
Alfred, 600 g	2·61	3·12	3·03	2·92
Clara, 600 g	2·12	3·36	2·99	2·83
Hay				
Alfred, 688 g	2·59	2·65	3·00	2·75
Clara, 675 g	2·64	2·88	2·68	2·73

The flow was intermittent. Usually the digesta was propelled from the cannula in discrete 20–30 ml. volumes, a series of such propulsions following each other over a period of some 10–30 min. These periods of activity were separated by intervals of 1 to 2 hr during which there was little or no flow. Figure 1 shows clearly this periodic activity, but the individual propulsions are fused together by the 10 min measurement procedure. Occasionally the flow stopped altogether for as long as 5 hr at a time. Once this appeared to be due to blockage of the cannula as suction released an abnormally rapid and copious flow, but on two other occasions the flow started again without assistance and at its normal rate.

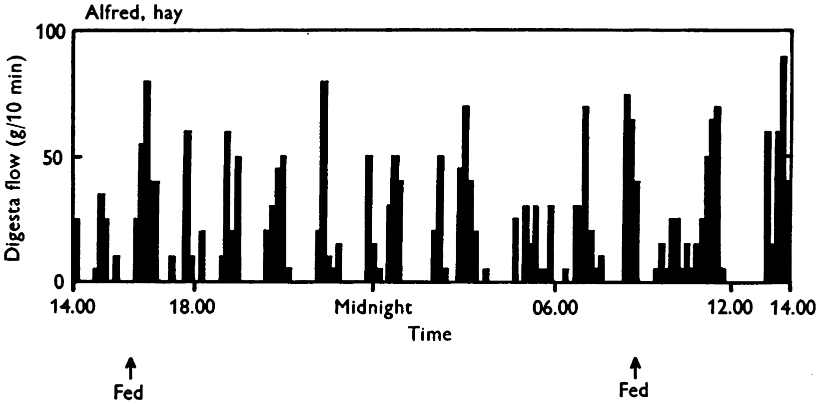

Fig. 1. The flow of digesta through the terminal ileum. This has been measured at 10 min intervals for a 24 hr period.

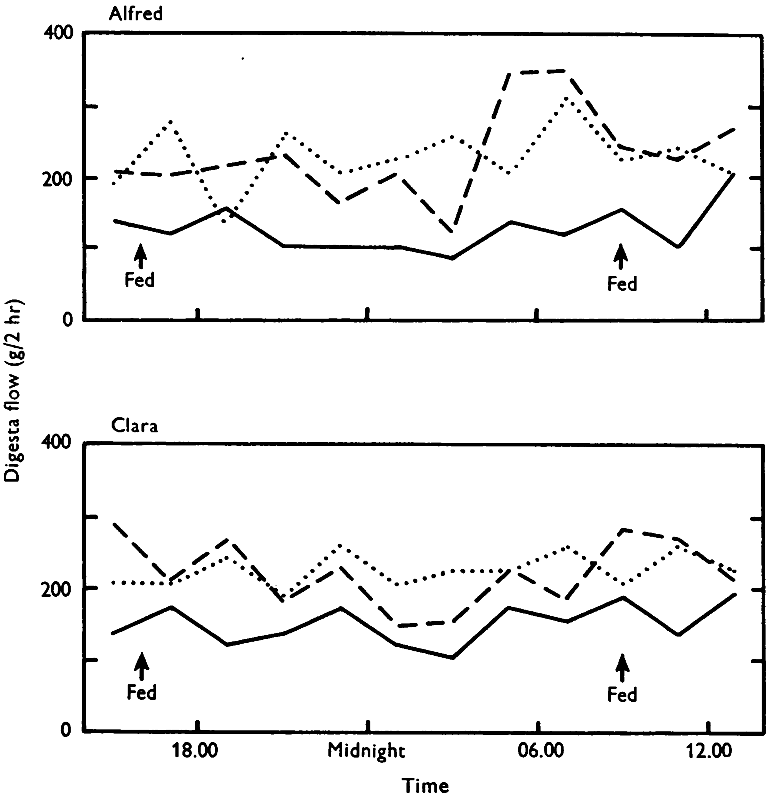

Fig. 2. The flow of digesta through the terminal ileum. Each point is the mean 2 hr flow for 3 consecutive days. Diets: dried grass, continuous line; hay and meals, interrupted line; hay, dotted line.

Figure 2 shows that the flow fluctuated considerably from time to time during the day. It was not possible to find any statistically significant diurnal pattern in these fluctuations, in spite of the twice-daily feeding regime, but there is a suggestion of a slight slowing around 2 a.m. Periods of rumination did not have any apparent effect on the flow.

Composition. The concentrations of dry matter, cellulose and total nitrogen are shown in Table 3. The concentrations of cellulose and total nitrogen in the digesta clearly depended on the nature of the diet, but the dry-matter content only varied within the range 6·9–8·8%, being consistently lower in Alfred. Nevertheless, the digesta varied noticeably in consistency from time to time in that the first material to appear during a period of flow was much less fluid than that which followed, and the digesta were more viscous on the dried-grass diet than when the sheep

TABLE 3. The concentrations, in g/100 g wet weight, of dry matter, cellulose and total nitrogen in digesta passing through the terminal ileum and in faeces. Each figure is the average of three consecutive 24 hr periods

	Digesta			Faeces		
	Dry matter	Cellulose	Total nitrogen	Dry matter	Cellulose	Total nitrogen
Dried grass						
Alfred	8·1	0·7	0·34	27	3	1·2
Clara	8·8	1·0	0·35	28	3	1·1
Hay + meals						
Alfred	6·9	1·5	0·15	50	13	1·0
Clara	8·7	2·0	0·17	48	13	0·9
Hay						
Alfred	7·2	1·1	0·22	42	8	1·1
Clara	8·3	1·4	0·24	45	8	1·2

TABLE 4. The concentrations, in m-equiv/kg water, of sodium, potassium and chloride in digesta passing through the terminal ileum and in faeces. Each figure is the average of three consecutive 24 hr periods

	Digesta			Faeces		
	Na^+	K^+	Cl^-	Na^+	K^+	Cl^-
Dried grass						
Alfred	123	12	72	62	54	26
Clara	129	27	79	31	99	28
Hay + meals						
Alfred	145	11	63	27	59	10
Clara	129	23	72	8	38	12
Hay						
Alfred	137	13	61	64	63	3
Clara	140	18	65	39	82	3
Over-all mean	134	17	69	39	66	14

received hay. The concentrations of sodium, potassium and chloride in digesta and faecal water are shown in Table 4. In the ileum the concentration of sodium was roughly ten times that of potassium but in the faeces potassium usually exceeded sodium and the concentration of chloride became very low. Alfred's faeces usually contained more sodium and less potassium than Clara's although their ileal digesta were similar in composition.

Net changes. The digesta flowing down the gut gain or lose various constituents as a result of secretion, degradation and absorption. Figure 3

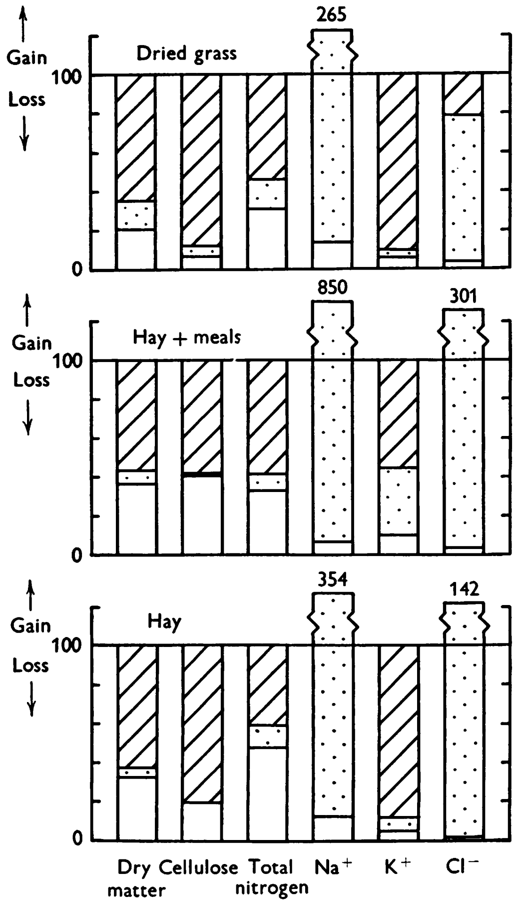

Fig. 3. The net gain (by secretion) or loss (by degradation and absorption) of various constituents of the digesta during their passage through the compartments of the stomach and the small intestine (cross-hatched) and through the large intestine (stippled). The lowest, unshaded part of each column represents the amounts excreted in the faeces. The values are the means for 72 hr periods for Alfred and Clara combined.

The amounts eaten have been given an arbitrary value of 100. The columns for sodium and chloride which rise above 100 indicate that a net movement into the gut has occurred between the mouth and the terminal ileum, net absorption only occurring beyond this point.

shows diagrammatically the relative magnitude of the net changes that occurred before the ileal cannulae were reached, in the chambers of the stomach and in the small intestine, compared with the changes occurring

TABLE 5. The amounts of various constituents disappearing from digesta during passage through the large intestine (amount returned into distal ileal cannula minus amount in faeces). Each figure is the average of three consecutive 24 hr periods

	g/24 hr				m-equiv/24 hr		
	Dry matter	Cellulose	Total nitrogen	Water	Na^+	K^+	Cl^-
Dried grass							
Alfred	31	3	1·3	1010	134	4	80
Clara	44	6	1·6	1190	178	13	107
Hay + meals							
Alfred	27	0	0·9	2510	382	19	165
Clara	38	0	0·9	2320	327	49	180
Hay							
Alfred	3	−6	0·7	2270	334	16	152
Clara	33	4	1·3	2240	335	25	158

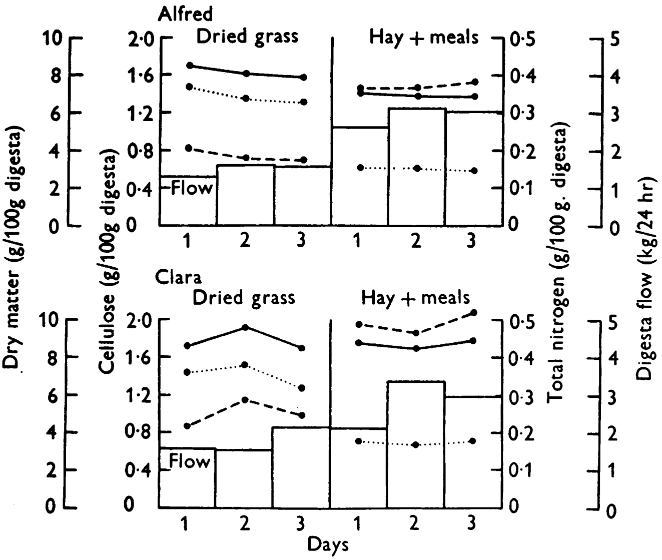

Fig. 4. The flow and composition of digesta passing through the terminal ileum during three consecutive 24 hr periods. Dry matter, continuous line; cellulose, interrupted line; nitrogen, dotted line.

beyond the cannulae, in the large intestine. Digestion and absorption of the organic constituents of the diet were largely complete before the digesta reached the terminal ileum but considerable amounts of water and salts passed into the large intestine. On average, 88% of this water was absorbed, together with 96% of the sodium, 53% of the potassium, and 98% of the chloride.

The net amounts of various constituents that were lost from the digesta passing through the large intestine are given in Table 5.

Variations in flow and composition. On any one diet there were quite large variations from day to day in the flow and composition of the digesta passing through the terminal ileum. In Table 2 it can be seen that the flow was always below average on the first day and usually above average on the second day. Figure 4 shows the changes in flow and composition that occurred on the two diets on which the greater variation was found. The concentrations of dry matter, cellulose and nitrogen changed in parallel; changes in their concentrations were rather smaller than changes in the rate of flow and did not seem to depend on them. For each sheep and diet the concentration of sodium varied by up to 29 m-equiv/kg water from day to day, potassium varied by up to 16 m-equiv/kg water and chloride by up to 10 m-equiv/kg water, and again these variations were not related to the rate of flow. A similar independence between the flow and composition of ileal digesta was found in a later experiment on four other sheep in which the flow was measured for two consecutive 24 hr periods.

Day-to-day variations in the weight and electrolyte concentration of the faeces were relatively greater than those of the digesta but the concentrations of nitrogen and cellulose varied little.

DISCUSSION

The intermittent nature of the flow of digesta through the terminal ileum of sheep has been described by Hogan & Phillipson (1960), on whose work at this Institute the present experiments are partly based. Dr J. B. Coombe, in unpublished observations on our sheep, Alfred and Clara, found that a briefly maintained rise in pressure moved swiftly down the lumen of the ileum upstream from the cannulae immediately before each expulsion of digesta. Propulsion through the terminal ileum therefore appears to be due to grouped series of peristaltic contractions which thrust segmented columns of digesta down the intestine at intervals of an hour or two. It is not clear whether the occasional prolonged periods of inactivity, also observed by Hogan & Phillipson (1960), are normal or whether they reflect an inhibitory condition caused by the experiment.

A rise and fall in the flow of digesta from the abomasum to the duodenum, associated with the feeding and rumination cycle, was found by Harris & Phillipson (1962) and a similar rhythm was sought in the flow through the terminal ileum. But in fact no such rhythm could be detected although the sheep ate their food rapidly at meal times, so it seems that any pattern of flow into the duodenum is lost through delays and the reduction in the volume of the digesta before it reaches the terminal ileum.

The concentrations of total nitrogen and cellulose in the ileal digesta were characteristic of each diet. On the very digestible dried-grass diet the digesta had roughly twice the concentration of nitrogen and half the concentration of cellulose that were found when the diets containing hay were fed. The differences in nitrogen concentration were largely smoothed out during passage of the digesta through the large intestine so that the concentration of nitrogen in the faeces was much the same, whatever the diet. On the other hand the differences in cellulose concentration persisted and appeared more strongly in the faeces. The dry-matter and nitrogen contents of the digesta for the hay and meals diet were similar to those reported by Hogan & Phillipson (1960) with this diet although the net losses of nitrogen from the large intestine were twice as large.

The degradation of cellulose by bacterial action in the large intestine of sheep appears to be of minor nutritional significance. In the present experiments almost all the cellulose passing through the terminal ileum appeared in the faeces and in later experiments (Goodall, Kay, Phillipson & Vowles, in preparation) only about 12 g of cellulose, 12 % of the total digested, disappeared in transit through the large intestine. Cellulolysis in the large intestine is of subsidiary importance in cattle also, for Hale, Duncan & Huffman (1947) showed that the digestion of cellulose in the reticulo-rumen accounted for all but 11·6 % of the total amount digested. On the other hand Gray (1947) found that in successive sections of the large intestine of slaughtered sheep the concentration of cellulose relative to lignin decreased to an extent that accounted for the digestion of about 30 % of the digestible cellulose of the diet. The divergence between Gray's results and our's may be due to a number of factors, such as the use of different diets and different methods for estimating cellulose, as well as to the fact that the digesta removed from a section of the gut of slaughtered animals are not readily comparable with the digesta flowing past a point within that section in conscious animals.

Schmidt-Nielsen & Osaki (1958) have shown that when sheep are given a low-protein diet urea is reabsorbed from the glomerular filtrate so that little is excreted in the urine. They suggest that the urea conserved in this way passes to the reticulo-rumen where some is converted to microbial protein, which is of high nutritive value. The consistent retrieval of about 1 g of nitrogen daily from the residues in the large intestine, even though most is probably absorbed as ammonia and converted to urea, could therefore be a considerable advantage to sheep of low-nitrogen diets. On such diets the total net amount of nitrogen absorbed is often only about 3 g daily. Houpt (1963) has shown that rabbits are able to make good use of urea in a similar manner. In their case, however, the urea apparently diffuses into the fermenting contents of the caecum and is converted into microbial products which are subsequently ingested with the night faeces.

Despite variations in the concentrations of individual constituents, the dry-matter content of the ileal digesta remained constant at about 8% on all diets. This means that the ileal flow, and so the amounts of water and electrolytes presented to the large intestine for absorption, will be determined largely by the amount of indigestible material eaten. On the natural pastures of sheep and other herbivores the digestibility of the fodder is least, and the ileal flow presumably is greatest, during dry seasons when water and salts may be hard to obtain. A large intestine which can efficiently re-absorb the huge amounts of water and electrolytes secreted into the gut is therefore a particularly important adaptation in such animals. The importance of the large intestine of sheep in the absorption of water, sodium and chloride has previously been reported by Hydén (1961) and the organ has a similar function in non-herbivores as well. Levitan, Fordtran, Burrows & Ingelfinger (1962) found that when the colons of healthy men were perfused with 0·85% NaCl solution net absorption occurred at rates amounting to about 2·45 l. of water, 403 m-equiv of sodium, and 562 m-equiv of chloride per 24 hr.

The sodium intake of our sheep, about 50–100 m-equiv daily, was quite enough to maintain sodium balance. In these sodium-replete sheep the concentration of sodium in digesta at the terminal ileum was nearly ten times that of potassium and approached the concentration found in the plasma—about 155 m-equiv/kg water in these sheep. The same is found in other mammals such as cattle (van Weerden, 1961), dogs (Field, Dailey, Boyd & Swell, 1954), horses and pigs (Alexander, 1962) and man (e.g. Welch, Wakefield & Adams, 1936). In the sheep, as in these other mammals, sodium was absorbed much more fully than potassium during passage through the large intestine. Consequently in the faeces potassium, which is normally abundant in a sheep's diet, usually replaced sodium, which is sometimes very scarce, as the dominant cation and faecal sodium losses were only between 2 and 17 m-equiv daily. When sheep are depleted of sodium, part of the sodium in ileal digesta is replaced by potassium, and faecal sodium losses are still lower (Goodall & Kay, 1965).

The tedious procedure of collecting, sampling and returning digesta for 3 days at a time was adopted in order to obtain reasonably reliable average figures for flow and composition and to find out how much variation occurred from day to day. The flow varied considerably, changing by as much as 60% from one day to the next. Much of the variation was associated with the low flow found on the first day's collection and may well have been due to the animal being disturbed by the experiment. It is clear that under our conditions a single day's collection would yield quite unreliable information about the flow of digesta, though not about its composition, and even for the mean flows over the 3-day periods the pooled standard error was $\pm 0{\cdot}2$ kg.

One way to reduce the uncertainty associated with a single day's collection is to measure the amount of some inert and indigestible reference substance that it contains. By comparing this with the normal daily intake of the substance the extent to which the observed flow of digesta deviates from the average daily flow can be assessed. An attempt was therefore made to use acid-insoluble ash, the mixture of grit and plant silica spicules present in the food, as a reference substance, though as such it was known to compare poorly with lignin (Badawy, Campbell, Cuthbertson, Fell & Mackie, 1958). This reduced the day-to-day variation in flow and removed certain anomalies, such as the apparent addition of cellulose to the digesta flowing through Alfred's large intestine on the hay diet (Table 5). However, it was not a satisfactory reference substance in that less could be recovered from the faeces than was eaten in the food and in later experiments, where collection of digesta for more than a day was impracticable, chromium sesquioxide, introduced into the rumen at meal-times, proved to be more suitable.

SUMMARY

1. The flow of digesta through re-entrant cannulae placed in the terminal ileum of two sheep was measured over 72 hr periods. Diets of dried grass, hay and meals and hay were fed.

2. The flow was intermittent, a series of flows over a period of about 30 min alternating with rather longer periods of inactivity.

3. The total flow and the concentrations of cellulose and total nitrogen in the digesta depended on the diet but the dry-matter content remained constant at about 8 %. The mean concentrations of sodium, potassium and chloride were 134, 17 and 69 m-equiv/kg water in the digesta and 39, 66 and 14 m-equiv/kg water in the faeces respectively.

4. Large quantities of water, sodium and chloride and about 1 g of nitrogen per day were absorbed from the food residues passing through the large intestine but little degradation of cellulose took place.

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