Factors Affecting the Utilization of Food by Dairy Cows

1. The Rate of Passage of Food through the Digestive Tract

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This paper is an account of the first stages in an investigation of factors that may influence the efficiency of the digestive processes in cows. The first factor to be studied as a possible influence on the efficiency of digestion was the rate at which foods pass through the cow. As a result of a series of experiments, which form the subject of this first paper, it became clear that although changes in the rate of passage of foods undoubtedly affected the efficiency of digestion, it was also necessary to investigate the factors that affect the rate at which digestion proceeds in any part of the gut, and in particular to determine what factors affect the rate of breakdown of foods in the reticulo-rumen. It is proposed to deal in subsequent publications with experiments in which some of these factors were investigated.

It has been suggested that changes in the rate of passage of foods influence their voluntary intake (Wright, 1929) and the degree of their digestion (Ewing & Smith, 1917; Mitchell, Hamilton & Kick, 1928; Columbus, 1936), and it has been generally assumed that an increased rate of passage of food is accompanied by an increased voluntary intake of food (appetite) and a lowered digestibility. These relationships appear to have received scanty attention, and such data as are available are inadequate either to support or to disprove the assumption. Changes in the fluidity of the faeces suggest that in cows maintained under British conditions the rate of passage of foods must vary considerably during the year. The difference between faeces produced at different seasons and from different diets is probably more marked in the cow than in most animals, and therefore in the cow any relationship between the rate of passage and the digestibility of the diet may be expected to be particularly prominent.

Study of the rate of passage of food in ruminants is complicated by the peculiar arrangement of the stomach compartments which leads to great mixing and sifting of their contents. Consequently the conventional method of measuring rates of passage by using markers ingested as a loose mixture with the food is not satisfactory, since the markers tend to become separated from the food with which they were originally fed. Markers such as sliced rubber hose (Ewing & Smith, 1917; Moore & Winter, 1934), ferric oxide (Mitchell *et al.* 1928; Moore & Winter, 1934), maize and sorghum seeds (Warth, 1927) are therefore likely to be unsuitable. A method which is physiologically more sound has been described by Lenkeit & Habeck (1930). In this method the marker was either hay or straw coloured with magenta or acid fuchsin and recovery was made by counting stained particles in samples of faeces. Habeck (1930), Lenkeit (1932) and Columbus (1936) reviewed work with this and with a more rudimentary

technique for measuring the rate of passage of foods in ruminants. It appears that the most reliable work on cattle was that of Usuelli (1933) who, in a preliminary experiment, determined the rate of passage of coloured oats twice in each of three cows. More extensive investigations on sheep and goats were made by Lenkeit (1930) and Columbus (1936). In these experiments and also in those of Usuelli the concentration of stained particles in the reticulo-rumen was determined by examining samples taken with a stomach tube. The results showed that the passage of foods through ruminants was rarely completed within a week, and under some conditions was prolonged for as much as 3 weeks. The prolonged time of passage was due to retention in the reticulo-rumen and this was affected by the physical and chemical properties of the foods.

This communication is an account of studies with dairy cows designed to expand available information. In addition to determining the time foods take to pass through the cow, the experiments were designed to demonstrate some of the causes and effects of different rates of passage. An attempt was also made to find whether treatments known to change the digestibility of hay do so by changing its rate of passage through the cow.

METHODS

Cows and their treatment

Five experiments were conducted on Dairy Shorthorn cows from the herd of this Institute. The cows were housed in a special shed in which temperature variation was reduced by central heating, and the standings were designed to prevent food wastage and to allow the animals to lie freely on either flank. Rubber mats in the floor made bedding unnecessary. Food offered and that left uneaten were weighed daily and in two of the experiments the daily intake of water was recorded. Cows with rumen fistulas were used for some of the experiments and in these the fistulas were closed by means of the rubber cannula and bung described by Balch & Johnson (1948).

Collection of excreta

Determinations of the digestibility and rate of passage of food were made in 10-day periods after a preliminary period of 3 weeks on the same diet. During the experimental periods faeces were collected on iron sheets raised above the gutter behind the cows; urine was allowed to drain away. At frequent intervals the faeces were scraped from the sheets and placed in buckets. Although the method did not entirely prevent contamination of faeces with urine, the effect of contamination on the results was very small.

Measurement of rate of passage of food

At a single meal the cows were given small amounts of the normal diet stained so that undigested particles could be identified visually in the faeces. The stains used were magenta, rhodamine B, brilliant green, crystal violet and chrysoidene in concentrations of 0·5 g./l. water. The foods were coloured by steeping them for 6 hr. in hot solutions of the stains and were then thoroughly washed with cold water and dried. Tests in which hay was suspended in the rumen in silk bags showed that the presence of these dyes may have slightly depressed the rate of breakdown of the particles.

Apart from hay in various forms, the only other food to be stained was the husk

fraction which remains in cottonseed meal after decortication. The husks were sieved off, steeped in rhodamine B for 24 hr., washed, placed back in the meal and dried.

On the first of the 10 days which formed the experimental period, small amounts of the normal diet were given stained. A suitable amount of hay for this purpose was about 4% of the daily intake of dry matter, i.e. 450 g. for a cow receiving 11 kg. hay. Half an hour was allowed for eating and the mid-point in this half-hour was taken as the 'time of feeding'. Collection of faeces began at this time, the first sampling being normally at 12 hr. and then at 4 hr. intervals for the first 2 days, every 6 hr. on the 3rd day and at longer intervals for the remainder of the 10 days. The intervals were varied slightly in different experiments but never exceeded 24 hr. At each time of sampling the accumulated faeces were weighed, thoroughly mixed and sampled, the sample being stored at 0° in a 400 ml. jar with screw top. Additional portions of 20 g./kg. faeces were taken for dry-matter determinations, the dried material being retained for the analyses connected with the digestibility trial.

The stained particles were counted in subsamples of 2·5 g. faeces from the jar samples. Each subsample was placed on a cotton-gauze filter stretched across the mouth of a 12·5 cm. funnel and washed thoroughly with a thin jet of water. Four subsamples were examined from each jar. Each gauze was transferred to a white dinner plate ruled with parallel lines 2·5 cm. apart. When the plate was placed in a good light any stained particles among the residue on the gauze could be easily seen and counted. The gauzes were dried and weighed before and after use and the weight of dried residue was calculated by difference. The recovery of stained particles was then expressed as the number of particles per 0·1 g. faecal dry matter on the gauze. This correction compensated for variations in the washing procedure because the relationship between the number of stained particles counted and the dry matter retained was found to be linear whether variations were caused by abnormal washing or by the amount of material examined. The number of particles excreted in each sampling period was then calculated and each period total was expressed as a percentage of the grand total for 10 days. Cumulative addition of these figures gave excretion curves (see, for example, Fig. 1) showing the percentage of the total residues voided by the cows at each sampling time.

Repetition of the counting procedure on numbers of samples from the same jar proved that counts corrected to 'particles per unit of dry matter' showed only the variation to be expected in samples from a normally distributed population, i.e.

$$c = \frac{1}{\sqrt{R}} \times 100,$$

where c = coefficient of variation and R = mean corrected count. With practice in washing, the same accuracy could be achieved with uncorrected counts, but the precaution of correcting was maintained in order to guard against possible over- or under-washing.

Digestibility trials

During the experimental periods the foods were sampled daily, samples of roughage being chopped, and their dry-matter content was determined in a steam oven at 90°.

The samples of faeces were dried in the same oven. Dried samples were bulked until the end of the period and then ground and subsampled for analysis. Uneaten food was bulked daily and was sampled, dried, ground and subsampled at the end of the period. Analyses were done on air-dry material and corrected to percentage dry matter by a dry-matter determination at the time of analysis. The following determinations were made: nitrogen, by the Kjeldahl method on 2 g. samples; ether extract, by extraction of 5 g. samples with light petroleum (b.p. 40–60°) in a Soxhlet apparatus; crude fibre, by the official method (Great Britain, Parliament, 1932) using 2 g. samples; nitrogen-free extract, by difference; ash, using 5 g. samples and a muffle furnace at 600°. Coefficients of apparent faecal digestibility were calculated for the 10-day collection periods.

Plan of experiments

Either two or four cows were used for each of the five experiments. Details of the cows are given in Table 1.

Table 1. *Details of the Shorthorn cows used in the five experiments*

Exp. no.	Index letter of cow	Name of cow	Age of cow (years)*	Mean weight of cow during experiment (kg.)	No. of times cow had calved*	Whether dry, lactating or fistulated
1	A	Flora 70	5	499	2	Dry
	B	Winsome 20	6	543	3	Dry
2	A	Lottie 23	5	554	2	Dry
	B	Flora 69	6	534	3	Dry
3	A	Lottie 23	5	571	2	Dry
	B	Flora 69	6	550	3	Dry
4	W	Winsome 22	6	518	1	Dry, fistulated
	X	Flora 69	7	670	3	Dry
	Y	Halora	6	482	2	Lactating, fistulated
	Z	Lottie 26	5	548	2	Lactating
5	A	Winsome 22	5	453	1	Dry, fistulated
	B	Rosalie 25	4	542	1	Dry
	C	Flora 69	6	562	3	Dry
	D	Rosalie 17	7	538	5	Dry

* The apparent discrepancies between the age of the cows and the number of calves are explained by the fact that Exp. 4 could not be done until after Exp. 5 and that the fistulated cows did not calve after the operation.

With the exception of Exp. 3 each experiment was divided into two or more parts. Each part consisted of a preliminary period of 3 weeks and a collection period of 10 days (p. 362).

The treatments in the experiments were as follows.

Exp. 1, parts 1 and 2. Rates of passage of hay and concentrates. The two cows used in this experiment were given daily 7·26 kg. coarse meadow hay and 2·72 kg. of a mixture balanced for milk production and consisting of maize meal, weatings and decorticated cottonseed meal, with an added mineral supplement. The daily foods

were given in two meals and the normal feeding programme was followed on the days when the stained meals were given. Thus, the cows received 0·45 kg. stained hay between 2.45 and 3.15 p.m., followed by 3·63 kg. normal hay, and between 5.50 and 6.10 p.m. they received 1·36 kg. concentrates in which the cottonseed husks were stained. The only difference between the treatments in the two parts of the experiment was that in part 2 the concentrates were given as a mash with water. There was no digestibility trial in this experiment.

Exp. 2, *parts* 1–4. *Variation in replicated determinations of digestibility coefficients and of the rate of passage of foods. Rates of passage of hay, chaff, ground hay and concentrates given in the same diet.* Two cows were kept on the same type of diet for 4 months while the four parts of the experiment were being completed. The time between collection periods was never less than 14 days. Both cows received 2·27 kg. chaffed hay and 3·18 kg. concentrates daily. In addition, one of the cows received 5·44 and the other 9·07 kg. unchaffed hay. Refusals were negligible.

During collection periods the rate of passage of hay and the digestibility of the whole diet were determined. Stained particles were counted three times in every sample of faeces, instead of the usual single count.

In parts 1 and 2 the rate of passage of hay only was measured, but during parts 3 and 4 stained foods were included when the cows were given concentrates at 2.0 p.m., chaff at 4.0 p.m. and hay at 6.0 p.m. on the afternoon of the 1st day of each collection period. The cottonseed husks in the concentrates and the hay were stained with magenta. Chaff was stained with crystal violet (part 3) and brilliant green (part 4). Ground hay was stained with chrysoidene, brilliant green and crystal violet and was given with the chaff and, in part 4 only, as a marker in the concentrates.

Exp. 3. *Rates of passage of hay and of ground hay in the same diet.* There were two cows in this small test. They were given daily hay without stint, 1·36 kg. chaff and 4·54 kg. of a concentrate mixture. The stained foods were hay and ground hay given with chaff. The chaff was given 3 hr. earlier than the hay.

Exp. 4, *parts* 1 *and* 2. *Effect of grinding hay on its rate of passage and digestibility in the cow.* Four cows were used; two were fistulated, and these two were paired with two unfistulated cows so that one of the pairs was lactating. The daily diets were as follows:

Cow	Hay (kg.)	Concentrates (kg.)	Cow	Hay (kg.)	Concentrates (kg.)
W*†	9·07	—	Y*	8·62	3·63
X†	11·34	—	Z	9·53	3·63

* Fistulated. † Non-lactating.

The concentrate mixture was made up of equal amounts of dried skim milk and maize starch; its palatability was increased by the addition of some molasses.

The arrangement of the experiment was:

Part of experiment	Feeding commenced	Collection period	Type of hay given: Long	Type of hay given: Ground
1	13 Nov.	4–14 Dec.	Cows Y, Z	Cows W, X
2	15 Dec.	3–13 Jan.	Cows W, X	Cows Y, Z

Digestibility trials and determinations of the rate of passage of hay were made during the collection periods.

The hay was well cured from ley grasses and the ground hay was made from bales chosen at random from the stack. Both foods were given daily in two meals. The marked meals of long hay were stained with magenta and of ground hay with brilliant green. Cows on the ground-hay diet received only marked ground hay, but those being fed long hay received marked ground hay with their marked long hay. The amounts of marked hay fed were calculated as described on p. 363.

At intervals during the collection periods samples of digesta were removed from the dorsal sac of the rumen and from the reticulum of each fistulated cow. (Throughout this paper the term 'digesta' will be used to describe food or its residues in any part of the digestive tract.) In these samples the concentration of stained particles and the mean weight of the stained particles from unground hay were determined.

Ground hay stained with crystal violet was introduced, through a rubber hose, directly into the abomasum of each fistulated cow immediately before the stained meals were offered. The tube by which this marker was introduced was passed from the reticulum through the reticulo-omasal orifice until its end was 18 cm. beyond the orifice. The ground hay was first soaked in water for several hours and introduced as a suspension in about ten times its own weight of water at 39°. In part 1 of the experiment, 400 g. (dry weight) of hay were used, but in part 2 this amount was reduced to 50 g.

Exp. 5, *parts* 1 *and* 2. *Influence of mangolds on the rate of passage of hay and on the digestibility of the whole diet.* Four cows were used; the daily amounts of food and order of feeding were:

	Hay		Mangolds			Hay		Mangolds	
Cow	Part 1 (kg.)	Part 2 (kg.)	Part 1 (kg.)	Part 2 (kg.)	Cow	Part 1 (kg.)	Part 2 (kg.)	Part 1 (kg.)	Part 2 (kg.)
A*	7·71	5·90	—	22·68	C	7·71	8·62	22·68	—
B	10·43	9·53	—	22·68	D	7·26	7·71	22·68	—

* Fistulated.

Cows A and D refused some of their hay on several occasions. The mangolds were chopped before feeding and both foods were given in two meals daily.

The marked foods were hay (450 g.) stained with magenta and ground hay (200 g.) stained with brilliant green and given with the marked hay; ground hay stained with crystal violet was added to a meal of mangolds eaten 3 hr. before the meal of marked hay.

Samples of digesta from the region of the reticulo-omasal orifice were removed through the fistula in cow A. In these samples the numbers of stained particles and of those from long hay exceeding 5 mm. in length were counted.

RESULTS

Accuracy of measurements of rate of passage and digestibility (*Exp.* 2)

Estimates of the accuracy of these two determinations were obtained by maintaining two cows on a constant diet and repeating the collection periods four times at intervals of not less than 14 days. The lower section of the curve of mean values for the

excretion of hay by both cows in all parts of the experiment is shown twice in Fig. 1 (in *a* and in *b*). The variation of values resulting from the two sources of error is shown with the duplicated curve. The sources of error are, firstly, the cumulative effects of inaccuracies of counting and, secondly, the error between values obtained from any one cow in different periods of an experiment; they are both shown as the standard deviation of any single determination of points on an excretion curve. These estimates show the degree of variation obtained under the conditions of experiment.

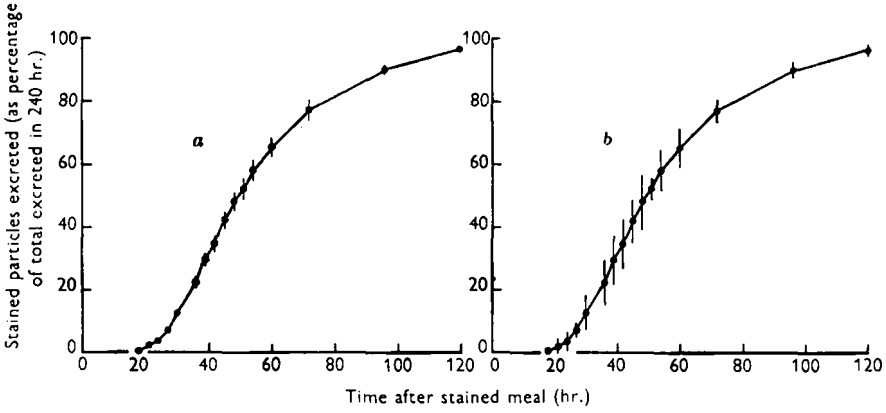

Fig. 1. Exp. 1. Curve of mean values for the excretion of undigested hay residues at intervals after feeding, when values were obtained from two cows on four occasions and on each occasion three separate determinations were made. The curve, ●——●, is shown twice and with it are shown, as vertical strokes, errors due to two causes, (*a*) the standard deviation of the results of any single determination resulting from inaccuracies in counting stained particles, and (*b*) a similar standard deviation resulting from the between-period variation in values obtained from any one cow; this includes (*a*). Standard deviations less than ±1·0% are not shown. Excretion is shown as the percentage of the total stained particles excreted within 240 hr. of a stained meal.

The standard deviations of single determinations of digestibility coefficients made in the course of the four experimental periods described above are given in Table 2. Differences between the rates of passage of the different foods in Exp. 2 are given in the following section.

Relative rates of passage of hay, chaff, ground hay and concentrates offered in one diet (Exps. 1, 2, 3 and 5)

Exp. 1. Hay and concentrate husks. This experiment provided a comparison of the rates of excretion of residues from hay and concentrates. Excretion curves for those foods are presented in Fig. 2. The difference between hay and husks was most marked in cow A, and in this animal the passage of the husks was apparently accelerated in part 2 when the concentrates were given as a mash. There can be no doubt that such residues of the husks, the least digestible part of the concentrate mixture, as passed undigested, were excreted at a considerably faster rate than the hay.

Exp. 2. Hay, chaff, ground hay and concentrate husks. The means of points on excretion curves for foods given in the last two parts of Exp. 2 were used to plot Fig. 3. The difference between hay and concentrate husks was again apparent. In cow B chaffing produced a rate of excretion faster than that for hay but in cow A the

Table 2. *Exp. 2. The variation in replicated determinations of the digestibility of diets of hay, chaff and concentrates by two cows*

		Digestibility coefficient (%)				
Cow	Part of experiment	Dry matter	Crude protein	Ether extract	Nitrogen-free extract	Crude fibre
A	1	59·3	65·8	59·4	63·7	58·6
	2	60·4	64·2	57·0	63·6	61·8
	3	59·2	67·8	60·7	63·2	55·1
	4	59·8	67·3	63·5	64·4	54·5
	Mean	59·7	66·3	60·2	63·7	57·5
	S.D.*	±0·6	±1·6	±2·7	±0·5	±3·4
B	1	59·3	63·1	58·1	63·2	59·8
	2	60·3	65·5	52·7	62·6	63·4
	3	60·8	67·1	52·6	65·0	59·7
	4	59·3	65·4	63·1	63·4	55·7
	Mean	59·9	65·3	56·6	63·5	59·7
	S.D.*	±0·7	±1·7	±5·1	±1·0	±3·2

* Standard deviation of single reading.

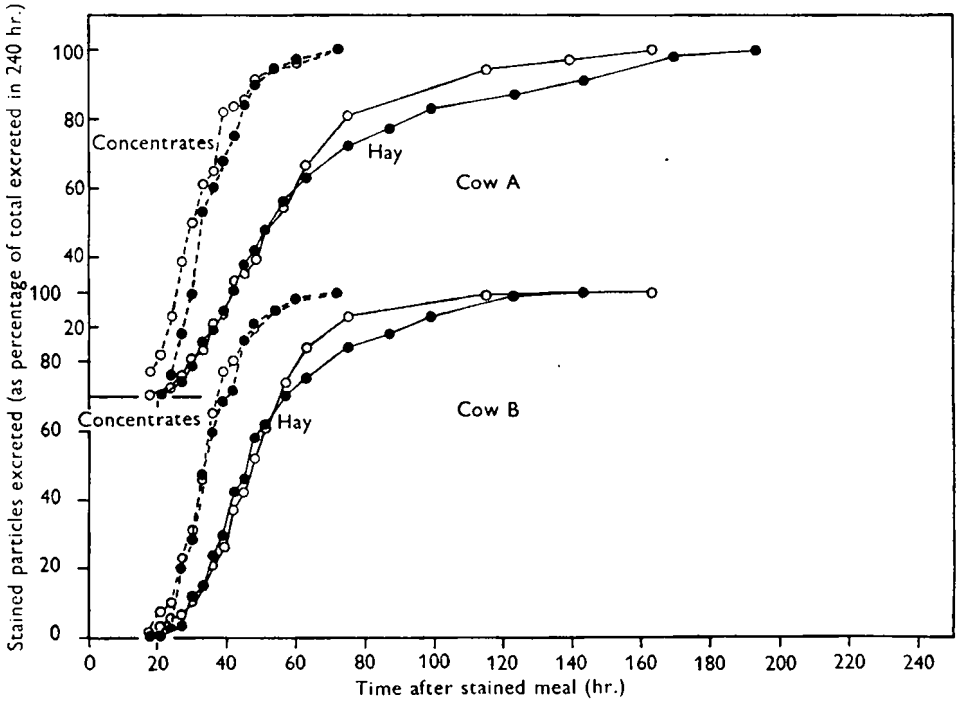

Fig. 2. Exp. 1. Values for the excretion (for definition of excretion see legend to Fig. 1) by two cows of undigested residues of stained hay and of the husks in cottonseed meal which formed part of a concentrate mixture. ●, values obtained in part 1 of the experiment; ○, values obtained in part 2.

rates of passage of the two foods were similar. In cow A ground hay was excreted faster than the chaff with which it was given, but the passage of ground hay which had been given with concentrates (not shown in Fig. 3) was still more rapid. These differences were greatest in the initial stages of excretion.

Exps. 3 *and* 5. *Further results demonstrating the rates of passage of different foods in the same diet.* Further observations confirmed that undigested ground hay was excreted more rapidly than long hay with which it was given. This is illustrated by the curves, shown in Fig. 4, obtained in Exp. 3.

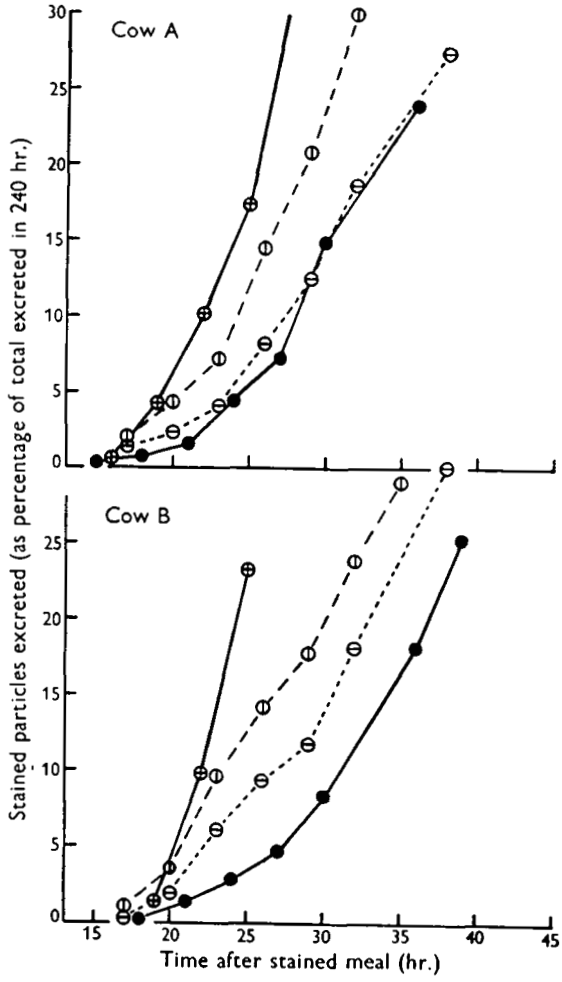

Fig. 3. Exp. 2. Values for the initial stages of excretion (for definition of excretion see legend to Fig. 1) by two cows of undigested residues from: ●——●, stained hay; ⊖- - -⊖, chaff given 3 hr. after the hay; ⓘ--ⓘ, ground hay given with the chaff; ⊕——⊕, cottonseed husks in concentrates given 6 hr. after the hay. The curves are for means of readings obtained in two parts of the experiment.

Exp. 5 was designed primarily to study the effect of mangolds on the rate of passage of hay; the results are described in detail below. However, the rate of excretion of various foods in these diets again confirmed the faster excretion of the smaller particles (Table 5). Mangolds given with ground hay appeared to alter its rate of passage in a similar way to concentrates, the initial rate of excretion being higher in both cases than the initial rate of excretion when ground hay was fed mixed with a meal of chaff.

The digestibility coefficients obtained in these experiments are given in Table 3.

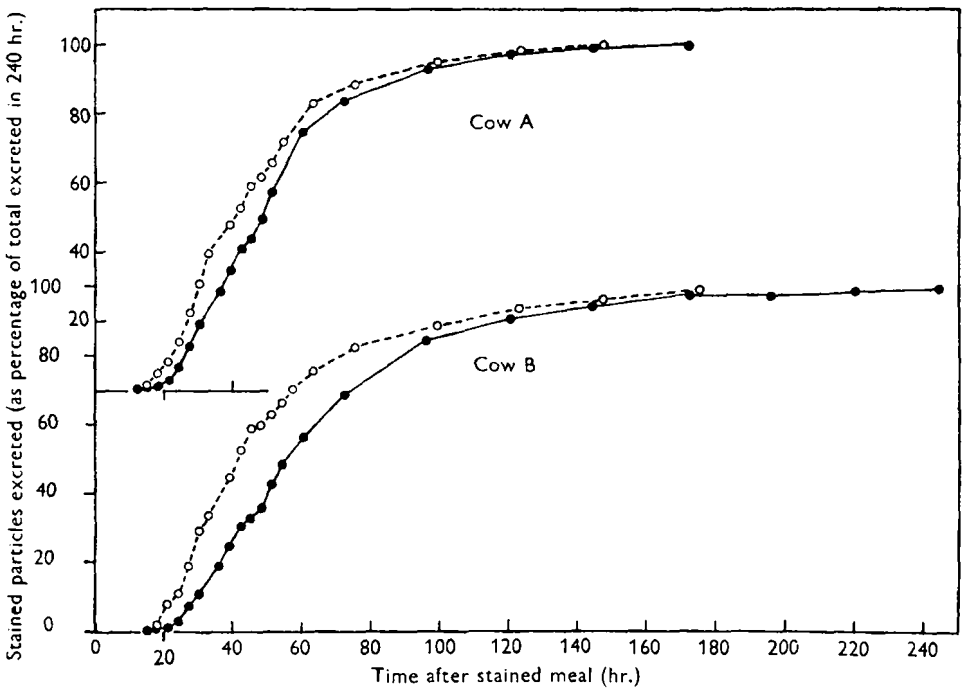

Fig. 4. Exp. 3. Further values for the excretion (for definition of excretion see legend to Fig. 1) by two cows of the undigested residues from: ○- - -○, stained ground hay given with chaff; ●——●, stained long hay.

Table 3. *Exps.* 3, 4 *and* 5. *Digestibility coefficients for the diets fed to cows*

Exp. no.	Diet	Cow	Part of experiment	Digestibility coefficient (%) Dry matter	Crude protein	Ether extract	Nitrogen-free extract	Crude fibre
3	Hay and concentrates	A	—	59·9	64·8	54·9	64·1	55·6
		B	—	60·9	67·3	61·2	64·1	57·0
4	Long hay	W	2	58·2	47·8	24·0	60·8	61·9
		X	2	61·2	47·8	23·7	62·9	67·1
	Ground hay	W	1	61·9	55·9	46·0	65·9	60·8
		X	1	59·6	51·1	39·7	63·7	59·8
	Long hay and concentrates	Y	1	68·3	59·9	28·0	76·6	55·1
		Z	1	70·8	63·8	25·2	78·6	58·2
	Ground hay and concentrates	Y	2	59·8	52·6	4·6	70·9	36·3
		Z	2	59·3	54·2	7·5	70·3	36·5
5	Hay alone	A	1	68·5	59·4	18·9	69·0	74·8
		B	1	62·7	52·5	9·3	63·7	70·6
		C	2	62·6	57·7	21·4	65·1	66·8
		D	2	65·8	62·1	31·7	73·8	70·7
	Hay and mangolds	A	2	70·9	66·7	33·2	78·7	69·2
		B	2	66·1	59·8	18·7	73·5	68·6
		C	1	68·6	60·1	6·8	75·3	68·9
		D	1	71·5	56·9	9·3	78·9	73·0

Relative rates of passage of long hay and ground hay when either constituted the sole roughage in a diet (Exp. 4)

Earlier results (Exps. 2 and 3) had shown that when small amounts of ground hay were given with chaffed hay the finer particles were excreted more rapidly. Exp. 4 was conducted to find out whether whole diets in which all the roughage was ground were also excreted more rapidly than diets in which the roughage was fed long.

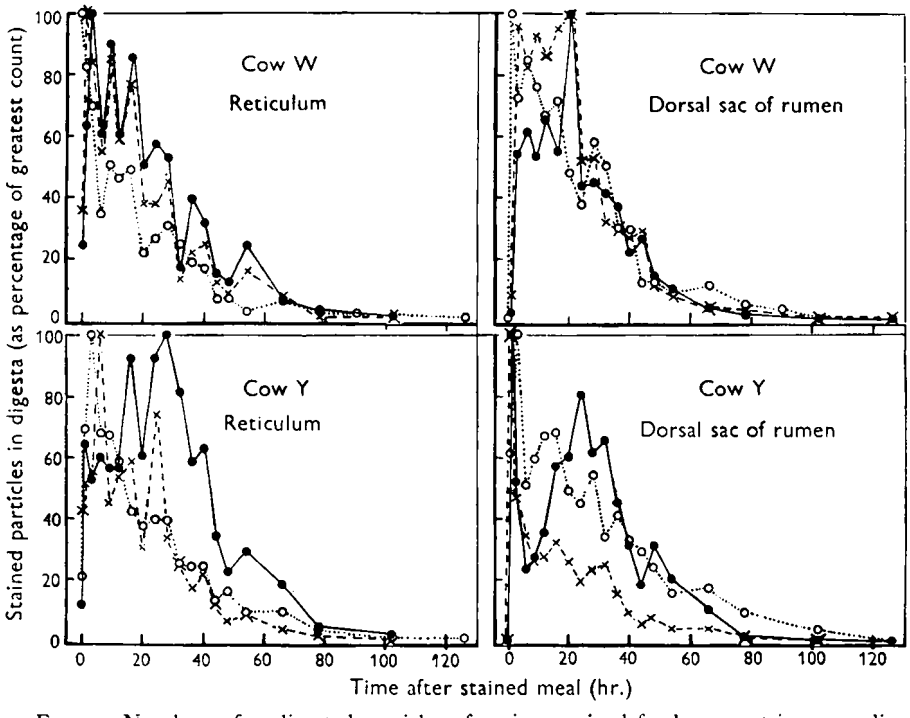

Fig. 5. Exp. 4. Numbers of undigested particles of various stained foods present in 0·1 g. digesta in the reticulum and the dorsal sac of the rumen of two cows at intervals after stained meals. ●——●, hay in a hay diet; ×- - -×, ground hay in a hay diet; ○·····○, ground hay in a ground-hay diet. Values are expressed as percentages of the greatest count.

Samples of digesta were removed at intervals from the dorsal sac of the rumen and from the reticulum of each fistulated cow. Curves showing the concentration of stained particles in these samples are given in Fig. 5. Comparison of the curves was aided by plotting them against a scale on which the greatest count was 100. The curves for long hay and for ground hay given with long hay showed a tendency for the numbers of particles of long hay to remain constant or to rise during the first 20–30 hr. but for those of ground hay to decrease. Ground hay in a diet of ground hay showed a faster initial decrease in numbers than long hay but there was a suggestion that, in the later stages, passage from the dorsal sac was less rapid.

Particles of digesta derived from the long hay were removed from some of the samples from the reticulo-rumen, dried and weighed. The particles found in the dorsal sac tended to be somewhat larger than those in the reticulum; peak size in the dorsal

sac was reached in less than 10 hr. and was followed by a steady decrease. From a comparison of the size and number of particles in the dorsal sac it seems likely that rumination of the stained hay began about 10 hr. after feeding, and that following rumination a high proportion of the particles must have re-entered the dorsal sac.

In addition to marked food, ground hay, stained with crystal violet, was introduced into the abomasum of each fistulated cow. Curves for the excretion of this material in the faeces are given in Fig. 6. The excretion of marker from the abomasum was very much more rapid than that of food that had entered the reticulo-rumen. From the abomasum the time required for 95% of the marker to be excreted varied from 16 to 32 hr., being greatest when the larger amounts (2 l. of marker in suspension) were administered. These large amounts were unsuitable because they gave rise to very fluid faeces for about 6 hr. during the time of excretion of the marked hay from the abomasum and because they produced a very high concentration of stained particles in the faeces (up to 1000/0·1 g. dry matter retained by a double-gauze filter), thus probably causing secondary staining of other particles and making the counting of the stained particles very difficult.

The difference in the rate of excretion of long and ground hay that had been given together, or almost together, is also shown in Fig. 6; it is very similar to the differences found in Exps. 2, 3 and 5. The faster initial excretion of the finer material was observed in every cow and a faster excretion continued throughout the major part of the period of excretion. Table 4 shows that when ground hay was given in a long-hay diet the

Table 4. *Exp.* 4. *Rate of excretion of hay by four cows (W, X, Y and Z) fed diets of long hay and ground hay*

Proportion of total residues from stained hay (%)	Time required for excretion of undigested residues from stained hay (hr.): Long-hay diet (*a*) W	X	Y	Z	Ground-hay diet (*b*) W	X	Y	Z	Change due to grinding (*b*) − (*a*) W	X	Y	Z
5*	22	31	30	22	24	25	18	16	+2	− 6	−12	− 6
80−5*	41	47	40	48	37	57	44	70	−4	+10	+ 4	+22

	Ground hay given with long-hay diet (*c*) W	X	Y	Z	Change in ground hay due to grinding whole diet (*b*) − (*c*) W	X	Y	Z
5*	21	27	26	18	+3	− 2	− 8	− 2
80−5*	34	39	31	39	+3	+18	+13	+31

* For explanation of these indices of the rate of excretion, see below.

excretion of 5% of the ground hay residues (called '5% excretion time') invariably took less time than excretion of the undigested long hay. Similarly, if the time required for excretion of 5% of the stained residues was subtracted from the time required for the excretion of 80% (called the '80−5% excretion time'), this also was less for ground hay given with long hay than for the long hay. It will be shown below (p. 374) that the 80−5% excretion time and the 5% excretion time were indicative of

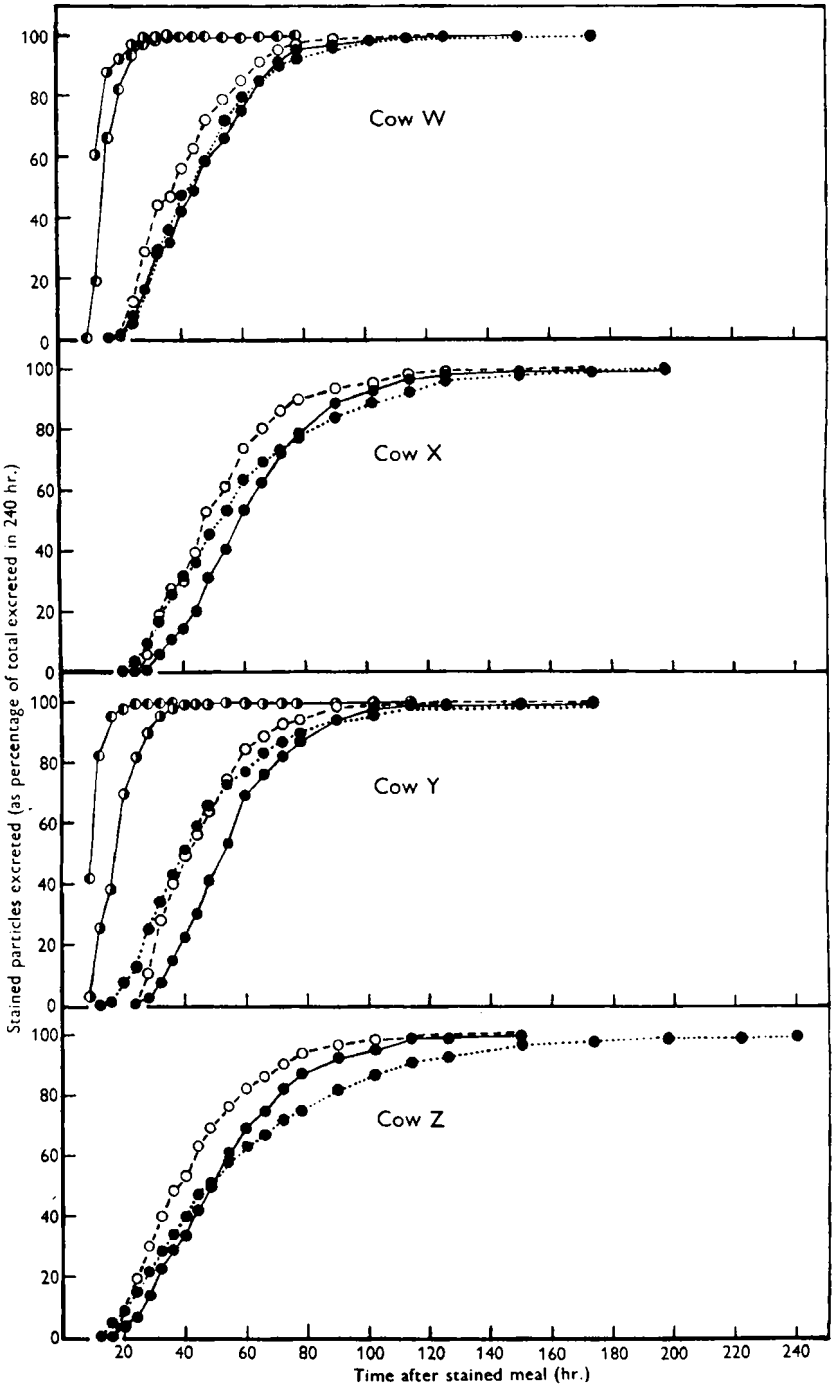

Fig. 6. Exp. 4. Values for the excretion (for definition of excretion see legend to Fig. 1) by four cows of undigested particles of stained hay and ground hay in two diets. ●——●, hay given in a hay diet; ○– – –○, ground hay in a hay diet; ●·····●, ground hay in a ground-hay diet. Values for the faecal excretion of ground hay introduced into the abomasum through rumen fistulas are shown for cows W and Y. Values for this material were obtained in: ◑——◑, the hay diets; ◐——◐, the ground-hay diets.

the time a stained meal took to pass through the reticulo-rumen and through the remainder of the gut respectively.

Excretion curves (Fig. 6) for the excretion of ground hay given in a completely ground diet showed characteristics very different from those of curves for ground hay given with long hay or for the long hay. In cow W the initial appearance, as shown by the time required for 5% excretion, was 2 hr. later than the initial appearance of long hay and 3 hr. later than that of ground hay given with long hay (Table 4). In the other three cows the time required for the excretion of 5% of the ground-hay diet was probably shorter than that for the excretion of 5% of the long-hay diet, even between ground hay in the long-hay diet and ground hay in the ground-hay diet. The initial excretion of the ground-hay diet was therefore more rapid than that of the long-hay diet. This faster excretion was not continued. In three cows the 80 – 5% excretion of the ground-hay diet was more prolonged than that of the long hay (Table 4). In the fourth cow (W) there was a slight reduction in the time necessary for this level of excretion. All the cows excreted a small meal of ground hay more rapidly when the diet consisted mainly of long hay than when the hay was all ground. It may therefore be concluded that, although a small proportion of ground hay in a diet of long hay is excreted from the reticulo-rumen more rapidly than the long hay, the grinding of all the hay produces a decrease in rate of passage of hay through the reticulo-rumen. In comparison with long-hay diets ground-hay diets tended to be excreted more slowly or at the same rate, but never faster.

The data obtained from samples of the digesta in the reticulum (Fig. 5) showed that stained particles were continuously present in the digesta close to the reticulo-omasal orifice from the beginning of the marked meal. Any digesta passing to the omasum after the meal had started would therefore have contained at least a few stained particles. Since passage to the omasum seems likely to be a fairly continuous process (Phillipson, 1948) some stained particles might be expected to have entered the omasum very shortly after the beginning of the stained meal. The time taken for passage through the omasum, the abomasum and the intestines should therefore have been represented by the time taken for the first appearance of stained foods in the faeces. This theory was checked by comparison of the excretion of marked foods with that of marked residues from the abomasum. Since the first appearance of a marker is a very uncertain measurement in ruminants, the time taken for 5% excretion was preferred; it was usually 3–6 hr. later than the first appearance but could be determined with greater certainty than the first appearance. The percentages of marked hay from the abomasum excreted in the time necessary for the appearance in the faeces of 5% of the main food constituent were remarkably constant, varying from 93 to 97%.

This showed that some confidence might be placed in the '5% excretion time' as an index, and to some extent as an absolute measurement, of passage through the hind gut.

A measure of the spread of the excretion curves was obtained by subtracting the 5% excretion time from the time required for 80% excretion (80 – 5% excretion time). The very much greater spread of excretion curves for material that had passed

through the reticulo-rumen showed that the spread of excretion curves for eaten food (as opposed to food introduced directly into the abomasum) was an index of the time it had been retained in the reticulo-rumen.

Influence of mangolds on the rate of passage of hay (Exp. 5)

Changes in the consistency of faeces are frequently observed when cows are given access to succulent foods. This experiment was undertaken in order to find whether mangolds produced any change in the rate of passage of other foods and if so, whether that change influenced the digestibility of the diet.

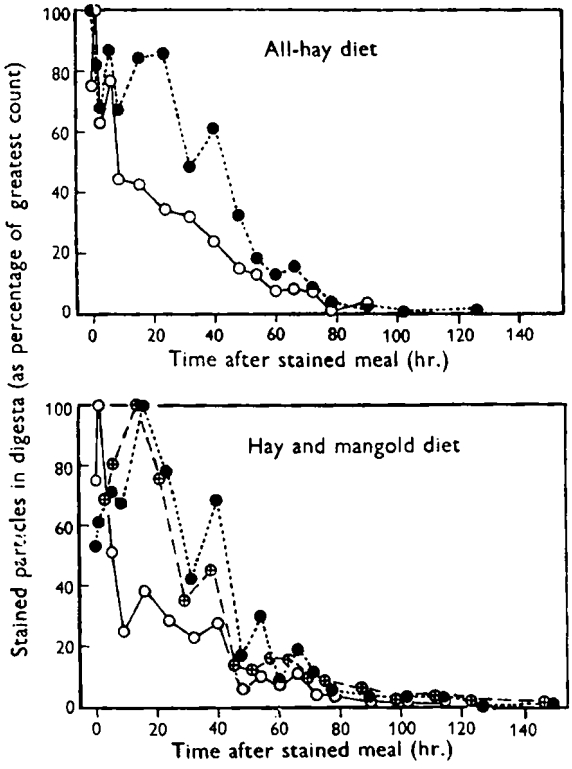

Fig. 7. Exp. 3. Numbers of undigested particles of various stained foods present in 0·1 g. digesta in the reticulum of cow A at intervals after stained meals. ●·····●, hay; ○——○, ground hay given with hay; ⊕– – –⊕, ground hay given with mangolds. Values are expressed as percentages of the greatest count.

Samples of digesta from the region of the reticulo-omasal orifice were removed through the fistula in cow A. The concentration curves shown in Fig. 7 are based on examination of these samples. The method of plotting was that used for similar figures in Exp. 4 (Fig. 5). The concentration in the reticulum of stained particles derived from hay was usually lower in the first 3 hr. than at any other time during the first 24 hr. The only exception was one in which a high count was obtained at 0·5 hr. after the stained meal. Particle size was estimated by counting those particles over 5 mm. in length. It was found that the largest particles were present 3 hr. after feeding in part 1

(all-hay diet) and 6 hr. after feeding in part 2 (hay and mangold diet). The average size of particles dropped appreciably after these times, whereas the greatest concentration was approximately maintained until 24 hr. in part 1 (ignoring the count made after 30 min.) and 15 hr. in part 2. These data suggest that the stained hay was being ruminated in the period between 6 and 24 hr. after feeding.

In both parts of the experiment the concentration in the reticulum of particles from the ground hay given with long hay showed a steady decline following feeding. The curves resembled those for similar ground hay in Fig. 5 and data for the concentration of oats in the rumen given by Usuelli (1933). Ground hay given with mangolds yielded a concentration curve resembling that for hay alone. This suggests that at least a part of the mangolds entered the rumen, carrying ground hay with it. However, since the faecal excretion curves for this ground hay given mixed with mangolds usually indicated a rapid rate of excretion, it is probable that not all the mangolds entered the rumen; a considerable proportion probably passed rapidly to the omasum.

The proportion of particles of digesta derived from stained hay that were over 5 mm. in length remained greater than 10% for 9 hr. in both parts of the experiment. The highest proportion was in both parts greater than 20%. In the faeces the proportion of these particles greater than 5 mm. was very rarely in excess of 7%. This difference could only have arisen if (*a*) the larger particles were screened off at the reticulo-omasal orifice, (*b*) they were further broken down after leaving the reticulo-rumen, or (*c*) passage from the reticulo-rumen was halted for 9 hr. after feeding.

The faecal excretion curves for hay and ground hay in the two diets are given in Figs. 8 and 9 respectively, and Table 5 contains a summary of the times required for

Table 5. *Exp.* 5. *The rate of excretion of hay by four cows* (*A*, *B*, *C and D*) *fed diets of hay and of hay and mangolds*

Type of hay and manner of feeding	Proportion of total residues from stained hay* (%)	Time required for excretion of undigested residues from stained hay (hr.)								Change due to mangolds			
		All-hay diet				Hay and mangold diet							
		A	B	C	D	A	B	C	D	A	B	C	D
		(*a*)				(*b*)				(*b*) − (*a*)			
Long	5	23	25	32	29	24	26	31	27	+1	+1	− 1	− 2
	80 − 5	57	63	56	54	48	61	71	78	−9	−2	+15	+24
		(*c*)				(*d*)				(*d*) − (*c*)			
Ground, given mixed with long hay	5	23	22	29	26	22	21	25	19	−1	−1	− 4	− 7
	80 − 5	51	49	44	55	43	45	64	68	−8	−4	+20	+13
						(*e*)							
Ground, given mixed with mangolds	5					51	20	28	20				
	80 − 5					39	43	56	66				

	Change due to grinding and mixing with hay											
	(*c*) − (*a*)				(*d*) − (*b*)				[(*d*) − (*b*)] − [(*c*) − (*a*)]			
5	0	− 3	− 3	− 3	−2	− 5	−6	− 8	−2	−2	− 3	− 5
80 − 5	−6	−14	−12	+1	−5	−16	−7	−10	+1	−2	+ 5	−11

* For explanation of these indices of the rate of excretion, see p. 372.

5% and 80 – 5% excretion of the hay and ground hay. The result of adding mangolds to the diet was obviously not the same with each cow, thus differing from results obtained here in a preliminary experiment (Anonymous, 1947). In cows A and B the spread of the excretion curve for hay (as shown in Table 5 by the time required for

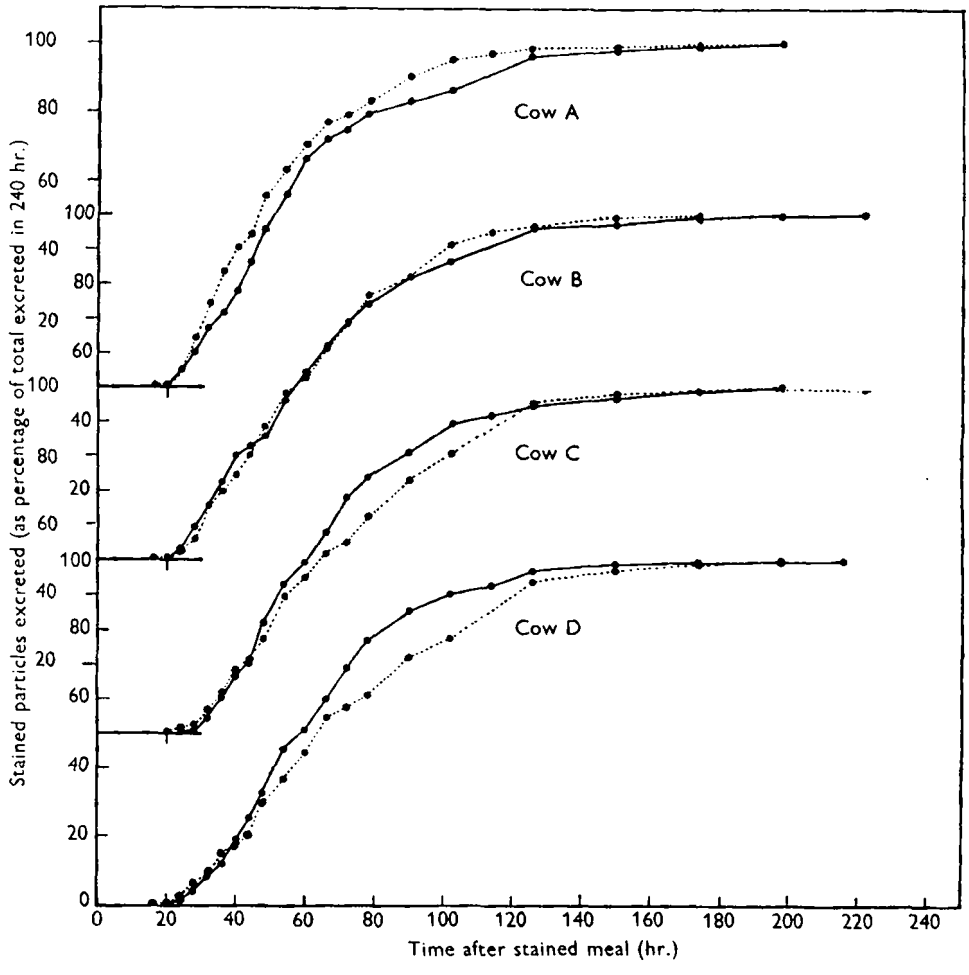

Fig. 8. Exp. 5. Values for the excretion (for definition of excretion see legend to Fig. 1) by four cows of undigested particles of stained hay in: ●— —●, all-hay diet; ●·····●, hay and mangold diet.

80 – 5% excretion) was decreased by the addition of mangolds; in the other two cows the roots caused a substantial increase in the spread of the curve. There was little change in the initial rate of excretion (5% excretion time in Table 5) although such changes as did occur were in an opposite direction to the changes in the spread of the excretion curve (80 – 5% excretion time).

The digestibility coefficients for these diets are given in Table 3. They were generally high, particularly for crude fibre, for which no reason can be given.

Relationship between variations in the rate of passage of food and variations in other factors

In the five experiments reported the rate of passage of foods was found to vary considerably both between and within cows. The causes of these variations and their influence on the determination of the degree of digestion are discussed below.

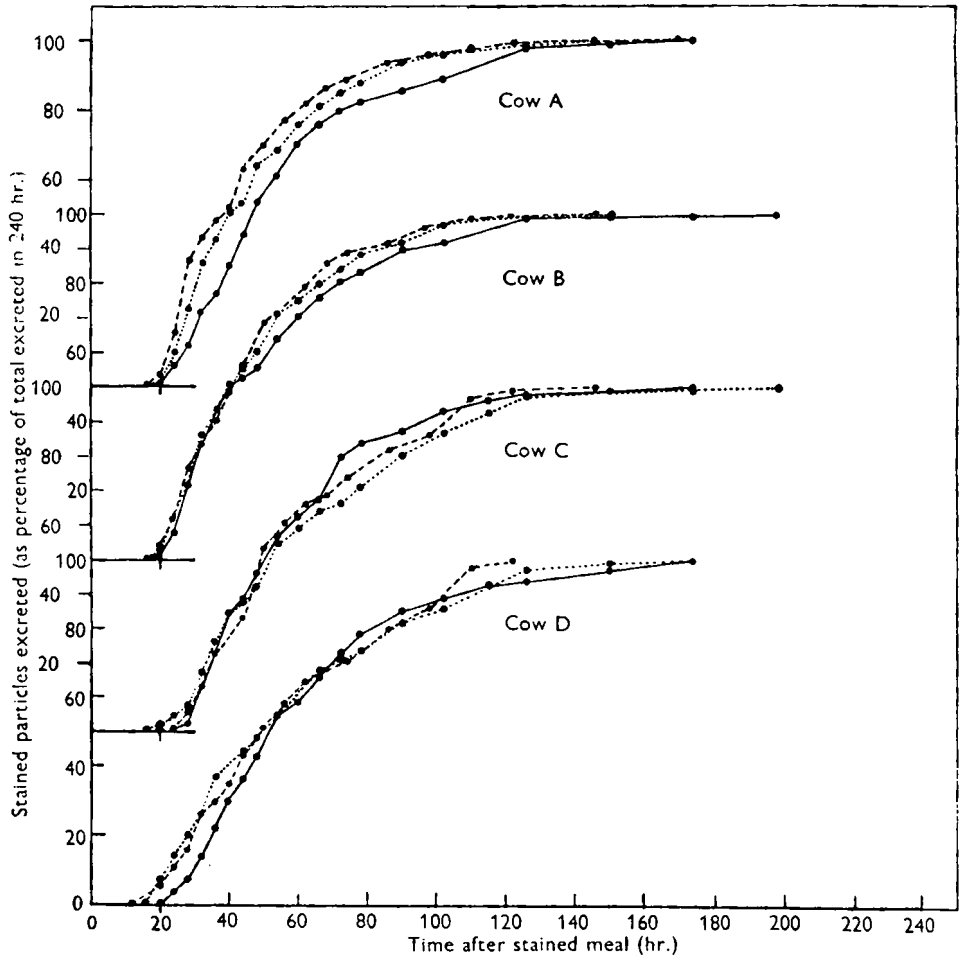

Fig. 9. Exp. 5. Values for the excretion (for definition of excretion see legend to Fig. 1) by four cows of undigested particles of stained ground hay given: ●——●, with hay in an all-hay diet; ●·····●, with hay in a mixed diet; ●– – –●, with mangolds in a mixed diet.

Relationship between variations in the rate of passage of food and variations in the size of cow and in the intake and faecal excretion of food and water. The importance of particle size in determining the rate of passage of constituents of normal diets has been fully demonstrated and will receive no further attention in this section.

Exp. 5, which showed the effect of mangolds on the rate of passage of hay, was most suited to an analysis depending very largely on between-cow differences. In Exp. 4 the cows were divided into two groups of two, and in each of the earlier experiments

only two cows were concerned. The data from Exp. 5 were accordingly examined in some detail, although the small number of cows concerned did not permit statistical interpretation of the results.

In Fig. 10 the two indices of rate of passage are plotted against the weight of the cows. There appeared to be some relationship between size of cow and variations in the time necessary for food to traverse the hind gut (5% excretion time), but there is

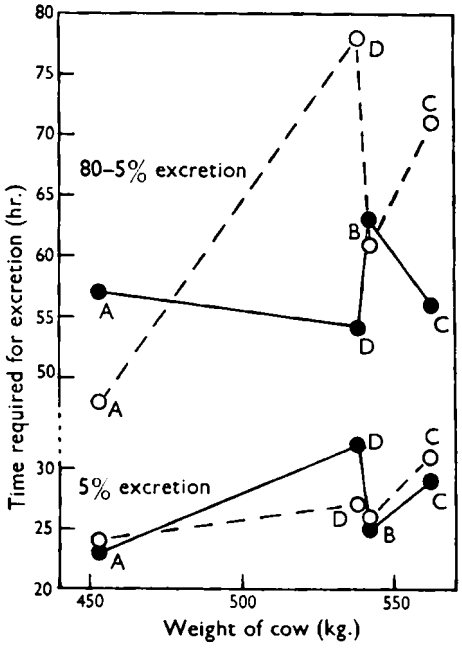

Fig. 10

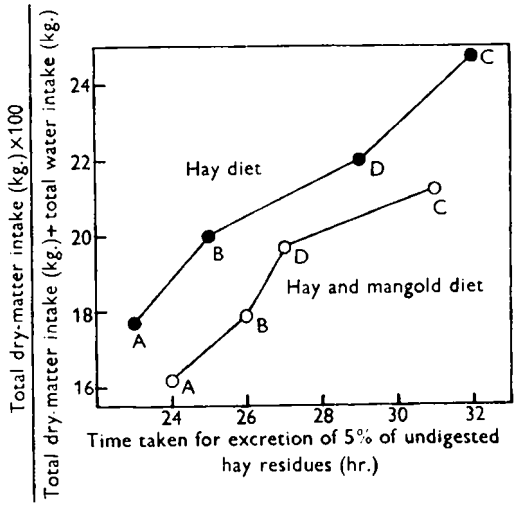

Fig. 11

Fig. 10. Exp. 5. Relationship between cow size in cows A, B, C and D and the time required for the excretion of 5% and 80−5% (for explanation of these indices of the rate of excretion see p. 372) of the residues from small meals of hay in diets of: ●——●, hay; ○----○, hay and mangolds.

Fig. 11. Exp. 5. Relationship in cows A, B, C and D between the percentage of dry matter in the total intake (food and water) and the time required for the excretion of 5% (for explanation of this index of the rate of excretion see p. 372) of the residues from a small meal of stained hay given with: ●——●, hay in diets of hay; ○——○, hay and mangolds.

little to suggest that size of cow was related in the same way to variations in the index of passage through the reticulo-rumen (80−5% excretion time). This observation may have been influenced by the fact that the cows were not fed to appetite.

The relationship of the indices of rate of passage to various measurements representing the physical condition and bulk of the diets was also studied. These measurements were plotted against the rate of excretion and they included the intake of hay and of total food, the production of faeces and the consumption of water, each factor being expressed per cow and per unit of body-weight. As shown in Fig. 11, between-cow variations in the time required for 5% excretion were closely related to between-

cow variations in the percentage of dry matter in the whole diet calculated as follows:

$$\text{Dry-matter content of whole diet (\%)} = \frac{\text{total dry-matter intake (kg.)} \times 100}{\text{total dry-matter intake (kg.)} + \text{total water intake (kg.)}}.$$

This suggests that wet conditions favoured passage through the hind gut. It is interesting to note that the addition of mangolds to the all-hay diet did not decrease the total dry-matter percentage of the diet very much because there was a reduction in the voluntary intake of water.

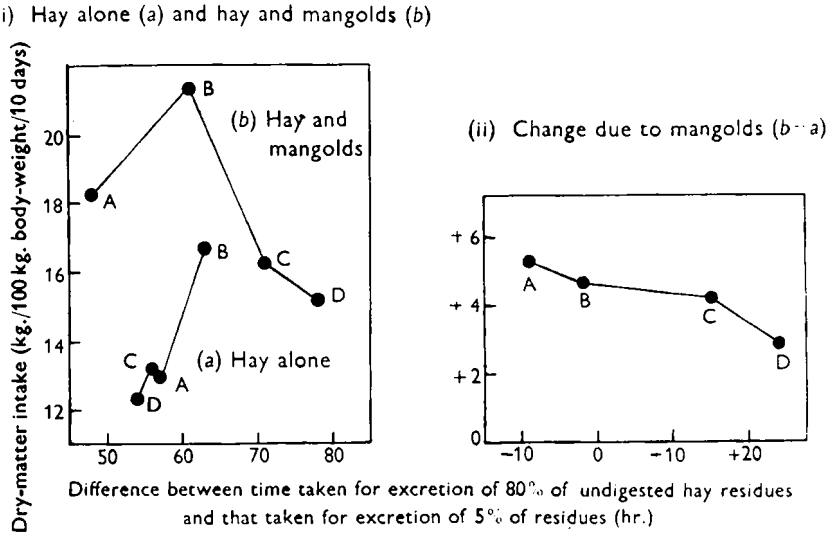

Fig. 12. Exp. 5. (i) Relationship in cows A, B, C and D between the total intake of dry matter and the time required for the excretion of 80−5 % (for explanation of this index of the rate of excretion see p. 372) of the residues from small meals of hay given in two diets. (ii) Relationship between the changes in these values caused by mangolds.

When cows were fed the diet of hay alone, between-cow variations in the index of rate of passage through the reticulo-rumen (80−5% excretion time) appeared to be related to the total intake of dry matter, especially when this was expressed as intake of dry matter/100 kg. cow weight (Fig. 12). The changes produced by mangolds in the 80−5% excretion time appeared to bear an inverse relationship to changes in the total intake of dry matter. It therefore appears that though hay was retained longest in the reticulo-rumen of the cow with the largest intake, even though that intake was not to appetite, the addition of extra dry matter as mangolds did not always cause a more rapid excretion of hay. In cows A and B, in which the daily addition of 22·7 kg. mangolds raised the total dry-matter intake by an amount greater than 0·47 kg./100 kg. live weight/day, there was a decrease in the index of passage through the reticulo-rumen. In cows C and D, in which the increase in dry matter was below 0·47 kg., the passage of hay was prolonged (Fig. 12). Similar relationships were found in the data for production of faeces, but the dry-matter percentage of the whole diet was unimportant in affecting passage from the reticulo-rumen.

In view of earlier claims, particularly those of Ewing & Smith (1917), it is interesting to note that none of the measures of rate of passage appeared to be related to the percentage of dry matter in the faeces.

The changes in rate of passage resulting from the grinding of hay have been traced to changes in the time the material was retained in the reticulo-rumen. Visual observation of the digesta in the rumen showed that when the cows were receiving a diet of long hay alone, with mangolds or with concentrates the reticulo-ruminal contents were arranged in two layers. These consisted of a tightly packed mass of dry fibrous digesta above a very fluid layer. When all the hay in the diet was ground, there was very little tendency for dry fibrous material to be packed into the dorsal sac of the rumen. Further exploration showed that the digesta derived from ground-hay diets were of a very even consistency throughout, and were apparently not divided into well-marked dry and liquid layers. These observations were confirmed by taking the mean dry-matter percentages of numerous samples of digesta removed during both day and night.

		Dry-matter content of digesta	
Type of hay in diet	Cow	Reticulum (%)	Dorsal sac of rumen (%)
Long	W	6·1	13·1
	Y	5·0	14·4
Ground	W	10·1	13·4
	Y	9·8	15·6

Cow W drank rather less water when she was eating ground hay than when her hay was not ground. The remaining three cows drank most water on the ground-hay diet. Therefore a higher dry-matter content throughout the digesta in the reticulo-rumen of cow Y may have been caused by an increased total amount of dry matter in the reticulo-rumen, a decreased flow of saliva, an increased absorption of water from the reticulo-rumen or an increased flow through the reticulo-omasal orifice.

When all the hay in the diet was ground the resulting arrangement of digesta in the reticulo-rumen produced a more rapid initial excretion of hay, possibly because the newly arrived food was retained longer in the reticulum and anterior rumen and was therefore in a position to pass the reticulo-omasal orifice, but the bulk of the marked meal was retained in the reticulo-rumen for longer than the bulk of diets containing unground hay.

Relationship between the rate of passage of food and digestibility. The correlation of the rate of passage and digestibility of food was studied in the data collected during the test of the reproducibility of readings (Exp. 2, p. 366). The correlation coefficients in the table on p. 382 show the relationship between these variables during the four parts of the experiment.

For significance at the 5% level r must equal $\pm 0{\cdot}95$. These factors did not therefore appear linked, and it seems unlikely that period-to-period differences in digestibility are the result of changes in the rate of passage of the food.

When an all-hay diet was ground the digestibility of the crude fibre of the hay was depressed; the digestibility of the crude protein, ether extractable substances and

nitrogen-free extract were all slightly raised (Table 3). Where the diet consisted of hay and concentrates the depression in the digestibility coefficients for crude fibre caused by grinding was very much more marked than in the all-hay diet, and the coefficients for other nutrients were also depressed (Table 3). These changes did not result from a more rapid passage of ground hay from the reticulo-rumen. Neither could the comparatively lower digestion of crude fibre by those cows that received concentrates than by those cows that did not receive them be explained by a more rapid passage of food through the reticulo-rumen.

Exp. 2. Correlation (r) between rate of passage (hr. for 80–5% excretion) and percentage digestibility of diet

Nutrient	Cow A	Cow B
Dry matter	+0·756	−0·772
Crude protein	−0·927	−0·570
Ether extract	−0·901	+0·796
Nitrogen-free extract	−0·352	+0·103
Crude fibre	+0·851	−0·754

Exp. 5 was used for a more exhaustive examination of between-cow variations in the digestibility and rate of passage of foods. In Fig. 13 the digestibility coefficients for the four cows are shown plotted against the time required for 80–5% excretion of hay. Values for the two diets are shown plotted separately and the changes produced by the mangolds are also compared. A more prolonged retention of hay in the reticulo-rumen apparently caused a less complete digestion of crude protein and ether extractable substances. Between cows on the two diets there was little relationship between the rate of passage of hay and the digestibility of crude fibre, but the magnitude of the changes produced by mangolds in the rate of passage of hay and in total digestibility seemed to be linked. In this experiment a shortened period of retention of food in the reticulo-rumen (80–5% excretion time) was accompanied by a depressed digestion of crude fibre, and a lengthened period of retention was accompanied by a raised digestion. The change in fibre digestion was about 0·4%/hr. in the 80–5% excretion time. There was no discernible relationship between the digestibility of nitrogen-free extract and the rate of passage of hay. The correlation between the times required for 5% excretion and digestibility coefficients, in the four cows, was no higher than would be expected from the small negative relationship which existed between the time required for 5% and the time required for 80–5% excretion (Table 5).

Between-cow variation in the digestibility of the important crude fibre fraction during Exp. 5 could not be entirely explained by variations in the rate of passage of hay. It was therefore permissible to search the data obtained for other variables that might have been concerned. Variations in crude-fibre digestion were accordingly compared with the measures (p. 379) of the physical condition and bulk of the diet. The most apparent relationship was with the dry-matter content of the total intake (food eaten and water drunk) during the all-hay diet (Fig. 14). The digestibility of crude fibre appeared to increase with the proportion of water in the total intake. It is not unlikely that this effect was due to an increased fluidity of digesta in the reticulo-

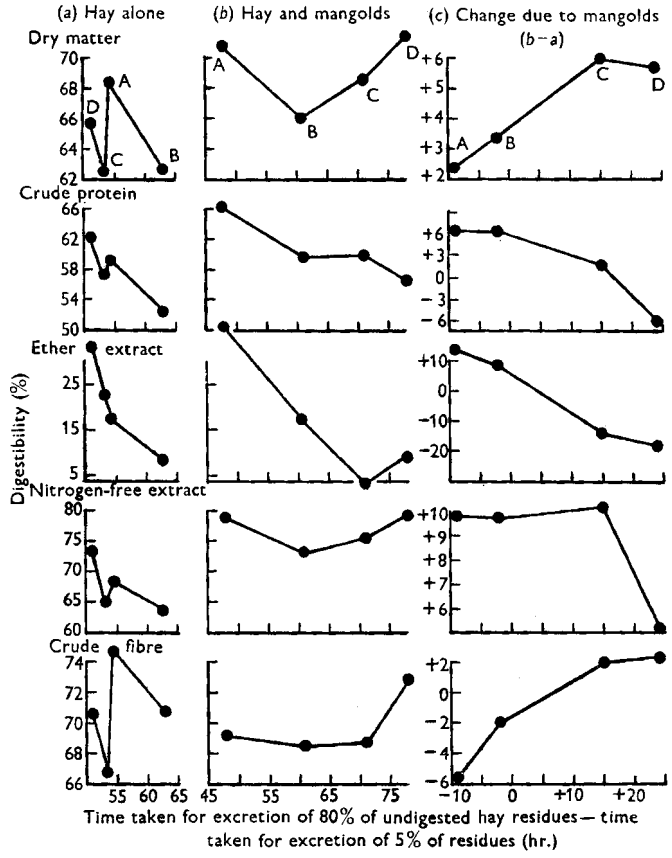

Fig. 13. Exp. 5. Relationship in cows A, B, C and D between digestibility and the time required for the excretion of 80−5% (for explanation of this index of the rate of excretion see p. 372) of the residues from small meals of (*a*) an all-hay diet, and (*b*) a hay and mangold diet. The relationships between changes in these values (*b*−*a*) resulting from the addition of mangolds are shown in (*c*).

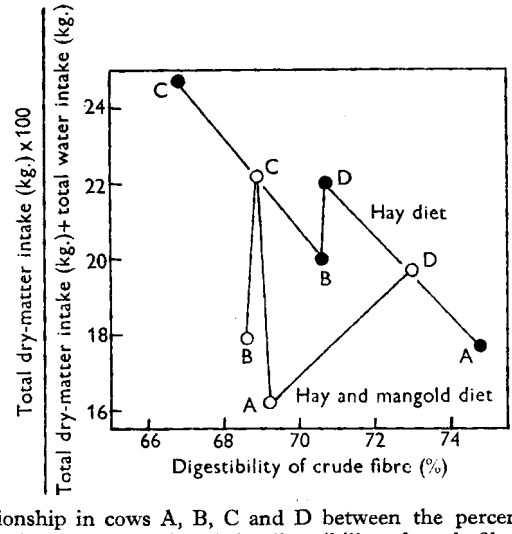

Fig. 14. Exp. 5. Relationship in cows A, B, C and D between the percentage of dry matter in the total intake (food and water) and the digestibility of crude fibre of two diets.

rumen. When mangolds were given, the changes in the total percentage of dry matter were small and it has already been shown that the resultant change in fibre digestion may be explained by a changed rate of passage of hay.

DISCUSSION

Rate of passage. The term 'rate of passage' has been used in this paper to denote the time taken by undigested residues of a marked meal to pass through the digestive tract or through some part of the digestive tract. This is by no means the same thing as 'the flow of digesta', a term which is used (e.g. by Phillipson, 1948) for the rate at which digesta pass a point in the digestive tract. In tube-like organs such as the intestine, successive portions of a meal may be expected to change places relatively little. In fact, if the entire gut was of a tube-like construction rate of passage and rate of flow would mean much the same thing. However, in the ruminant, the reticulo-rumen causes so much mixing that at any given time the digesta passing any point posterior to the reticulo-omasal orifice contain residues from many meals.

Previous measurements of the rate of passage of foods and food residues in ruminants have been expressed as curves showing the concentration of stained particles per unit of faeces at intervals after feeding (see, for example, Usuelli, 1933; Columbus, 1936). Individual readings have sometimes been expressed as a percentage of the total of all readings, but this was no measure of the progress of excretion because the amount of faeces produced between samplings was not considered. Concentration curves could only be compared by means of the time taken for the first appearance, peak excretion or final appearance of the marker. In ruminants all these points are likely to vary and their exact position may be uncertain. Concentration curves were accordingly only used in this work for recording the concentration of stained particles in the reticulo-rumen of fistulated cows. Comparison of excretion rates was made by means of excretion curves showing the cumulative percentage of the total undigested particles produced at any time after feeding. Curves of this type were used by Moore & Winter (1934) to show the excretion of inert markers.

Hay was the basis of all the diets used in this series of experiments. Excretion curves for its excretion in faeces had a typical sigmoid shape and showed that in any one cow hay was excreted at a slower rate than any of the other foods studied. The initial appearance of stained hay in the faeces varied between 12 and 24 hr. after feeding and excretion of the first 10% was slow, frequently requiring a further 10–15 hr. Through the main part of the curve, excretion of the next 70% of the residues was more rapid, rates of 1·5%/hr. being quite usual, so that 80% of the residues were typically excreted in 70–90 hr. The curves then rapidly flattened and excretion continued at a slowly decreasing rate until 7–10 days after the marked meal. Retention in the rumen and rumination were shown to be the major factors in determining the spread of the excretion curves, and the time of the first appearance of the marker in the faeces was determined by the rate of its passage through the omasum, the abomasum and the intestines. The results obtained agree, as far as comparison can be made, with the concentration curves of Usuelli (1933) for cows. Excretion of roughage in cows appeared to be rather less prolonged than excretion in sheep and goats (cf. Columbus, 1936).

Excretion curves for chaff and ground hay mixed with hay showed that finer particles were excreted more rapidly than large ones; in some cows chaff behaved like hay, in others like ground hay. The difference was apparently due to a more rapid removal of fine particles from the reticulo-rumen. Schalk & Amadon (1928) suggested that such particles would absorb water most rapidly and therefore sink into the liquid layer and be removed. This explanation would fit the present data, but measurements of particle size in the digesta close to the reticulo-omasal orifice and in the faeces suggested that either sifting of large food particles occurred at the orifice or else the particle size was reduced at a later stage in the gut. The high initial excretion of ground hay would therefore have occurred before the particle size of the long hay was reduced by rumination. The rapid excretion of residues from concentrate husks and from ground hay given with concentrates may also have been partly due to their rapid initial passage from the reticulo-rumen because ground hay mixed with the concentrates was excreted more rapidly than ground hay mixed with chaff or hay. The small spread of excretion curves for cottonseed husks in the concentrates supports this view, but could also have resulted if the husks had been more digestible than hay. However, experiments (Balch, unpublished data) in which hay and husks were suspended in silk bags inside the rumen of cows suggested that there was little difference in the rate of breakdown of husks and hay.

The experiments produced some evidence (Exp. 5) that in cows with a high intake of dry matter, consisting only of hay, the passage of hay from the reticulo-rumen was more prolonged than in cows with a smaller intake. When, in the same experiment, the total intake of dry matter was raised by reducing the hay and adding daily 22·7 kg. mangolds, the rate of passage of hay through the reticulo-rumen was increased provided the total increase in dry matter exceeded 0·47 kg./100 kg. live weight/day. In the two cows in which the total increase was less than 0·47 kg. the rate of passage of hay through the reticulo-rumen was decreased. If the hay intake had not been reduced the mangolds would probably have caused a more rapid excretion in all of the cows. The mechanism responsible for this property of mangolds was not discovered. If it was due to the additional water carried into the rumen by the mangolds, that water must have functioned differently from water entering the rumen after drinking, because the total dry-matter percentage of the diet and the weight of water drunk by the cow had little influence on the time hay remained in the reticulo-rumen.

The introduction of marked ground hay into the abomasum showed that passage from the abomasum to the faeces was rapid. The time required for the excretion of 5% of a marked meal could also be used as an index of passage through the omasum, the abomasum and the intestines. Since the faecal excretion of material from the abomasum was spread over a very short period the amount of mixing in later stages must have been small. Therefore, as there was no break between the final excretion of this marker and the initial appearance of the meal passing from the reticulum, the material by-passed in the omasum cannot have been large, neither can any digesta free of stained particles have left the reticulo-rumen after the marked meal was fed. The first appearance of material from the abomasum preceded that of the meal from the reticulo-rumen by 3–7 hr. As the ground hay was suspended in water when placed in the

stomach, this difference may have been due to some of the marker being washed ahead. It may also have been due to a delayed passage from the reticulum to the omasum following feeding. In this instance it may not be without significance that the apparent delay was greater when 2 l. of suspension were inserted in the abomasum than when only 0·5 l. was used.

The percentage of water in the complete diet appeared to exert some influence on passage through the hind gut, a high percentage being associated with a fast passage. However, with the diets studied the dry-matter percentage of the faeces of different cows did not appear to be related to their rates of passage.

Relationship between rate of passage and digestibility. The variations from period to period of digestibility coefficients for one cow on the same diet could not be explained by changes in rate of passage. The ability to digest the crude-protein and ether-extract fractions of hay or hay and mangold diets was greatest in cows that retained hay particles for the least time in the reticulo-rumen. As these also tended to be the cows with the slowest index of rate of passage through the hind gut the exact cause of the changed digestibility could not be established from the data obtained. In the same experiment variations between cows in the digestibility of the crude fibre of all-hay diets were not related to the rate of passage of food. The efficiency of fibre digestion was greatest when the moisture intake was highest in relation to dry-matter intake. However, the change in the digestibility of fibre caused by mangolds could not be explained by the small changes that took place in the water percentage of the diet. It could, however, be explained by changes in the rate of passage of foods. The digestion of crude fibre may be presumed to have largely occurred in the reticulo-rumen. Therefore, these results suggest that the digestion of crude fibre must have proceeded most rapidly when the food was accompanied by the greatest amount of water. It is not unreasonable to assume that digesta in the reticulo-rumen were then most fluid. Since the addition of mangolds to the diet changed the time hay was in the reticulo-rumen but did not greatly change the proportion of water to dry food, it is logical that the resultant change in fibre digestibility should vary, as it was found to vary, with the rate of passage of hay.

Exp. 4 reproduced the changes in digestibility that were known to result from grinding hay (e.g. Bechdel & Williams, 1929; Heller, Wall & Briggs, 1941) and adding concentrates to hay diets (Bechdel & Williams, 1929; Burroughs, Gerlaugh, Edgington & Bethke, 1949). Simultaneous measurements of the rate of passage of foods showed that changes in this factor were not the cause of the changes in the digestibility of the foods. The depression of crude fibre digestibility that followed grinding may have been influenced again by a change in the fluidity of digesta in the reticulo-rumen. Observations by means of rumen fistulas showed that when all the hay in the diet was fed ground the contents of the ventral parts of the reticulo-rumen were drier than when the cows were eating the same diets containing unground hay. The general depression of the digestibility of food in the cows receiving concentrates was greatest when the hay was ground, although the reason for this was not apparent.

SUMMARY

1. Existing techniques were elaborated to give a method of measuring the rate of passage of undigested food residues in cows. The method consisted of feeding a small meal of stained food and counting the stained particles in subsequent voidings of faeces. The principal marked food was hay. The amounts of faeces voided were used to determine the percentage of the total stained particles that had been excreted at any given time after feeding, and the data were used to plot excretion curves.

2. The time between feeding and the initial appearance of the marker in the faeces was found to be an index of the rate of passage of digesta (see p. 374) through the omasum, the abomasum and the intestines. The spread of the excretion curves proved to be indicative of the rate of passage of the marked meal through the reticulo-rumen.

3. In five experiments with dairy cows excretion curves for hay were characterized by an initial appearance of marker in the faeces varying from 12 to 24 hr. after feeding, a slow excretion of the first 10% of the residues followed by a higher rate of excretion typically resulting in the passage of 80% of the residues within 70–90 hr. Excretion then proceeded more slowly and was completed 7–10 days after feeding.

4. Ground hay given as a small addition to unground hay was invariably excreted more rapidly than the unground hay. Ground hay in diets in which all the hay was ground was usually excreted over a longer period than hay in a similar diet in which the hay was not ground. Both these differences were due to changes in the movement of the foods in the reticulo-rumen.

5. In two cows the addition of mangolds to a diet of hay increased the spread of the excretion curves for hay, suggesting that the hay had remained longer in the reticulo-rumen; in two other cows on the same experiment the results suggested that the hay had remained in the reticulo-rumen for a shorter time. The magnitude of these differences in the spread of the excretion curves appeared to be related to simultaneous increases in the total intake of dry matter. In this experiment between-cow variations in the ratio of the dry matter consumed by the cows to their water consumption appeared related to the rate of passage of hay through the omasum, the abomasum and the intestines; in general, the passage of foods through this section of the gut tended to be rapid when the diet included a high proportion of water. Indirect evidence suggested that the rate of passage of mangolds from the reticulo-rumen was more rapid than that of hay.

6. Differences in the rate of passage of hay were not correlated with the digestibility of the diet in an experiment in which the same diet was given continuously. Changes in the digestibility of the total diet following the addition of mangolds to an all-hay diet were correlated with simultaneous changes in the rate of passage of hay. These relationships suggested that a decreased rate of passage of food through the reticulo-rumen was accompanied by a raised digestion of crude fibre and a lowered apparent faecal digestibility coefficient for crude protein and ether extractable substances.

7. The breakdown of crude fibre in the reticulo-rumen was more rapid when the ruminal contents were more fluid than when they were less fluid.

8. The depressions in the digestibility of the crude fibre of hay, known to occur

when hay is ground or where highly digestible carbohydrates are added to diets of hay, were not the result of changes in the rate of passage of the hay.

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