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Post-abomasal digestion of carbohydrate in the adult ruminant

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Gray (1947) studied sites of digestion in sheep of the cellulose contained in a mixed ration of lucerne hay and wheat straw by applying the lignin ratio technique to analyses of digesta obtained from slaughtered animals. The technique has also been used by Hale, Duncan & Huffman (1947) to study cellulose digestion in cows fed lucerne hay, by Marshall (1949) to study the digestion of pentosans in sheep fed hay and by Rogerson (1958) to study digestion of crude fibre and nitrogen-free extractives contained in three rations fed to sheep. Apart from errors that may arise from the use of lignin as an indigestible marker, results obtained using the above method suffer the disadvantage that they relate to conditions pertaining in the tract at specific times after feeding. The development of techniques for inserting re-entrant cannulas into various parts of the alimentary tract of the ruminant has greatly facilitated studies in this field (Phillipson, 1952; Ash, 1962).

Extent and sites of digestion of starch

Table 1 shows the extent and sites of digestion of starch in rations fed to both sheep and cattle, and Table 2 gives additional information for starch contained in diets fed to sheep only. The results presented in Table 1 show that for the feeds examined there is good agreement between sheep and cattle regarding overall digestibility of starch and, in four of the six feeds examined, the extent to which it is digested in the reticulo-rumen. In the case of the rations containing 20 and 80% ground maize the results suggest that more starch enters the small intestine in cattle than in sheep. The results in Table 1 do not allow a comparison to be made between sheep and cattle on the extent to which starch entering the small intestine is digested therein or is lost in subsequent passage through the caecum and colon. The slightly lower values shown in Table 1 for digestibilities of starch for sheep (Tucker, Mitchell & Little, 1968) compared to cattle, when rations containing 20–60% ground maize were fed, are of doubtful significance. Each coefficient is the mean of

Table 1. *Extent and sites of digestion of starch contained in diets fed to both sheep and cattle*

Feed*	Animal	Starch ingested (g/24 h)	Digestibility of starch (%)	Disappearance of digested starch (%)				Reference
				Before small intestine	In small intestine	In caecum and colon		
Ground maize 20, ground lucerne hay 76	Sheep	172	94.5	84.2	33.4	15.8	→	Tucker <i>et al.</i> (1968)†
	Cattle	1002	98.8	65.2	33.4	1.4	→	Karr <i>et al.</i> (1966)‡
Ground maize 40, ground lucerne hay 53	Sheep	326	96.6	72.8	27.2	→	→	Tucker <i>et al.</i> (1968)†
	Cattle	1948	99.0	72.8	24.0	3.2	→	Karr <i>et al.</i> (1966)‡
Ground maize 60, ground lucerne hay 31	Sheep	460	97.2	71.2	28.8	→	→	Tucker <i>et al.</i> (1968)†
	Cattle	2438	98.4	69.2	25.4	5.4	→	Karr <i>et al.</i> (1966)‡
Ground maize 80, ground lucerne hay 7.5	Sheep	576	98.4	76.4	23.8	11.3	→	Tucker <i>et al.</i> (1968)†
	Cattle	2684	97.7	64.9	23.8	0.2	→	Karr <i>et al.</i> (1966)‡
Barley (grain with husk) 85, soya-bean oil meal 7.5 (fed pelleted)	Sheep	208	99.6	94.4	5.4	→	→	Toppers, Kay & Goodall (1968)§
	Cattle	(285)	(99.4)	(93.8)	(4.5)	(1.7)	→	Toppers, Kay, Goodall, Whitelaw & Reid (1968)¶
Hay, milled and pelleted	Sheep	1334	99.5	95.9	4.1	→	→	Toppers, Kay & Goodall (1968)
	Cattle	(1273)	(99.8)	(95.7)	(4.3)	→	→	Reid (1968)¶
	Sheep	34	88.0	84.4	-3.3	18.9	→	Toppers, Kay & Goodall (1968)
	Cattle	128	64.3	79.6	20.4	→	→	Toppers, Kay, Goodall, Whitelaw & Reid (1968)

*Only major feed constituents are shown; numerals indicate percentages of individual constituents present.

†Mean values calculated for Expts 1 and 2.

‡Values obtained in Expt 1.

§Mean values calculated from the values for starch determined enzymically by the method of MacRae & Armstrong (1968); values for the sheep Ingrid were not included (see authors' comments, p. 270). The mean values in parentheses have been calculated from the values for starch determined by the anthrone procedure of Clegg (1956).

¶Mean values calculated from the values for starch determined by the method of MacRae & Armstrong (1968). Those shown in parentheses have been calculated from the values for starch determined by the method of Clegg (1956).

Table 2. *Extent and sites of digestion of starch contained in diets fed to sheep*

Feed*	Starch ingested (g/24 h)	Digestibility of starch (%)	Disappearance of digested starch (%)			Reference
			Before small intestine	In small intestine	In caecum and colon	
(a) Diets containing cereals						
Hay 75, dairy cubes 25	45	97.6	90.0	←—— 10.0 ———→	} Sutton & Nicholson (1968)	
Hay 20, dairy cubes 34, and flaked maize 45	168	99.8	96.2	←—— 3.8 ———→		
Hay 20, dairy cubes 18, and flaked maize 62	363	99.8	94.7	←—— 5.3 ———→		
Hay 19, dairy cubes 12, and flaked maize 69	579	99.6	94.5	←—— 5.5 ———→		
Hay 67, rolled barley 33	171†	100	90.7	8.9	0.4	} MacRae & Armstrong (1969)
Hay 33, rolled barley 67	321	100	92.5	7.1	0.4	
Hay 33, flaked maize 67	323	100	89.7	10.4	0.0	
Rollled barley	396	100	92.0	8.0	0.0	
Rollled barley	543	ND	96.8‡	←—— 3.2 ———→		
Whole barley	552	ND	94.8‡	←—— 5.2 ———→		
(b) Forages						
Hay chopped	14	100	81.8	18.2	0.0	MacRae & Armstrong (1969)

ND, not determined.

*For mixed diets, only major feed constituents are shown; numerals indicate percentages of individual constituents present.

†Glucose yielded × 0.90.

‡Digestibility assumed to be 100%.

three values; thus for example on the 20% maize ration, the coefficients were 87.1, 98.4 and 98.2. The digestibility coefficients shown in Table 2 confirm the virtually complete digestion of starch contained in a wide variety of rations fed to sheep.

Both cattle and sheep are able to digest completely the starch contained in certain cereal-based diets. The results obtained by MacRae & Armstrong (1969) for sheep fed whole or rolled barley suggest that its digestive system can handle with equal effectiveness either form of the grain (see Table 2). This is borne out by the close agreement obtained in these studies for digestibility coefficients of dry matter (88.1 whole; 87.9 rolled) for nitrogen (83.5; 82.1) and for gross energy (87.7; 88.0). The same might not be true for cattle fed whole and rolled barleys, and Morrison (1959) quotes evidence that in dairy cows fed whole shelled maize 18–35% of the grain passes through the entire tract virtually undigested.

With cattle and sheep fed hay the values in Tables 1 and 2 give a mean value for the starch entering the small intestine, expressed as a percentage of that digested, approximating to 18. Quantitatively the amount of starch entering the small intestine on such diets is of little significance because of the small amounts occurring in the feed. The values presented for forages in Tables 1 and 2 agree well with the conclusions of Heald (1951), Weller & Gray (1954) and Porter & Singleton (1965) that on roughage diets very little α -linked glucose polymer passes the pylorus of the sheep.

From the results shown in Tables 1 and 2 for the sites of digestion of starch in cereal-based diets it is apparent that the diets fall into two categories, namely, those containing barley or flaked maize and those containing ground maize. Table 3 gives overall mean values for the results from Tables 1 and 2 for each of these categories; the means shown are those derived only from experiments in which the extent of digestion in the small intestine and in the caecum and colon has been considered separately. This restriction necessarily results in the exclusion of a

Table 3. *Mean values for the extent and sites of digestion of starch in cereal-containing diets fed to cattle or sheep calculated from values given in Tables 1 and 2. Only the results of those experiments in which digestion in the small and large intestines has been considered separately have been included. Mean values for all the values in Tables 1 and 2 are shown in parentheses.*

Feed category	Fed to	Digestibility of starch (%)	Disappearance of digested starch (%)		
			Before small intestine	In small intestine	In caecum and colon
Diets containing barley or flaked maize	Sheep	99.9* ± 0.25 (99.8)†	91.8 ± 0.8 (93.8)	8.0 ± 0.8	0.2 ± 0.09
Diets containing ground maize	Cattle	98.5‡ ± 0.40 (97.6)§	68.0 ± 1.8 (72.1)	26.7 ± 2.2	5.3 ± 2.1

*Mean of five values for sheep.

†Mean of ten values for sheep and one value for cattle.

‡Mean of four values for cattle.

§Mean of four values for cattle and four values for sheep.

number of results for each feed category shown in Tables 1 and 2. However, mean values for all the results relating to overall digestibility and percentage of the digested starch that disappeared before reaching the small intestine for each feed category are shown in parentheses in Table 3: in no instance were the values appreciably different from the means of the selected results.

On diets where the cereal component is barley or flaked maize the overall mean value for the amount of starch entering the small intestine of the sheep as a percentage of that digested (or ingested since digestibility is virtually 100) is 8.0% (see Table 3) and this is almost completely digested in its passage through the small intestine. In the experiments of MacRae & Armstrong (1969) referred to in Table 2, the eight observations made with sheep on diets in which rolled or whole barley was fed alone or was the major feed constituent gave a value for starch entering the small intestine expressed as a percentage of that ingested of 6.0 ± 0.76 , which was significantly lower than that of 10.4 ± 1.3 found by these authors for a diet of 1 part hay: 2 parts flaked maize.

With diets containing ground maize the mean value for the amount of starch passing the pylorus of cattle approximates to 32% of that ingested (Table 3) and while the major part of this (83%) is apparently digested in the small intestine small but nevertheless significant amounts are lost in passage through the caecum and

colon. These amounts increase as the proportion of ground maize in the diet increases (see Table 1). Evidence of an appreciable digestion of starch occurring in the small intestine of ruminants fed maize is also provided by the studies of Wright, Grainger & Marco (1966).

With reference to the marked difference in sites of starch digestion for feeds containing barley or flaked maize on the one hand, and ground maize on the other, two points need emphasis. The values for the diets containing barley or flaked maize relate to sheep, those for the ground maize diets to cattle, and it has already been noted that in two of the four rations containing ground maize fed to both cattle and sheep (Table 1) the values for the amounts of starch entering the small intestine were lower for sheep. Secondly, in all the experiments relating to the feeding of ground maize, starch was estimated by the anthrone procedure of Hassid & Neufeld (1964), while in all the others an enzymic method for starch estimation has been used. To the extent that the two procedures may give rise to considerably different patterns of starch disappearance along the tract if used on the same experimental material then the different results for ground maize diets on the one hand and for barley and flaked maize diets on the other may be more apparent than real. Some indication that the difference between diets cannot be attributed to difference in analytical procedure used for estimating starch can be obtained from the values shown in Table 1 for a high-barley diet calculated using the results obtained by Topps, Kay & Goodall (1968) for sheep and Topps, Kay, Goodall, Whitelaw & Reid (1968) for steers. It can be seen that the anthrone method of Clegg (1956) used by these workers gave values comparable to those determined using the enzymic procedure of MacRae & Armstrong (1968).

It must also be recalled that in all the experiments referred to no distinction has been made between starch of feed origin that has escaped fermentation in the reticulo-rumen and that of microbial origin, particularly protozoal, that may be produced within that organ and subsequently enters the lower part of the alimentary tract.

Carbohydrases concerned in starch digestion in the small intestine

The enzymes concerned in the digestion of starch in the small intestine are the amylases and maltases of pancreatic juice and the amylase, maltase and oligo-1:6-glucosidase of intestinal mucosa. Siddons (1968) has shown that pancreatic juices from mature cattle have high amylase and weak maltase activities. In young (14-16 week old) calves maltase activities in pancreatic juice were similar to those in adult animals while pancreatic amylase levels, although appreciable, were lower.

The influence of diet at least in mature animals is clearly indicated by the results of Clary, Mitchell & Little (1967). These workers showed that as the maize level in the diet of yearling wethers increased from 20 to 80% the level of amylase activity in the pancreatic juice increased significantly and fell again as the proportion of maize in the diet decreased.

Activities of these enzymes in the mucosa of the small intestine have been measured in mature cattle by Siddons (1968) and in mature sheep by Hembry, Bell

& Hall (1967). Siddons showed the levels of amylase activity in homogenates of the intestinal mucosa to be little different from those found in 14–16 week old calves either weaned at 6 weeks or milk-fed. Levels of maltase activity were also reported to be similar to those found in young calves. In the studies of Hembry *et al.* (1967) both enzymes were present in each of the three regions of the small intestine (duodenum, jejunum and ileum), the highest level of each being found in the jejunum. Since in all regions intestinal maltase activity in intestinal mucosa exceeded amylase activity, these workers concluded that digestion of starch in the small intestine was not limited by maltase activity, a view that was supported by their failure to detect starch hydrolysis in the isolated segments of the intestinal tract in the absence of pancreatic amylases. Information is lacking on the activity of oligo-1:6-glucosidase in ruminant intestinal mucosa.

That hydrolysis of starch in the small intestine appears to be slow is shown by the failure of Huber, Jacobson, McGilliard & Allen (1961) to detect any response in blood sugar levels to administration of starch into the omaso-abomasal area of mature cattle.

It is of interest to comment on the area within the small intestine where pH conditions would most favour starch hydrolysis. The pH optima for α -amylase from pig pancreatic juice is 6.9 (Long, 1961), for maltase of calf intestinal mucosa is 6.8–7.0 (Siddons, 1968), and for oligo-1:6-glucosidase is 6.2–6.4 (Long, 1961). The pH range found in digesta passing the pylorus on hay plus barley diets lies in the range of 2.6–3.5 and at the ileum 8.0–8.3 (MacRae, 1967). In sheep fed grass cubes the pH values of digesta at various points along the small intestine have been reported by Lennox & Garton (1968). At the start of the jejunum the range was 2.5–4.0, at the end of the upper jejunum 3.9–5.0 and at the end of the jejunum 7.2–7.9. It would, therefore, seem reasonable to suppose that maximal hydrolysis of starch to glucose would occur in the proximal half of the jejunum, and in this connexion it is of interest to recall that activities of intestinal amylase and maltase were highest in the jejunum compared to the activities in duodenum and ileum (Hembry *et al.* 1967). It is also noteworthy that in the experiments of Wright *et al.* (1966) the major part of digestion of the considerable amount of starch entering the small intestine was virtually completed in the first third of the tract.

On diets containing much ground maize the quantity of starch reaching the terminal ileum was appreciable and increased as the level of maize in the ration increased (Karr, Little & Mitchell, 1966). The experiments of Little, Mitchell & Reitnour (1968), in which increasing amounts of maize starch were infused into the abomasum of mature cattle, also indicate that there is a limit to the ability of the small intestine to digest starch, although in these experiments the animals were fed a basal ration of lucerne hay and hence pancreatic amylase levels may have been low (Clary *et al.* 1967). Evidence suggesting increasing microbial fermentation in the distal part of the small intestine will be referred to later. It seems likely that starch which has not undergone host-enzyme digestion in the proximal part of the small intestine would be subjected to fermentation in the distal part; starch reaching the

caecum would certainly be subjected to microbial degradation yielding volatile fatty acids.

The contribution that starch digested and absorbed as glucose in the small intestine may make to glucose requirement

If it is assumed that the starch which disappears in the small intestine is broken down to glucose and absorbed as such, the contribution that such glucose would make to the overall glucose requirement can be calculated. The calculation has been made from the values shown in Table 1 for rations containing 40 and 60% ground maize (Tucker *et al.* 1968); the assumptions have been made that the magnitude of the loss of starch in the small intestine of the sheep is the same as that reported for cattle on these rations and that 1 g starch yields 1.111 g glucose. For a sheep of 40 kg live weight (W) glucose absorption from the small intestine would be 5.3 and 8.0 g/ $W_{\text{kg}}^{0.75}$ respectively; both figures are above the requirement of 4.4 g/ $W_{\text{kg}}^{0.75}$ calculated for the non-pregnant animal (Armstrong, 1965). Comparable values calculated for the cattle (360 kg live weight) fed these rations by Karr *et al.* (1966) are 6.2 and 8.2 g/ $W_{\text{kg}}^{0.75}$. If the same starch intakes received by the sheep on the 40 and 60% ground maize diets fed in the experiments of Tucker *et al.* (1968) were supplied in the form of barley or flaked maize then, using the mean values given in Table 3 for the magnitude of starch digestion in the small intestine on such diets, it can be calculated that the intake of glucose from the small intestine would amount to 1.8 and 2.6 g/ $W_{\text{kg}}^{0.75}$ respectively. It seems clear, if the assumptions made above are correct, that on diets containing much ground maize glucose requirements of sheep would be adequately covered from glucose absorbed from the small intestine. On diets high in barley or flaked maize such glucose would make an appreciable contribution to overall glucose requirements of sheep.

Digestion of cellulose

Values in the literature on the extent and sites of digestion of cellulose in diets fed to cattle, sheep and goats are shown in Table 4. With reference to forages it can be seen from the table that when sheep are fed hay or grass either fresh or dried the extent of cellulose digestion after passage of the digesta through the pylorus is relatively small and does not exceed 10% of the total amount digested. The same is true for the single values shown for cattle and goats. The site of this small post-ruminal cellulose digestion is not clearly indicated by the data. It has been noted that the pelleted hay fed to sheep by Topps, Kay & Goodall (1968) was also fed to cattle (Topps, Kay, Goodall *et al.* 1968). Overall cellulose digestibility was the same for both species (61%) and as already indicated post-ruminal digestion was less than 10% with both species. In the experiments of Hogan & Weston (1967) with lucerne hay digestion of cellulose beyond the reticulo-rumen was also of little significance, whereas with wheaten hay more than 30% of the cellulose digested disappeared after the digesta had passed through the pylorus. With neither of these diets did grinding the feed affect site of cellulose digestion, although with the wheaten hay

Table 4. *Extent and sites of digestion of cellulose contained in rations fed to ruminants*

Feed*	Cellulose ingested (g/24 h)	Digestibility of cellulose (%)	Disappearance of digested cellulose (%)				Reference
			Before small intestine	In small intestine	In caecum and colon		
Sheep fed forages							
Hay, chopped	249	72.6	91.0	0.2	8.8	MacRae & Armstrong (1969)	
Hay, milled and pelleted	306	61.4	107.7	-3.1	-4.5	Topps, Kay & Goodall (1968)	
Lucerne hay, chopped	284	51.8	89.8	↔	↔	Hogan & Weston (1967)	
Lucerne hay, ground and pelleted	311	49.4	89.2	↔	↔		
Wheaten hay, chopped	190	43.7	69.9	↔	↔		
Wheaten hay, ground and pelleted	205	40.5	68.7	↔	↔		
Lucerne, dried, chopped	274	58.0	85.4	-3.7	18.3	Thomson <i>et al.</i> (1969)	
Lucerne, dried, chopped and wafered	256	59.5	79.8	-2.9	23.2		
Lucerne, dried, ground and pelleted	263	59.0	63.3	9.3	27.5	Unpublished observations, this laboratory	
Grass, chopped, fresh	223	75.2	93.4	-4.2	10.8		
Grass, chopped, dried	224	75.7	91.6	4.4	4.0		
Sheep fed diets containing cereals							
Hay 67, rolled barley 33	179	75.7	84.1	0.4	15.5	MacRae & Armstrong (1969)	
Hay 33, rolled barley 67	107	61.3	56.2	14.4	29.4	Bruce <i>et al.</i> (1966)	
Hay 82, flaked maize 18	148	62.2	89.1	1.1	9.8		
Hay 82, flaked maize 9	149	65.8	86.7	2.0	11.3		
Cattle fed forages							
Hay, milled and pelleted	750	61.0	90.5	↔	9.5	Topps, Kay, Goodall <i>et al.</i> (1968)	
Cattle fed diets containing cereals							
Ground maize 20, ground lucerne hay 76	1754	60.0	93.4	↔	6.6	Mitchell <i>et al.</i> (1967)	
Ground maize 40, ground lucerne hay 53	1286	55.8	97.1	↔	2.9		
Ground maize 60, ground lucerne hay 31	673	45.0	101.3	↔	-1.3		
Ground maize 80, ground lucerne hay 75	298	40.9	76.2	↔	23.8		
Goats fed forages							
Hay	251	71.9	92.2	↔	7.8	Porter & Singleton (1965)	

*For mixed diets, only major feed constituents are shown; numerals indicate percentages of individual constituents present.

grinding significantly depressed ($P < 0.05$) overall cellulose digestion (Hogan & Weston, 1967).

In the studies of Thomson, Beever, Coehlo da Silva & Armstrong (1969) with a dried lucerne fed to sheep, the physical form of the feed had no effect on overall cellulose digestibility but had an appreciable influence on the contribution of the different sites to cellulose digestion (Table 4). Digestion of cellulose in the reticulo-rumen was reduced by grinding and pelleting ($P < 0.001$) and this was partly compensated for by increased digestion in the caecum and colon (pelleted *v.* chopped, $P < 0.01$). The explanation of the lack of agreement between the results of Hogan & Weston (1967) and Thomson *et al.* (1969) is not known, although differences in particle size may be a contributory factor. In the first-mentioned experiment the material was ground through a 3 mm sieve, in the second through one of 1.96 mm. In the experiments of Thomson *et al.* post-ruminal digestion of cellulose was restricted to the caecum and colon when the lucerne was fed chopped or chopped and wafered. On the pelleted ration, however, an appreciable digestion of cellulose appeared to occur in the small intestine. Evidence of a similar apparent digestion of cellulose in the small intestine is also to be seen when a diet comprising 33% hay and 67% rolled barley was fed (Table 4).

Apart from the last-mentioned result the values in Table 4 for sheep fed mixed diets containing cereals suggest that post-ruminal digestion of cellulose is confined to the caecum and colon and that the loss in passing through this part of the alimentary tract may account for between 9 and 30% of the cellulose digested, the higher value being associated with the inclusion of large quantities of grain in the diet.

It is generally agreed that digestion of cellulose in the alimentary tract of the ruminant is the result of microbial fermentation and that the end-products produced are the volatile fatty acids (VFA), carbon dioxide and methane. Studies on the concentration of VFA along the alimentary tract of cattle and sheep have been made by Elsdon, Hitchcock, Marshall & Phillipson (1945-6) and in sheep by Boyne, Campbell, Davidson & Cuthbertson (1956) and Badawy, Campbell, Cuthbertson & Mackie (1958). In these studies the importance of the caecum as a site for secondary fermentation has been clearly indicated. Furthermore although VFA concentrations were always low in the proximal small intestine, there was a pronounced rise in their concentration in the distal end. This was particularly marked with sheep fed diets high in ground maize (Badawy *et al.* 1958). According to Boyne *et al.* (1956) the increase in fermentation occurring as the digesta approaches the ileo-caecal valve is in agreement with the distribution of micro-organisms extending forward from the caecum but in ever diminishing numbers. VFA concentrations rise sharply in the caecum and decrease as the digesta pass along the colon. Absorption of VFA from caecum and colon in sheep has been demonstrated by Myers, Jackson & Packett (1967).

Digestion of hemicelluloses

The major constituents of plant hemicelluloses comprise the pentosans xylan and araban together with small amounts of glucans and uronic acids. Schemes of

analysis are available for determining the content of the individual fractions (Waite & Gorrod, 1959*a,b*; Salo, 1965), but no experiments have been found in the literature reporting results obtained by applying such schemes to the digesta of ruminant animals. Measurement of the non-glucose reducing sugar content in a protein-free extract obtained by subjecting feeds, digesta or faeces to hydrolysis with 0.36 N-H₂SO₄ for 8 h has been found to account for the major part of the pentosans present (Beever, unpublished observations). The results in Table 5 show the extent and sites of digestion of this fraction in a number of feeds. It appears

Table 5. *Extent and sites of digestion in sheep of a fraction designated non-glucose reducing polymer contained in feeds*

Feed*	Amount of polymer ingested (g/24 h)	Digestibility of polymer (%)	Disappearance of the digested polymer (%)			Reference	
			Before small intestine	In small intestine	In caecum and colon		
Hay	155	65.6	95.3	3.4	1.3	MacRac & Armstrong (1969)	
Hay 67, rolled barley 33	130	68.5	94.5	1.8	3.7		
Hay 33, rolled barley 67	103	60.0	82.1	5.1	12.8		
Hay 33, flaked maize 67	114	68.2	83.0	-2.1	19.1		
Grass, chopped, fresh	126	59.6	75.8	0.3	24.5		Unpublished observations, this laboratory
Grass, chopped, dried	120	57.9	72.2	0.5	27.3		

*For mixed diets, only major feed constituents are shown; numerals indicate percentages of individual constituents present.

that between 70 and 90% of the digested fraction disappears in the reticulo-rumen and that digestion of the remainder occurs in the caecum and colon. Presumably hemicelluloses entering the caecum are, like cellulose, subjected to a further microbial fermentation.

Digestion of soluble carbohydrates in grasses

Appreciable amounts of water-soluble carbohydrates such as glucose, fructose, sucrose and fructosans are found in grasses (MacKenzie & Wylam, 1957; Waite & Gorrod, 1959*b*) and as to be expected are completely digested (Waite, Johnston & Armstrong, 1964). When a grass was fed fresh (frozen) to sheep 98.2% of the total water-soluble sugars ingested had disappeared before reaching the pylorus; with the same grass fed dried the comparable value was 95.5% (unpublished observations, this laboratory). In both instances, although small quantities of fructosan were present in the feed, none (nor free fructose) was detected at the duodenum.

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Digestion and absorption of lipids in the ruminant

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Although this Symposium is concerned primarily with events in the abomasum and intestinal tract, it is necessary first to consider briefly the fate of dietary lipids in the reticulo-rumen since this has consequences which significantly affect the chemical and physical state of the lipids which pass on to the abomasum and small intestine. While many of the studies which are discussed refer to sheep, it is reasonable to suppose that the findings apply to ruminants in general.