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Carbohydrate digestion and glucose supply in the gut of the ruminant

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The ruminant is able to digest and utilize a wider range of carbohydrates than most other mammals, yet the means whereby it carries out this digestion also ensures that it may, during periods of high productivity, suffer from a shortage of glucose. Indeed the plight of the high-producing ruminant is not so very different from that of the ancient Mariner who had 'Water water every where. Nor any drop to drink.' The basic reason for this shortage of glucose is that some 90% of the digestion of carbohydrates is by fermentation to short-chain fatty acids (volatile fatty acids (VFA)) by the bacteria and protozoa of the rumen and large intestine. Thus, only small amounts of glucose, derived mainly by hydrolysis of starch in the small intestine, are absorbed from the gut, and to meet its glucose requirements the ruminant relies heavily upon gluconeogenesis from the propionic acid and microbial protein produced by fermentation in the rumen.

In the following discussion, those aspects of carbohydrate digestion recently reviewed for the Society by Armstrong & Beever (1969) will be covered only briefly.

Processes of carbohydrate digestion

Rumen. The first form of digestion which carbohydrates undergo involves an anaerobic fermentation in the rumen. Polysaccharides are hydrolysed and the resulting hexoses and pentoses are then oxidized to acetic acid and various reduced products, in particular propionic acid, n-butyric acid and methane. These products are formed in widely different proportions although, so far as is known, all carbohydrates are fermented by a common pathway, the Embden–Meyerhof glycolysis system, to pyruvate. It is in the further metabolism of pyruvate that the differences in products arise (Baldwin, 1965).

The products formed during fermentation are basically the resultant of the interaction between the microbial population and the substrate. Such relatively small differences in substrates as exist between glucose, galactose and xylose result in the formation of widely different proportions of VFA (Sutton, 1968), but there is no consistent relation between a substrate and the products of its fermentation as

these same sugars are fermented to quite different proportions of VFA when the type of basal fermentation changes (Sutton, 1969).

In practical terms, a reduction in the ratio of hay to concentrates in the ration usually causes a fall in the proportion of acetic acid in the rumen and increases in either propionic acid or butyric acid or both. A change from a fermentation characterized by a high proportion of butyric acid to one in which propionic acid is a major product has been related to the elimination of protozoa from the rumen (Eadie, Hyldgaard-Jensen, Mann, Reid & Whitelaw, 1970) but smaller changes in VFA proportions do not bear any simple relationship to the balance of bacterial species (Latham, Sharpe & Sutton, 1971).

The pH of the rumen contents can considerably modify the interaction between substrate and the microbial population, and proportions of VFA can sometimes be related more readily to the pH than to the ration composition (Sutton & Johnson, 1969). The elimination of protozoa by feeding high-concentrate rations is probably due to low rumen pH (Eadie *et al.* 1970) and intraruminal infusions of buffers into animals given such rations can completely alter the proportions of VFA (Sutton & Johnson, 1969, and unpublished). These interactions among the substrate (food), the microbial population and pH are complex, and the resultant, the proportions of VFA formed in the rumen, is still highly unpredictable, particularly when high-concentrate rations are given.

The fermentation of carbohydrates provides energy in the form of ATP to support microbial growth which in turn usually provides the principal source of protein for the host animal. Wide variations occur among species of bacteria in the amount of protein synthesized per unit of carbohydrate fermented (Hogan & Weston, 1970).

Small intestine. Amylase and maltase are secreted by the pancreas and small intestine, and lactase and dextranase by the small intestine; sucrase is virtually absent. Pancreatic amylase activity increases in response to increased maize in the ration (see Armstrong & Beever, 1969). Thus, of the carbohydrates that might normally reach the duodenum of the adult ruminant, one might expect that starch and associated polysaccharides would be hydrolysed and absorbed as glucose but that sucrose and fibrous carbohydrates would remain undigested; yet disappearance of all these carbohydrates has been found to occur between the abomasum and the terminal ileum. This almost certainly reflects a considerable microbial fermentation in the terminal ileum, the existence of which not only accounts for the digestion of cellulose and sucrose but probably also for an unknown proportion of the starch. Indeed, clear evidence that the digestion of starch in the small intestine leads to an increased absorption of glucose has yet to be reported.

Large intestine. The fermentation in the caecum has received relatively little attention but there is no reason to suppose that it differs from that in the rumen in any way other than may be dictated by the different positions of the two organs in the digestive tract. Thus, the carbohydrate reaching the caecum is less digestible than that entering the rumen and the microbial cells synthesized during the fermentation are not subsequently digested by the host.

Quantitative aspects

Carbohydrate digestion. When forages are given alone and in the chopped or long form, more than 85% of the digestible fibre and 90% of the total soluble carbohydrate are digested in the rumen (Weston & Hogan, 1968). The digestible fibre leaving the rumen must be presumed to be digested by fermentation in the terminal ileum and caecum, and the small amount of soluble carbohydrate, which is rarely more than 3–10 g daily and may well be mainly microbial polysaccharide, is probably hydrolysed to glucose in the small intestine. The relative importance of the rumen as a site for fibre digestion tends to be less when the quality of roughages declines (Hogan & Weston, 1967*a*; Weston & Hogan, 1968), when certain dried roughages are given in the finely ground form and when starchy concentrates are given with the roughage (see Armstrong & Beever, 1969).

With rations consisting mainly or even entirely of concentrates, starch is often the most abundant carbohydrate. Some 90–95% of the starch of most cereals is digested in the rumen and most of the remainder in the small intestine. Raw maize is an exception (Ørskov, Fraser & Kay, 1969); 25% or more may escape digestion in the rumen and, when large amounts are given, some may even reach the caecum.

The few experiments conducted with adult cattle suggest that the relative importance of different parts of the gut for carbohydrate digestion is broadly similar to that in sheep (Karr, Little & Mitchell, 1966; Gaillard & van't Klooster, 1969).

VFA production. Of the organic matter (OM) digested in the rumen, part is converted to microbial cells and about 80% is fermented to VFA, heat, methane and similar products. This fermented fraction approximates to 'apparently digested OM' which is the measured net loss of OM during passage of digesta through the rumen; it consists very largely of carbohydrate polymers.

Theoretical yields of VFA consisting, on a molar basis, of 65% acetic acid, 25% propionic acid and 10% n-butyric acid (65:25:10) are about 1·2 mol/100 g polysaccharide fermented when calculated according to stoichiometric principles (Walker & Nader, 1970) and about 1·3 mol/100 g OM fermented when based on the measurement of apparent energy digestion in the rumen (Nicholson & Sutton, 1969). In vivo measurements by isotope dilution procedures suggest that production is about 1·5 mol/100 g OM fermented (Hogan, Weston & Lindsay, 1969); in vitro techniques yield values about 35% lower than this and are almost certainly in error (Whitelaw, Hyldgaard-Jensen, Reid & Kay, 1970).

The estimates of VFA production based on isotope dilution procedures imply the capture of 90–95% of the fermented energy in VFA, yet 15–20% of the energy is known to be lost as heat and methane. Thus, either VFA production is overestimated by isotope dilution techniques by some 10% or, alternatively, the amount of OM fermented is underestimated by measurement of the apparent digestion of OM in the stomach. From these considerations, a reasonable estimate for the production of a 65:25:10 mixture of VFA is probably about 1·3 mol/100 g OM fermented.

When roughages are given alone and in the chopped or long form, about 55–70% of the digestible OM is fermented in the rumen (Weston & Hogan, 1968). Thus,

about 0·7–0·9 mol VFA, including 15–20% propionate, would be produced in the rumen per 100 g OM digested throughout the tract. A further 0·1 mol is probably produced in the caecum.

When mixed rations of hay and concentrates are given, the proportion of digestible OM fermented in the rumen averages about 65–75% (Hogan & Weston, 1967*b*; Nicholson & Sutton, 1969; Sutton, Smith & Corse, 1970) and probably results in the production of about 0·8–0·9 mol VFA for every 100 g OM digested throughout the tract. For high-concentrate rations, the amounts of glucogenic VFA produced would vary widely according to whether high-propionate or high-butyrate fermentations developed.

The few measurements of VFA production in lactating cows have yielded widely divergent results. Estimates of the net production of acetic acid in cows given normal rations range from 25 (Davis, 1967) to 77 (Satter & Wiltrout, 1970) mol/d according to isotope dilution procedures, but the relative importance of the rumen as a site for OM digestion seems to be similar to that in sheep (van't Klooster & Rogers, 1969) which would lead one to expect an intermediate value of about 55–60 mol/d. More accurate measurements with lactating cows are urgently needed.

Protein synthesis. Results of in vivo studies so far reported with sheep agree well with the theoretical estimates of 20 g crude protein being synthesized for every 100 g polysaccharide fermented (Walker & Nader, 1970; D. J. Walker, personal communication). Yields of 23 g crude protein/100 g OM fermented were found for hay rations (Hogan & Weston, 1970), 16–23 g for various rations of hay and concentrates (J. D. Sutton, R. H. Smith, D. A. Corse and A. B. McAllan, unpublished), and 14–23 g for purified rations (Hume, 1970*a*, *b*). Of this crude protein, only about 87% probably consists of true protein (McAllan & Smith, 1972). Although about 17 g true protein appears to be a reasonable average for most rations, variations in this value may occur that can be related to different types of fermentation in the rumen (Hume, 1970*a*; Jackson, Rook & Towers, 1971).

Microbial protein is about 80% digestible and a maximum of about 55 g glucose can be synthesized in the body for every 100 g protein metabolized (Krebs, 1964). Thus, the synthesis of 17 g microbial protein in the rumen would yield a maximum of 7·5 g glucose in the body.

Uptake of glucogenic materials

Despite the uncertainty associated with many of the values considered, it is useful to attempt to estimate the amounts of glucose that could be derived from various rations if all glucogenic materials absorbed from the gut were converted to glucose with maximal efficiency. In Table 1 such an attempt has been made for a roughage ration (A) and for two high-concentrate rations, one of which is fermented to two quite different proportions of VFA. All the rations supply sufficient metabolizable energy to maintain a 70 kg adult sheep. It is assumed that only 5% of ingested starch enters the duodenum for B and C, and that all is hydrolysed to

Table 1. *Estimates of the amounts of glucogenic materials, expressed as glucose (g/d), available for absorption from the gut of sheep given three rations (g dry matter/d)*

	1000 g hay A*	110 g hay – 440 g flaked maize B	110 g hay – 440 g flaked maize C	110 g hay + 440 g cracked maize D
Rumen VFA (molar %)	65:25:10	55:35:10	55:20:25	55:20:25
Glucose precursor (g/d glucose):				
Rumen propionic acid	103	121	69	55
Caecal propionic acid	11	8	8	11
Microbial protein	26	24	24	19
Glucose (from starch)	9	18	18	68
Total	149	171	119	153

VFA, volatile fatty acid.
*For explanation of A, B, C and D, see p. 246.

glucose, whereas for D, that 25% of the ingested starch leaves the rumen unfermented and, of this, 75% is hydrolysed to glucose in the small intestine, and that the remainder is fermented to VFA in the terminal ileum and caecum.

A comparison of the three situations when maize is given emphasizes that the type of fermentation in the rumen (B *v.* C) can increase the total supply of glucose precursors to a greater extent than can a large change in the site of digestion of starch (D *v.* C). On the other hand, the need for gluconeogenesis is much less with D than with any of the other situations.

According to estimates by Lindsay (1970), the entry rate of glucose into the tissue would be about 110 g/d for the intake of digestible energy supplied by these rations. It is only when cracked maize is given that the uptake of glucose from the gut provides more than about 15% of this total. With the other rations, propionic acid is the major precursor of glucose. For all situations except C, propionic acid and protein would have to be converted to glucose with an efficiency of about 50–70% to meet the difference between the amount of glucose absorbed from the gut and the estimated entry rate.

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Intestinal absorption of carbohydrates in man

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Carbohydrates provide about half the total calories in the diet of the average household in this country (Greaves & Hollingsworth, 1964). Typically, nearly two-thirds of this ingested carbohydrate are derived from starch, about a quarter from sucrose and about a tenth from lactose. All this carbohydrate is hydrolysed to monosaccharides prior to absorption, producing approximately 250 g glucose, 40 g fructose and 10 g galactose.

Rate-limiting factors in carbohydrate digestion and absorption

Digestion and absorption take place in three phases: the intraluminal phase, the brush-border phase and the final absorption of the resultant monosaccharides.

Intraluminal phase

Starch hydrolysis by pancreatic α-amylase (*EC* 3.2.1.1.) appears to be very efficient. Dahlqvist & Borgström (1961), using a post-liquid meal sampling technique at varying levels of the small intestine, found that each carbohydrate molecule consisted of, on average, less than three glucose units. Auricchio, Pietra & Vegnente (1967) took samples from the distal duodenum in infants and young children after a test-meal containing amylopectin. Although the mean number of glucose units per molecule was 5–9 in infants up to 6 months old, the amylopectin contained over 5000 glucose units per molecule, so this represents very efficient hydrolysis even at this proximal point of the intestine.

There is, however, evidence to suggest that starch absorption continues even after surgical removal of the whole pancreas (Gaston, 1948). While salivary amylase and gastric acid hydrolysis may be of some importance, there is much amylase activity in the intestinal brush borders.