
STARCH DIGESTION AND GLUCOSE METABOLISM IN THE RUMINANT: A REVIEW

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Carbohydrates are as important to the ruminant animal as they are to non-ruminants, since they provide the glucose necessary for the adequate function of cells. However, in the ruminant, ruminal fermentation transforms most of the cell wall polysaccharides and all of the intracellular carbohydrates present in the forage into short-chain volatile fatty acids, which are then absorbed by the rumen epithelium (Bird *et al.*, 1996).

Plant tissues contain about 75% carbohydrates, providing the primary sources of energy for both the rumen organisms and the host animal (Morrison, 1959; Church, 1979). The carbohydrates found in plant tissues are primarily polysaccharides, cellulose, hemicellulose, pectins, fructans and starches, with minor amounts of other compounds (Theander, 1981). Cellulose is the most abundant. However, grains are widely used in diets used in intensive production systems with highly productive animals (Waldo, 1973; Theurer, 1986), providing an appreciable amount of starch for ruminal and intestinal digestion (Armstrong and Smithard, 1979; Sutton, 1979). The purpose of this review is to summarize the present knowledge on starch digestion in the ruminant, as well as glucose metabolism in the rumen, post-ruminal absorption of starch and glucose requirements of the ruminant.

Starch Digestion in the Ruminant

In the non-ruminant, starch digestion occurs mainly in the small intestine. The situation in the ruminant differs due to the action of microorganisms in the rumen. Digestion of starch to glucose requires the action of several enzymes produced by the salivary glands, the rumen microorganisms or the pancreas and small intestine. Amylase secreted by the nasolabial glands is found at relatively high levels in the saliva of some ruminants, such as the buffalo (Church, 1979). Alpha-amylase is secreted by the pancreas, while isomaltase, maltase-glucoamylase, trehalase and lactase are secreted by the intestinal mucosa (Harmon, 1993). Alpha-amylase, beta-amylase, R-enzyme, pullulanase, iso-amylase or alpha-limit dextrinase are produced by the rumen microorganisms.

Several species of ruminal bacteria are able to digest starch. Amylolytic organisms are found in larger percentages of the total microbial population when rations high in starch are fed. Important species that have been enumerated in cattle fed high grain diets are *Bacteroides amylophilus*, *Butyrivibrio fibrisolvans*, *Bacteroides ruminicola*, *Selemonona lactylitica*, *Streptococcus bovis*, *Prevotella ruminicola*, *Eubacterium ruminantium*, *Ruminobacter amylophilus*,

Ruminococcus bromii, *Succinimonas amylolytica* and *Lactobacillus* sp. (Clarke and Bauchop, 1977; Church, 1979; Kotarski *et al.*, 1992).

In studies in which ruminants are switched abruptly from forage-based diets to grain based rations an acute ruminal lactic acidosis occurs, the numbers of *Streptococcus* sp. increase by 2-3 orders of magnitude within hours after feeding, protozoa populations are eliminated and lactobacilli become dominant within 24h (Krogh, 1963; Mann, 1970). Ciliated protozoa are found in large quantities in grain-fed ruminants. Low ruminal pH occurring during all or part of the daily feeding cycle is thought to limit protozoa populations (Eadie and Hobson, 1962; Eadie *et al.*, 1967), because many are unable to survive below pH 6.0 (Hino *et al.*, 1973).

In grain-fed animals, protozoa can exert an influence on ruminal starch hydrolysis rates in at least two respects: 1) by ingesting bacteria in numbers sufficient to decrease ruminal fermentation rates (Eadie and Hobson, 1962; Clark and Bauchop, 1977; Kurihara *et al.*, 1978), and 2) by ingesting starch granules and soluble sugars, thus decreasing the accessibility of these substrates to fermentation by the faster growing bacteria (Coleman, 1986; Coleman, 1992).

The presence of ciliates influences the site of starch digestion. It

KEYWORDS / Glucose Metabolism / Starch Digestion / Ruminants /

Received: 10/24/2002. Modified: 06/16/2003. Accepted: 06/18/2003

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has been reported that protozoa reduce the rate of starch digestion and ruminal starch digestibility, shifting the site of starch digestion to the small intestine (Mendoza *et al.*, 1993).

Most amilolytic microorganisms possess extracellular amylases, usually of the alpha-type, which is an endoenzyme acting randomly in the interior parts of the starch chain. The fragmentation by alpha-amylase initially leads to a rapid reduction in the molecular size of the starch with formation of water soluble dextrans and oligosaccharides. The final products from amylose are maltose, maltotriose and sometimes small amounts of free glucose. Maltotriose is generally stable to the action of both alpha and beta-amylases, unless massive quantities of enzyme are added. The final products from amylopectin are maltose, maltotriose, a little glucose and a mixture of alpha-limit dextrans. These latter oligosaccharides consist of 4-8 glucose moieties and still contain the alpha-(1-6) linkage(s) which cannot be hydrolyzed by amylases. Debranching enzymes (R-enzyme, pullulanase, iso-amylase, or alpha-limit dextrinase) are necessary to break these bonds (Clark and Bauchop, 1977).

Starch digestion in the total digestive tract of ruminants exceeds 95% (Tucker *et al.*, 1968). With roughage diets only small quantities of alpha-linked glucose polymers pass to the abomasums (Heald, 1951) and it is very likely that such material, which does leave the rumen, is mostly of microbial origin. Both rumen protozoa and bacteria store alpha-linked glucose polymers when available energy is in excess of growth requirements (Hungate, 1966; Walker and Nader, 1970; Cheng *et al.*, 1973; McAllan and Smith, 1974).

With roughage diets this would occur shortly after feeding, due to the rapid fermentation of the soluble sugars present in the higher quality roughages. McAllan and Smith (1974) reported values of 17-30g alpha-dextran per kg bacterial DM passing to the duodenum of hay-fed sheep and cows. Calculations based on these estimates yield a value of 3-6g alpha-dextran per day and per kg hay consumed, which is close to reported values of 5g·day⁻¹ with sheep (Armstrong and Beever, 1969). Thus, on hay diets the quantity of glucose available for absorption in the small intestine would be of minimal importance.

When diets containing grains are fed, depending on the type of the grain, the extent of processing prior feeding, and the species of animal fed, an appreciable amount of starch and protozoal glycogen may escape fermentation

in the rumen and enter the small intestine (Weeks, 1979).

It has been observed that the degree of processing is an important factor which influences the degree of fermentation of grains in the rumen and their post-ruminal digestibility. Xiong *et al.* (1991) observed that processing of sorghum by steam-flaking increased starch digestion in the rumen, there being less starch available for fermentation in the lower gastrointestinal tract. Ruminal retention time is another important factor which determines the degree of ruminal starch fermentation. It has been demonstrated that steam-rolling causes a greater ruminal retention time than dry-rolling (Zinn, 1993, 1994).

The inclusion of ionophores or Na bicarbonate cause minor changes in the site and extent of starch digestion, as observed by Zinn and Borques (1993) and Zinn (1987). Ionophores usually reduce intake, which results in less starch being fermented in the rumen, reducing incidence of acidosis in feedlot diets. Combination of slow (25-33%) and fast (75-66%) digesting grains improve gain and feed efficiency (Stock *et al.*, 1987), presumably because those combinations stimulate protozoal numbers (Mendoza *et al.*, 1998; Mendoza *et al.*, 1999) reducing ruminal starch digestion and acidosis.

Manipulation of starch fermentation in the rumen is important when slow digested grains such as sorghum are fed. The use of exogenous amyolytic enzymes from *Bacillus licheniformis* increased ruminal starch digestion and feed efficiency in sorghum based diets (Rojo *et al.*, 2001). Therefore, exogenous enzymes could be considered as an alternative treatment to improve ruminal starch digestion when diets with a high grain content are fed to ruminants.

It has been calculated that when rolled barley or ground maize is fed to sheep the total starch digestibility was 99.9% and the proportion of starch disappearance before the small intestine was 91.8%, whilst in cattle fed ground corn the total starch digestibility was 98.5% with 68.0% of the starch disappearing before the small intestine (Armstrong and Beever, 1969). Other authors (Nocek and Tamminga, 1991) indicate that rumen degradable starch as percentage of total starch varies from 73.2 to 90.3 for rolled barley, whilst whole and ground maize range from 58.9 to 75.0 and 51.4 to 93.0, when fed to sheep and cattle, respectively.

El-Shazly *et al.* (1961) noticed that dry matter (DM) digestibility of roughages is lowered in the presence

of starch or starchy feedstuffs, mainly due to competition for essential nutrients by amyolytic and cellulolytic microorganisms within the rumen, resulting in proliferation of starch digesting bacteria. Rapid fermentation of starch leads to a decrease in rumen pH which encourages amyolytic microorganisms to proliferate and compete successfully against cellulolytic bacteria, which grow at a higher pH (Mould and Orskov, 1983; Mould *et al.*, 1983).

Both cattle and sheep are able to digest completely the starch contained in certain cereal based diets (Armstrong and Beever, 1969). The results obtained by MacRae and Armstrong (1969) for sheep fed whole or rolled barley suggest that its digestive tract can handle with equal effectiveness either form of grain. However, the same might not be true for cattle fed whole or rolled barley, and there is evidence that in dairy cows fed whole shelled maize, 18-35% of the grain passes undigested through the entire digestive tract (Morrison, 1959).

The method of grain processing affects the site of digestion of starch in ruminants. Wu *et al.* (1994), found in cows fed steam flaked sorghum that the main site of starch digestion was the rumen, while in cows fed dry rolled sorghum it was the intestine. Type and variety of grain also affect the site of starch digestion. Hatfield *et al.* (1993) found differences in ruminal starch digestion in wethers fed different barley varieties. Herrera-Saldaña *et al.* (1990a) found that starch degradability *in vitro* was the highest for oats (98%), followed by wheat, barley, maize and sorghum (95, 90, 62 and 49%, respectively). Wilcox *et al.* (1994) compared two varieties of maize, Sugary-Brawn2 and dent maize, being the highest total starch digestion that of Sugary Brawn2. McCarthy *et al.* (1989) observed in lactating cows that passage of starch to the duodenum was greater for corn based diets than barley based diets. Streeter *et al.* (1990) fed steers with four sorghum grain hybrids and maize; ruminal starch digestibility, pre-cecal starch digestibility and total starch digestibility were higher for maize than for sorghum grains.

It has also been observed that when different grain processing methods are compared, some of them have a greater effect than others in improving starch digestibility in the rumen of cattle. Cheng *et al.* (1994) studied the effect of steam flaking of corn and sorghum grains on performance of lactating cows. They found that compared to rolling, flaking of both grains increased yields of milk, milk protein and fat, due

to a higher rumen digestibility of starch which increased ruminal volatile fatty acids (VFA) concentration, with more VFA absorption from the rumen and greater flow of bacterial protein to the duodenum. Oliveira *et al.* (1992) and Poore *et al.* (1993) also observed that steam flaked sorghum grain had a higher ruminal and total tract starch digestibility than dry rolled sorghum grain when fed to dairy cows.

The differences in apparent digestibility of grains between species may be related to the physical size of the reticulo-omasal orifice, which is considerably greater in cattle than in sheep or goats. In cattle un-masticated whole grains which are those still resistant to enzyme attack are able to pass from the reticulo-rumen into the abomasum, whereas in sheep or goats similar grains are retained within the reticulo-rumen and subjected to further mastication during rumination, which results in rupture of the seed coat of most of the cereal grains, so enzyme degradation can occur (Nordin and Campling, 1976).

However, excessive amounts of readily fermented carbohydrates might occur when diets rich in concentrate are fed to ruminants, causing marked acidosis as acids and glucose accumulate. These compounds damage the ruminal and intestinal walls, decrease blood pH, and cause dehydration that proves fatal. Feeding higher amounts of dietary roughage, processing grains less thoroughly and limiting the quantity of feed should reduce the incidence of acidosis, although these practices may depress performance and economic efficiency. Therefore, it is necessary to continue research on grain processing, dietary cation-anion balance, narrow spectrum antibiotics, glucose or lactate utilizing microbes and feeding management in order to reduce the incidence of acute and chronic acidosis (Owens *et al.*, 1998).

Glucose Metabolism in the Rumen

The carbohydrate components in ruminant diets are mainly hexose polymers like cellulose, starch, fructans, and pentose polymers, mostly xylan; (Walker, 1965; Martin, 1994). The most important pathway of hexose fermentation in the rumen is the Embden Meyerhof pathway, resulting in the degradation of glucose to pyruvate (Baldwin, 1965). The 3-carbon intermediates arising as a result of hexose and pentose degradation may be utilized via, at least, two alternative pathways. One involves the release of lactate or another 3-carbon intermediate into the medium by the

microorganism which carried out the initial fermentation, followed by the conversion of the free lactate to the VFA and other products by a second microorganism. The other process simply involves a direct conversion of a 3-carbon intermediate to acetate and formate or acetate, CO₂, and a reduced product such as H₂, succinate, propionate, or butyrate, by the same microorganism that carried out the initial degradation (Baldwin, 1965).

Phosphoroclastic reactions are the major reactions involved in acetate synthesis. Two of them appear to be prominent in the rumen, the clostridial phosphoroclastic type and the coliaerogenes phosphoroclastic (formate phosphoroclastic) type. The requirements for both systems include thiamine pyrophosphate, coenzyme A and phosphate. The clostridia system also requires ferredoxin (Baldwin, 1965).

Groups of organisms differ in the fate of the pairs of electrons removed in this reaction. Clostridia transfer them to protons which are then liberated as molecular H₂. Other bacteria transfer them to CO₂ and produce formate. Formate is oxidized rapidly in the rumen, probably by the ferredoxin-dependent formic dehydrogenase, with formation of H₂ and CO₂ (Baldwin, 1965; Leng, 1970a).

There are two mechanisms known for the conversion of lactate or pyruvate to propionate. The first pathway involves the formation of oxaloacetate and succinate, and the second involves the formation of acrylate. Deficiencies of sulphur may change the routes of propionate production which is probably due to a change in microbial population where the acrylate pathway assumes a more important role. The acrylate pathway may be more important in the rumen of animals given grain rations (Baldwin *et al.*, 1963; Leng, 1970a).

Butyrate synthesis may occur in the rumen from acetate, or from compounds giving rise to acetyl-CoA, such as pyruvate or glutamate. Two pathways may be available for butyrate synthesis from acetate in anaerobic ruminal organisms. The most likely pathway is the reversal of beta-oxidation. The synthesis of long chain and branched-chain fatty acids of the bacterial cells of rumen organisms suggests the possibility of butyrate synthesis via a second pathway involving malonyl-CoA. In the malonyl pathway 2 moles of ATP are required for the formation of 1 mole of butyrate from 2 moles of acetate, as compared with 1 mole of ATP for the synthesis of butyrate by the reversal of beta-oxidation (Leng, 1970a).

Post-ruminal Digestion and Starch Absorption

The residence time of a feed particle in the rumen is a major determinant of the extent it will be fermented. However, with regard to starch digestion, the rate of starch digestion in the rumen is an important factor because of competition of passage and digestion (Allen and Mertens, 1988). It is evident that a decrease in starch digestion in the rumen can be accomplished by increasing the fluid dilution rate. The dilution rate of rumen fluid is higher with long than ground roughage (Hodgeson and Thomas, 1975) and is probably related to the greater amount of time spent ruminating. This could explain the twofold increase in ground maize starch passing to the duodenum of sheep when ground straw was replaced with long straw (Thompson and Lamming, 1972; Thompson, 1973). Orskov *et al.* (1969) observed a larger proportion of dietary starch passing to the duodenum when hay and ground barley was fed to lambs in comparison to an all ground barley diet. A higher amount of dietary starch may escape ruminal fermentation and thus become available post-ruminally for possible absorption as glucose. However, other researchers (Topps *et al.*, 1968a, b; Nicholson and Sutton, 1969) did not find any significant increase in the concentration of starch escaping rumen fermentation with animals on high-concentrate diets.

Starch and N₂ metabolism are closely linked in the rumen since energy released from starch degradation is required for the incorporation of N₂ into microbial cells but, conversely, insufficient N₂ may limit microbial growth and enzyme production (Herrera-Saldana *et al.*, 1990b). In support of this latter statement Orskov *et al.* (1972) found the starch flow at the duodenum of growing lambs to be 14.2% of intake with a 10% CP rolled barley diet; this decreased to 6.8, 3.4 and 3.4% when urea was added to bring the diets to 12.4, 16.6 and 16.45% CP respectively, suggesting that N₂ was limiting microbial growth when the non-supplemented diet was fed.

The capacity of the ruminant small intestine to digest large amounts of starch has been questioned (Croome *et al.*, 1992; Waldo, 1973), as a consequence of the low levels of pancreatic amylase, intestinal maltase and isomaltase (Keller *et al.*, 1958; Siddons, 1968; Coombe and Siddons, 1973; Coombe and Smith, 1974) and also because low glucose absorption (Orskov, 1986; Kreikemeier *et al.*, 1991; Tanigushi

et al., 1995). However, it has also been suggested that starch digested postruminally is used more efficiently than that digested in the rumen (Nocek and Tamminga, 1991), and ruminant animals may be capable of digesting large amounts of starch in the small intestine through an adaptation in the activity of the host carbohydrases (Janes *et al.*, 1985a).

It has been shown that the activity of amylase absorbed on the mucosa of the small intestine is greatest in the proximal region of the small intestine. The activity generally declines with increasing distance away from the pylorus with the highest activity in the jejunum (Janes *et al.*, 1985a).

The knowledge of specific mechanisms that regulate amylase secretion by the pancreas is important. It has been found that the presence of glucose or starch hydrolysate in the small intestine decreases secretion of amylase in cattle (Swanson *et al.*, 2002) as well as enzyme activity (Kreikemeier *et al.*, 1990). Pancreatic secretion might be regulated by gastrointestinal hormones. Kreikemeier *et al.* (1990) reported a higher amylolytic activity when a high protein alfalfa hay diet was fed vs. a grain diet, with equal amounts of energy. This could be related to the stimulation of the pancreas by the protease-sensitive cholecystokinin releasing peptide due to the presence of protein in the intestine (Fushiki *et al.* 1989).

The stimulatory effect of protein on pancreatic amylase secretion has been shown to occur in non-ruminants. Johnson *et al.* (1977) fed a high carbohydrate diet to rats, finding that amylase synthesis was stimulated only in the presence of high quality proteins. It is possible that pancreatic secretion in ruminants might be mediated by a monitor peptide in a similar way to that described by Fushiki and Iwai (1989) and Fushiki *et al.* (1989). Results from Kreikemeier *et al.* (1990) suggest that the amount of protein in the diet could play an important role in starch digestion in the small intestine. Mendoza *et al.* (1993) found a linear response in starch digested in the small intestine as a response to duodenal infusions of casein.

There is evidence for the digestion of starch, hydrolysis of starch to glucose and absorption from the small intestine (Janes *et al.*, 1984). Increased concentrations of glucose in venous portal blood in sheep fed ground maize and an increase in total reducing substances in the blood from the mesenteric vein have been observed in cows fed maize meal (Weeks, 1979). Janes *et al.* (1985b)

observed that 90-92% of maize starch (100-120g·d⁻¹) disappeared from digesta through the small intestine of sheep and was carried by the mesenteric vein and subsequently the portal vein to the liver.

Intestinal glucose transport takes place via the apical Na⁺ dependent glucose transporter and by the basolateral facilitative glucose transport. Results from Feng-Qi *et al.* (1998) showed that active transport of glucose from the lumen across the brush border membrane of the epithelial cells is possible in the gastrointestinal tract of lactating dairy cows. However, some studies indicate that one of the possible limitations for starch digestion in the small intestine could be glucose absorption in the intestine, or its transport through the intestinal lumen, like the decline in the activity and expression of the glucose co-transporter SGLT1 in adult ruminants (Wood *et al.*, 2000). Bauer *et al.* (2001) found that Na⁺/glucose co-transport activity may limit starch assimilation in the distal small intestine.

In order to get more glucose absorbed in the small intestine, protecting starch from rumen fermentation has been investigated (Ortega *et al.*, 1999a, 1999b). However, a suitable method of protecting starch from rumen microbial attack has not been found yet. Besides, there is still controversy about the capacity of the ruminant to digest and absorb large amounts of starch, as stated previously.

Glucose Requirements of Ruminants

As mentioned above, in ruminants dietary carbohydrates are fermented to short chain VFA in the rumen and often less than 10% of the body glucose requirements are absorbed as pre-formed glucose from the ruminant digestion tract (Young, 1977; Donkin and Armentano, 1995). Thus, the main source of glucose for ruminants arises from gluconeogenesis with propionate being the major substrate, providing from 27-59% of the carbon in the body pool (Amaral *et al.*, 1990; Chow and Jesse, 1992). Amino acids, glycerol and lactate make minor contributions for glucose carbon. Gluconeogenesis in ruminants occur mainly in the liver with kidneys accounting for a maximum of about 15% (Leng, 1970b; Bergman, 1973). During fasting, glycerol is available through lipolysis in adipose tissue, becoming an important substrate in the fasting state (Bergman, 1973).

Although not absorbed in large quantities, glucose is of equal importance as a metabolite in ruminants as in non-ruminants. It is a major source of energy for nervous tissues and is es-

sential in the synthesis of structural polysaccharides, glycoproteins and glycolipids of cell membranes, cartilage, mucopolysaccharides, etc. However, ruminants differ from non-ruminants in that acetate is the major source of energy for non-nervous tissue and of carbon for lipogenesis (Weeks, 1979).

The amount of propionate absorbed from the rumen of well fed animals is frequently sufficient to meet the animals requirements for glucose synthesis (Bergman, 1973). It increases slightly in pregnancy (Steel and Leng, 1973b), but there is no evidence for an appreciable redirection of propionate metabolism towards glucose synthesis when the supply of glucose precursors is limited (Weeks, 1979).

Alternate metabolic pathways have developed in ruminant tissues which have lowered the metabolic requirements for glucose. However, during pregnancy and lactation a large proportion of the maternal glucose supply can be taken up by the fetus and mammary gland. The metabolism of glucose in the fetal ruminant is more similar to that of the non-ruminant than to that of an adult ruminant. Battaglia and Meschia (1973) found that glucose metabolism could account for 50% of sheep fetal oxygen uptake, indicating that it is a major energy source for the fetus whilst fatty acid oxidation is quite small. The rate of fetal growth increases markedly in the last trimester of pregnancy and this is accompanied by increases in maternal glucose loss (Steel and Leng, 1973a). Christenson and Prior (1978) calculated that the uterus of a twin-bearing ewe will consume 77g glucose per day at 105 days of gestation, and 92g per day at 121 days.

Lactation presents the greatest challenge to glucose metabolism in ruminants. In lactating cows, sheep and goats 60-80% of the glucose entry can be taken up by the mammary gland (Linzell, 1960; Annison and Linzell, 1964; Bergman, 1973; Bickerstaffe *et al.*, 1974), increasing from 32 to 45% the glucose derived from propionate (Wiltrout and Satter, 1972). Horsfield *et al.* (1974) reported that the total glucose entry rate in cows with a body weight of 459kg and producing 12.9kg of milk per day was 2.1g·min⁻¹, while in cows weighing 521kg and producing 20.5kg per day it was 6.8g·min⁻¹. Glucose is the major precursor of milk lactose and smaller amounts of glucose are also used for the synthesis of milk citrate, non essential amino acids and glycerol. It has been found (Bergman and Hogue, 1967) that about 60% of the glucose entry is used for lactose production in sheep. Lactose output accounts for

40-75% of the glucose loss in dairy cows producing 12-26kg of milk per day (Bickerstaffe *et al.*, 1974).

The lack of glucose absorption when roughage diets are fed or the small amount absorbed with grain diets, compels the use of gluconeogenesis to meet the metabolic demands of the high producing ruminant which implies a high energetic cost and the danger of metabolic disorders (Otchere *et al.*, 1974; Sauvant *et al.*, 1991).

The metabolic disorders of primary ketosis in dairy cows and pregnant ewes are considered to be a consequence of an imbalance in the rate of gluconeogenesis and the supply of glucose precursors (Krebs 1966; Bergman, 1971; Schultz, 1971; Bickerstaffe *et al.*, 1974). A shortage of carbon precursors to maintain adequate levels of oxaloacetate in liver mitochondria prevents the oxidation of acetyl CoA via the tricarboxylic acid cycle and leads to the formation of ketone bodies. This situation arises when the demand for glucose is higher than the supply of glucogenic precursors, occurring in early lactation in dairy cows and in late pregnancy in ewes, especially those bearing multiple fetus, and results in the metabolic disorders mentioned above.

Conclusions

Carbohydrates contained in forages and grains are a very important part of the ruminant diet. However, although there has been extensive research in this area, there are still many questions to solve, mainly related to the extent in which carbohydrates are used by rumen microbes and the ruminant itself, and to find the most suitable ways of feeding them to ruminants in order to make the most of them.

REFERENCES

- Allen MS, Mertens DR (1988) Evaluating constraints on fiber digestion by rumen microbes. *J. Nutr.* 118: 261-270.
- Amaral MD, Veenhuizen JJ, Drackley JK, Cooley MH, McGilliard AD, Young JW (1990) Metabolism of propionate, glucose and carbon dioxide as affected by exogenous glucose in dairy cows at energy equilibrium. *J. Dairy Sci.* 73: 1244-1254.
- Annisson EF, Linzell, JL (1964) Oxidation and utilization of glucose and acetate by the mammary gland of the goat in relation to their overall metabolism and to milk formation. *J. Physiol.* 175: 372-385.
- Armstrong DG, Beever, DE (1969) Post-abomasal digestion of carbohydrates in the adult ruminant. *Proc. Nutr. Soc.* 28: 121-131.
- Armstrong DG, Smithard RR (1979) The fate of carbohydrates in the small and large intestines of the ruminant. *J. Sci. Food Agric.* 30: 1021-1022.
- Baldwin RL (1965) Pathways of carbohydrate metabolism in the rumen. In Dungherty RW (Ed.) *Physiology of Digestion in the Ruminant*. Butterworths. London, UK. pp. 379-389.
- Baldwin RL, Wood WA, Emery RS (1963) Conversion of glucose-C¹⁴ to propionate by the rumen microbiota. *J. Bacteriol.* 85: 1346-1349.
- Battaglia FC, Meschia G (1973) Foetal and neonatal physiology. *Proceedings of Sir Joseph Barcroft Centenary Symposium*. University Press. Cambridge, England. p. 382.
- Bauer ML, Harmon DL, Bohner DW, Branco AF, Huntington GB (2001) Influence of α -linked glucose on sodium-glucose cotransport activity along the small intestine in cattle. *J. Anim. Sci.* 79: 1917-1924.
- Bergman EN (1971) Hyperketonemia-Ketogenesis and ketone body metabolism. *J. Dairy Sci.* 54: 936-948.
- Bergman EN (1973) Glucose metabolism in ruminants as related to hypoglycemia and ketosis. *Cornell Vet.* 63: 341-382.
- Bergman EN, Hogue DE (1967) Glucose turnover and oxidation rates in lactating sheep. *Amer. J. Physiol.* 213: 1378-1384.
- Bickerstaffe R, Annison EF, Linzell JF (1974) The metabolism of glucose, acetate, lipids and amino acids in lactating dairy cows. *J. Agric. Sci. (Camb.)* 82: 71-85.
- Bird AR, Croome WJr, Fan YK, Black BL, McBride BW, Taylor IL (1996) Peptide regulation of intestinal glucose absorption. *J. Anim. Sci.* 74: 2523-2540.
- Cheng KJ, Hironaka R, Roberts DWA, Costerton JW (1973) Cytoplasmic glycogen inclusions in cells of anaerobic gram-negative rumen bacteria. *Can. J. Microbiol.* 19: 1501-1506.
- Cheng KH, Huber JT, Theurer BC, Swingle RS, Simas J, Chan SC, Wu Z, Sullivan JL (1994) Effect of steam flaking corn and sorghum grains on performance of lactating cows. *J. Dairy Sci.* 77: 1038-1043.
- Christenson RK, Prior RL (1978) Uterine blood flow and nutrient uptake during late gestation in ewes with different number of foetuses. *J. Anim. Sci.* 46: 189-200.
- Chow JC, Jesse EW (1992) Interactions between gluconeogenesis and fatty acid oxidation in isolated sheep hepatocytes. *J. Dairy Sci.* 75: 2142-2148.
- Church DC (1979) *Digestive Physiology and Nutrition of Ruminants*. Vol. 1. 3rd ed. O & B Corvallis. Oregon, USA. 350 pp.
- Clark RTJ, Bauchop T (1977) *Microbial Ecology of the Gut*. Academic Press. New York, USA. pp. 83-115.
- Coleman GS (1986) The amylase activity of 14 species of entodiniomorphid protozoa and the distribution of amylase in rumen digesta fractions of sheep containing no protozoa or one of seven different protozoal populations. *J. Agric. Sci. (Camb.)* 107: 709-721.
- Coleman GS (1992) The rate of uptake and metabolism of starch grains and cellulose particles by *Entodinium* species, *Eudiplodinium maggii*, some other entodiniomorphid protozoal and natural protozoal populations taken from the ovine rumen. *J. Appl. Bacteriol.* 73: 507-513.
- Coombe NB, Siddons RC (1973) Carbohydrases of the bovine small intestine. *Br. J. Nutr.* 30: 269-279.
- Coombe NB, Smith RH (1974) Digestion and absorption of starch, maltose and lactose by the preruminant calf. *Br. J. Nutr.* 31: 227-235.
- Croome WJr, Bull LS, Taylor IL (1992) Regulation of pancreatic exocrine secretion in ruminants: A review. *J. Nutr.* 122: 191-202.
- Donkin SS, Armentano LE (1995) Insulin and glucagons regulation of gluconeogenesis in preruminating and ruminating bovine. *J. Anim. Sci.* 73: 546-551.
- Eadie JM, Hobson PN (1962) Effect of the presence or absence of rumen ciliate protozoa on the total rumen bacterial count in lambs. *Nature* 193: 503-505.
- Eadie JM, Hobson PN, Mann SO (1967) A note on some comparisons between the rumen content of barley fed steers and that of young calves also fed on a high concentrate ration. *Anim. Prod.* 9: 247-250.
- El-Shazly K, Dehorty BA, Johnson RR (1961) Effect of starch on the digestion of cellulose *in vitro* and *in vivo* by rumen microorganisms. *J. Anim. Sci.* 20: 268-273.
- Feng-Qi Z, Okine EK, Cheeseman CI, Shirazi-Beechev SP, Kennelly JJ (1998) Glucose transporter gene expression in lactating bovine gastrointestinal tract. *J. Anim. Sci.* 76: 2921-2929.
- Fushiki T, Iwai K (1989) Two hypothesis on the feedback regulation of pancreatic enzyme secretion. *FASEB J.* 3: 121-124.
- Fushiki T, Kajiura H, Fukuoka S, Kido K, Semba T, Iwai K (1989) Evidence for an intraluminal mediator in rat pancreatic enzyme secretion: Reconstitution of the pancreatic response with dietary protein, trypsin and the monitor peptide. *J. Nutr.* 119: 622-630.
- Harmon DL (1993) Nutritional regulation of post-ruminal digestive enzymes in ruminants. *J. Dairy Sci.* 76: 2102-2111.
- Hatfield PG, Petersen MK, Clark CK, Glimp HA, Hememway KJ, Ramsey WS (1993) Effects of barley variety and restricted versus *libitum* intake on rate, site and extent of digestion by wethers fed a high energy diet. *J. Anim. Sci.* 71: 1390-1394.
- Heald PJ (1951) The assessment of glucose-containing substances in rumen microorganisms during a digestion cycle in sheep. *Br. J. Nutr.* 5: 84-93.
- Herrera-Saldaña RE, Huber JT, Poore MH (1990a) Dry matter, crude protein, and starch degradability of five cereal grains. *J. Dairy Sci.* 73: 2386-2393.
- Herrera-Saldaña RE, Gómez-Alarcón R, Torabi M, Huber JT (1990b) Influence of synchronizing protein and starch degradation in the rumen on nutrient utilization and microbial protein synthesis. *J. Dairy Sci.* 73: 142-148.
- Hino T, Kametaka M, Kandtsu M (1973) The cultivation of rumen oligotrich protozoa. I. Factors affecting the life of *Entodinium*. *J. Gen. Microbiol.* 19: 305-315.
- Hodgeson JC, Thomas PC (1975) A relationship between the molar proportion of propionic acid and the clearance rate of the liquid phase in the rumen of the sheep. *Br. J. Nutr.* 33: 447-456.
- Horsfield S, Infield JM, Annison EF (1974) Compartmental analysis and model building in the study of glucose kinetics in the lactating cow. *Proc. Nutr. Soc.* 33: 9-15.
- Hungate RE (1966) *The rumen and its microbes*. Academic Press. New York, USA.

- Janes AN, Parker DS, Weeks TEC, Armstrong DG (1984) Mesenteric venous flow and the net absorption of glucose in sheep fed dried grass or ground maize-based diets. *J. Agric. Sci. (Camb.)* 103: 549-553.
- Janes AN, Weeks TEC, Armstrong DG (1985a) Carbohydrase activity in the pancreatic tissue and small intestine mucosa of sheep fed dried-grass or ground maize-based diets. *J. Agric. Sci. (Camb.)* 104: 435-443.
- Janes AN, Weeks TEC, Armstrong DG (1985b) Absorption and metabolism of glucose by the mesenteric-drained viscera of sheep fed on dried-grass or ground, maize-based diets. *Br. J. Nutr.*: 54: 449-458.
- Johnson A, Hurwitz R, Kretchmer N (1977) Adaptation of rat pancreatic amylase and chymotrypsinogen to changes in diet. *J. Nutr.* 107:87-96.
- Keller PJ, Cohen E, Neurath H (1958) The proteins of bovine pancreatic juice. *J. Biol. Chem.* 233: 344-349.
- Kotarski SF, Waniska RD, Thurn KK (1992) Starch hydrolysis by the ruminal microflora. *J. Nutr.* 122: 178-190.
- Krebs HA (1966) Bovine ketosis. *Vet. Record* 78: 187-195.
- Kreikemeier KK, Harmon DL, Peters JP, Gross KL, Armendariz CK, Krehbiel CR (1990) Influence of dietary forage and feed intake on carbohydrase activities and small intestinal morphology of calves. *J. Anim. Sci.* 68:2916-2929.
- Kreikemeier KK, Harmon DL, Brandt RTJr, Avery TB, Johnson DE (1991) Small intestinal starch digestion in steers: Effect of various levels of abomasal glucose, corn starch, and corn dextrin infusion on small intestinal disappearance and net glucose absorption. *J. Anim. Sci.* 69: 328-338.
- Krogh N (1963) Clinical and microbiological studies on spontaneous cases of acute indigestion in ruminants. *Acta Vet. Scand.* 4: 27-40.
- Kurihara Y, Takechi T, Shibata F (1978) Relationship between bacteria and ciliate protozoa in the rumen of a sheep fed a purified diet. *J. Agric. Sci. (Camb.)* 90: 373-382.
- Leng RA (1970a) Biochemistry I (Nitrogen and carbohydrate metabolism). In Phillipson AD (Ed.) *Physiology of Digestion in the Ruminant*. Oriel Press. Newcastle Upon Tyne, UK. pp. 406-421.
- Leng RA (1970b) Glucose synthesis in ruminants. *Adv. Vet. Sci.* 14: 209-292.
- Linzell JL (1960) Mammary-gland blood flow and oxygen, glucose and volatile fatty acid uptake in the conscious goat. *J. Physiol.* 153: 492-509.
- MacRae JC, Armstrong DG (1969) Studies on intestinal digestion in the sheep. 2. Digestion of some carbohydrate constituents in hay, cereal and hay-cereal rations. *Br. J. Nutr.* 23: 377-387.
- Mann SC (1970) Some effects on the rumen microorganisms of overfeeding a high barley ration. *J. Appl. Bacteriol.* 33: 403-409.
- Martin SA (1994) Nutrient transport by ruminal bacteria: A review. *J. Anim. Sci.* 72: 3019-3031.
- McAllan AB, Smith RH (1974) Carbohydrate metabolism in the ruminant. Bacterial carbohydrates fermented in the rumen and their contribution to digesta entering the duodenum. *Br. J. Nutr.* 31: 77-88.
- McCarthy RDJr, Klusmeyer TH, Vicini, JL, Clark JH, Nelson DR (1989) Effects of source of protein and carbohydrate on ruminal fermentation and passage of nutrients to the small intestine of lactating cows. *J. Dairy Sci.* 72: 2002-2016.
- Mendoza MGD, Britton RA, Stock RA (1993) Influence of ruminal protozoa on site and extent of starch digestion and ruminal fermentation. *J. Anim. Sci.* 71: 1572-1578.
- Mendoza MGD, Britton RA, Stock RA (1998) Ruminal fermentation and *in situ* starch digestion with high moisture corn, dry rolled grain sorghum or a mixture of these grains. *Feed Sci. Technol.* 74:329-335.
- Mendoza MGD, Britton RA, Stock RA (1999) Effect of feeding mixtures of high moisture corn and dry rolled grain sorghum on ruminal fermentation and starch digestion. *Small Rum. Res.* 32: 113-118.
- Morrison FB (1959) *Feeds and Feeding*. 22nd ed. Morrison. Iowa, USA. 721 pp.
- Mould FL, Orskov RE (1983) Manipulation of rumen fluid pH and its influence on cellulolysis *in sacco* dry matter degradation and the rumen microflora of sheep offered either hay or concentrate. *Anim. Feed Sci. Technol.* 10: 1-14.
- Mould FL, Orskov RE, Mann SO (1983) Associative effects of mixed feeds. I. Effects of type and the influence of the rumen fluid pH on cellulolysis *in vivo* and dry matter digestion of various roughages. *Anim. Feed Sci. Technol.* 10: 15-30.
- Nicholson JWG, Sutton JD (1969) The effect of diet composition and level of feeding on digestion in the stomach and intestines of sheep. *Br. J. Nutr.* 23: 585-601.
- Nocek JE, Tamminga S (1991) Site of digestion of starch in the gastrointestinal tract of dairy cows and its effect on milk yield and composition. *J. Dairy Sci.* 74: 3598-3629.
- Nordin N, Campling RC (1976) Digestibility studies with cows given whole and rolled cereal grains. *Anim. Prod.* 23: 305-315.
- Oliveira JS, Huber JT, Theurer CB, Sullivan JL, Pessaraki M (1992) Effect of sorghum grain processing on site and extent of starch digestion in lactating dairy cows. *J. Dairy Sci.*, 75 (Suppl. 1): 296.
- Orskov ER (1986) Starch digestion and utilization in ruminants. *J. Anim. Sci.* 63: 1624-1633.
- Orskov ER, Fraser C, Kay RNB (1969) Dietary factors influencing the digestion of starch in the rumen and small and large intestine of early weaned lambs. *Br. J. Nutr.* 23: 217-226.
- Orskov ER, Fraser C, McDonald I (1972) Digestion of concentrates in sheep. 4. The effects of urea on digestion, nitrogen retention and growth in young lambs. *Br. J. Nutr.* 27: 491-501.
- Ortega CME, Finlayson HJ, Armstrong DG (1999a) The effect of chemical treatment of barley on starch digestion in ruminants. *Anim. Feed Sci. Technol.* 77: 73-81.
- Ortega CME, Finlayson HJ, Armstrong DG (1999b) Protection of starch in barley against rumen degradation by glutaraldehyde and formaldehyde as assessed by the dactron bag technique. *Anim. Feed Sci. Technol.* 77: 83-90.
- Otchere EO, McGilliard AD, Young JW (1974) Quantitation of alpha-linked glucose polymers passing to the small intestine in cattle. *J. Dairy Sci.* 57: 1184-1195.
- Owens FN, Secrist DS, Hill WJ, Gill DR (1998) Acidosis in cattle. A review. *J. Anim. Sci.* 76: 275-286.
- Poore MH, Moore JA, Eck TP, Swingle RW, Theurer CB (1993) Effect of fiber source and ruminal starch degradability on site and extent of digestion in dairy cows. *J. Dairy Sci.* 76: 2244-2253.
- Rojo R, Mendoza G, González R, Bárcena R, Crosby M, Landois L (2001) Use of exogenous amylases from *Bacillus licheniformis* and *Aspergillus niger* in high grain diets. *J. Anim. Sci.* 79 (Suppl. 1): 280.
- Sauvant D, Chilliard Y, Morand-Fehr P (1991) Etiological aspects of nutritional and metabolic disorders of goats. In Moran-Fehr P (Ed.) *Goat. Nutrition*. Pudoc. Wageningen, Netherlands. pp. 124-142.
- Schultz LH (1971) Management and nutritional aspects of ketosis. *J. Dairy Sci.* 54: 962-973.
- Siddons RC (1968) Carbohydrase activities in the bovine digestive tract. *Biochem. J.* 108: 839-844.
- Steel JW, Leng RA (1973a) Effects of plane of nutrition and pregnancy on gluconeogenesis in sheep. I. The kinetics of glucose metabolism. *Brit. J. Nutr.* 30: 451-473.
- Steel JW, Leng RA (1973b) Effects of plane of nutrition and pregnancy on gluconeogenesis in sheep. 2. Synthesis of glucose from ruminal propionate. *Brit. J. Nutr.* 30: 475-489.
- Stock RA, Brink, DR, Britton, RA, Goedeken, FK, Sindt MH, Kreikemeier KK, Bauer ML, Smith KK (1987) Feeding combinations of high moisture corn and dry rolled grain sorghum to finishing steers. *J. Anim. Sci.* 65: 290-302.
- Streeter MN, Wagner DG, Hibberd CA, Owens FN (1990) Comparison of corn with four sorghum grain hybrids: site and extent of digestion in steers. *J. Anim. Sci.* 68: 3429-3440.
- Sutton JD (1979) Carbohydrate fermentation in the rumen. Variations on a theme. *J. Sci. Food Agric.* 30: 1021.
- Swanson KC, Richards CJ, Harmon DL (2002) Influence of abomasal infusion of glucose or partially hydrolyzed starch on pancreatic exocrine secretion in beef steers. *J. Anim. Sci.* 80: 1112-1116.
- Taniguchi K, Huntington GB, Glenn BP (1995) Net nutrient flux by visceral tissues of beef steers given abomasal and ruminal infusions of casein and starch. *J. Anim. Sci.* 73: 236-249.
- Theander O (1981) Chemical composition of low quality roughages as related to alkali treatment. In Kategile JA, Said AN, Sundstol F (Eds.) *Utilization of low quality roughages in Africa*. Agricultural Development Report 1. The Agricultural University of Norway. pp. 1-27.
- Theurer CB (1986) Grain processing effects on starch utilization by ruminants. *J. Anim. Sci.* 63: 1649-1662.
- Thompson F (1973) The effect of frequency of feeding on the flow and composition of duodenal digesta in sheep given straw-based diets. *Br. J. Nutr.* 30: 87-94.
- Thompson F, Lamming GE (1972) The flow of digesta, dry matter and starch to the duodenum in sheep given rations containing straw of varying particle size. *Br. J. Nutr.* 28: 391-403.

- Topps JH, Kay RNB, Goodall ED (1968a) Digestion of concentrate and of hay diets in the stomach and intestines of ruminants. 1. Sheep. *Br. J. Nutr.* 22: 261-280.
- Topps JH, Kay RNB, Goodall ED, Whitelaw FG, Ried RS (1968b) Digestion of concentrate and of hay diets in the stomach and intestines of ruminants. 2. Young steers. *Brit. J. Nutr.* 22: 281-290.
- Tucker RE, Mitchell GE, Little CO (1968) Ruminant and post-ruminal starch digestion in sheep. *J. Anim. Sci.* 27: 824-826.
- Waldo DR (1973) Extent and partition of cereal grain starch digestion in ruminants. *J. Anim. Sci.* 37: 1062-1074.
- Walker DJ (1965) Energy metabolism and rumen microorganisms. In Dougherty RW (Ed.). *Physiology of Digestion in the Ruminant*. Butterworths. London, UK. pp. 296-310.
- Walker DJ, Nader CJ (1970) Rumen microbial protein synthesis in relation to energy supply: diurnal with once-daily feeding. *Austr. J. Agric. Res.* 21: 747-754.
- Weeks TEC (1979). Carbohydrate Metabolism. In Church DC (Ed.) *Digestive Physiology and Nutrition in Ruminants*. Vol. 2, 2nd ed. O & B Books. Corvallis, Oregon, USA. pp. 187-209.
- Wilcox MC, Saver RD, Coors JG, Batajoo KK (1994) Influence of *Sugary-Brawn*² or dent corn at two forage levels on intake, digestion and milk production by dairy cows. *J. Anim. Sci.* 72: 220-228.
- Wiltout DW, Satter LD (1972) Contribution of propionate to glucose synthesis in the lactating and non-lactating cow. *J. Dairy Sci.* 55: 307-317.
- Wood IS, Dyer J, Hofmann RR, Shirazi-Beechey SP (2000) Expression of the Na⁺/glucose co-transporter (SGLT1) in the intestine of domestic and wild ruminants. *Pflugers Arch.* 441: 155-162.
- Wu Z, Sleiman FT, Theurer CB, Santos F, Simas JM, Francolin M, Huber JT (1994) Effect of isocaloric infusion of glucose in the rumen or propionate in the duodenum. *J. Dairy Sci.* 77: 1556-1562.
- Xiong Y, Bartle SJ, Preston RL (1991) Density of steam flaked sorghum grain, roughage level and feeding regime for feedlot steers. *J. Anim. Sci.* 69: 1707-1718.
- Young JW (1977) Gluconeogenesis in cattle: significance and methodology. *J. Dairy Sci.* 60: 1-15.
- Zinn RA (1987) Influence of lasalocid and monensin plus tylosin on comparative feeding value of steam flaked versus dry rolled corn in diets for feedlot cattle. *J. Anim. Sci.* 65: 256-266.
- Zinn RA (1993) Influence of processing on the comparative feeding value of barley for feedlot cattle. *J. Anim. Sci.* 71: 3-10.
- Zinn RA (1994) Influence of flake thickness on the feeding value of steam rolled wheat for feedlot cattle. *J. Anim. Sci.* 72: 21-28.
- Zinn RA, Borques JL (1993) Influence of sodium bicarbonate and monensin on utilization of a fat supplemented high energy growing finishing diet by feedlot steers. *J. Anim. Sci.* 71: 18-25.