Proceedings of
THE NUTRITION SOCIETY
of
AUSTRALIA

Volume 18

Eighteenth Annual Scientific Meeting
Newcastle, NSW, September 1994
STARCH DIGESTION IN RUMINANTS - PROBLEMS, SOLUTIONS AND OPPORTUNITIES

J. B. ROWE¹ AND D. W. PETHICK²

Summary

There have been significant advances in our understanding of starch fermentation and digestion in ruminants. The major problem in feeding starch to ruminants is the rapid fermentation of starch and the accumulation of acids in the gut which reduce the pH to the point where health and productivity are affected. Recent research has identified problems of hindgut acidosis which can be more common and as harmful as the better known problems of lactic acidosis in the rumen. The use of the antibiotic feed additive, virginiamycin, has been shown to reduce the risks of starch feeding to the extent where feeding cereal grain is safe and practical. These new feeding systems have the potential to deliver undigested starch post-ruminally for absorption as glucose. For this reason it has been appropriate to evaluate the effect of glucose on pathways of physiological and commercial importance such as glycogen and lipid synthesis. It is clear that intravenous infusions of glucose stimulate key enzymes involved in lipid synthesis including the citrate cleavage pathway which converts glucose to lipid and importantly acetylCoA carboxylase, the rate limiting step for lipogenesis.

I. INTRODUCTION

Cereal grain is an important source of feed for ruminants in Australia. Historically the main use of cereal grain has been for supplementary feed during periods of drought or seasonal pasture shortage. This pattern has changed with the rapid expansion of the feedlot industry over the last five years and grain fed in feedlots now constitutes around 30% of the total amount of cereal grain fed to ruminants in Australia. The use of grain in feedlots is as much an opportunity to market grain "through beef" as it is for beef producers to achieve a consistent product. This alternative use for grain for ruminant feeding in Australia is becoming more important as there is increased differentiation in the pricing of cereal grain based on quality. Therefore it is likely that increasing quantities of cereal grains which do not meet the specifications for profitable export will be available for animal feeding. Further factors suggesting increased animal use are forecasts for continued low prices of cereals on international markets, and for cereal grains to continue their dominance of broad acre cropping in Australia. Optimising the efficiency with which cereal grains are used for ruminant feeding is therefore an important task for Australian scientists and producers.

In many parts of Australia cereals are a cheaper source of digestible energy than hay or silage and they are also easier to store and handle than forages. Cereal grains also provide the potential for increased growth rate or higher levels of production than those achievable on low-quality roughages and conserved forages. The usefulness of cereal grains for herbivore feeding is, however, restricted by problems associated with the rapid fermentation of starch and the risk that this may lead to acidosis. The consequences of acidosis for animal health and production...
can be serious. The common effects are a reduction in feed intake, lower growth rates, low tensile strength in wool and, in serious cases, death can result. The problems associated with acidosis are widely recognised and have a profound impact on the selection of grain, and the methods by which it is fed. Table 1 shows how little wheat, which is the most dangerous grain to feed, is used for feeding grazing ruminants. In fact it represents 0.3% of the total wheat produced on the farms surveyed compared to 55% in the case of oats (unpublished information). Feedlot production systems have been developed to allow tight control in the way in which cereal grain is fed to cattle. The cost of equipment and infrastructure for feed processing and mixing, fencing and shelter as well as the indirect costs of animal health and waste management, makes lot feeding expensive and capital intensive. Almost all production feeding based on cereal grain is conducted under controlled feedlot conditions. Feeding cereal grain to grazing sheep is relatively common (approx 80% of the sheep flock in WA in most years), but the feeding of grain to grazing cattle is comparatively rare (approx 20% of the herd fed grain supplements in WA) (Table 1).

Table 1. Results of a survey of 784 sheep and cattle producers to determine grain use for supplementary feeding in WA during the 1990/91 season. (J.B. Rowe, unpublished). Most producers surveyed fed more than one type of grain. Amounts of each grain are given in t/year for the total number of producers using that type of grain.

<table>
<thead>
<tr>
<th></th>
<th>Wheat</th>
<th>Oats</th>
<th>Barley</th>
<th>Lupins</th>
<th>Total fed (t/year)</th>
<th>Average intake*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of producers</td>
<td>46</td>
<td>564</td>
<td>150</td>
<td>509</td>
<td>784</td>
<td></td>
</tr>
<tr>
<td>Grain fed to sheep</td>
<td>706</td>
<td>58,658</td>
<td>4,858</td>
<td>24,824</td>
<td>89,046</td>
<td>14</td>
</tr>
<tr>
<td>Grain fed to cattle</td>
<td>808</td>
<td>1,806</td>
<td>3,558</td>
<td>3,536</td>
<td>9,708</td>
<td>62</td>
</tr>
</tbody>
</table>

* Average amount of grain fed (kg/ head) as a supplement to sheep or cattle

There has been little effort to develop systems for safely feeding grain to grazing sheep and cattle. Most research has focussed on improving the utilisation of cereal starch by feedlot cattle. Here there have been two conflicting objectives. Firstly to maximise fermentation of starch in the rumen to provide both energy and microbial protein. Secondly to slow down fermentation in the rumen in order to reduce the risk of acidosis and to increase the absorption of glucose from starch digestion in the small intestine (Huntington 1994). In our research we have focussed on developing systems for the safe feeding of cereal grain to grazing ruminants without slowing down fermentation in the rumen. In this paper we review the major ways in which starch fermentation can be manipulated and the nutritional consequences of these changes. We also discuss some new developments in the control of acidosis which provides the basis of new feeding systems for ruminants. These feeding systems may allow us to exploit the potential advantages for ruminant production when preformed glucose is absorbed from the intestine.

II. DIFFERENCES BETWEEN GRAINS FOR RUMINANT ANIMALS

The extent to which different cereal grains are used for feeding grazing ruminants reflects the relative risk of acidosis associated with these grains (see Table 1). The risk of acidosis is related to the amount of starch consumed and the rate at which it is fermented. Wheat is the most dangerous grain to feed and the reason for this is clearly seen in Table 2. It
contains relatively high levels of starch which is highly soluble and fermentation is therefore both extensive and also very rapid. On the other hand, oats has the lowest level of starch compared to wheat and barley, even though oat starch is also readily fermentable. This low level of starch combined with the reasonable levels of fibre provided by the hull of the oat grain (25 to 30% of the dry matter) makes it relatively safe to feed to ruminants and explains why it is the traditional grain for ruminant feeding. The use of lupin grain is widespread in Western Australia and is gaining popularity elsewhere in Australia. Although it is not a cereal grain it is interesting and relevant to discuss its success as it indicates the potential use of cereal grains if we can overcome the risk of acidosis. Lupin grain contains little or no starch and can be fed to sheep and cattle with complete safety. This safety means that it can be fed out, even without a gradual period of introduction, at weekly or fortnightly intervals with no risk of ill health and without reducing its effectiveness as a supplement (Rowe and Ferguson 1984; Morecombe et al. 1986).

The normal practice for cereal grains is to slowly increase the amount offered through daily feeding for around two weeks, followed by feeding every two to three days. The convenience and savings in labour of the simplified system for feeding lupins justifies, to many producers, the higher cost of lupins compared to cereal grains (approximately twice the price). It has been suggested that the advantages of lupin grain result from the high levels of protein compared to cereal grain. This is not supported by experiments measuring wool growth in grazing sheep fed supplements of either lupin or cereal grain (Rowe et al. 1989) where wool growth has been directly related to the amount of grain fed irrespective of type of grain or amount of protein supplied. The protein of lupin is extensively degraded in the rumen (Hume 1974) and also has low levels of methionine for wool growth (Murray et al. 1991). The use of lupins in experiments and under commercial conditions has provided the breakthrough in demonstrating the range of benefits possible in feeding grain supplements to grazing animals. We believe that the challenge is to modify the fermentation and digestion of starch in order to facilitate the safe feeding of cereals in the same way as lupin grain is used now. Cereal grains may even have some advantages over and above lupins by supplying starch which, if digested post-ruminally, allows for absorption of glucose which could be beneficial under certain circumstances. There are a number of potential advantages in supplying preformed glucose in the form of starch to ruminants. The process of fermentation results in significant loss of energy in the form of methane, hydrogen and heat. Glucose units passing unfermented through the rumen and absorbed intact from the small intestine therefore represents an increase in the efficiency of energy utilisation by around 30%. There may also be advantages to the animal in absorbing intact glucose and this is discussed later in the paper.

III. PROCESSING OF CEREAL GRAINS FOR RUMINANTS

There is no indication that cereal grain should be processed before feeding to sheep. Through primary mastication and rumination the grain is cracked and ground to allow efficient fermentation and digestion of starch. On the other hand, for cattle, it is widely accepted that the grain should be milled by grinding or rolling to expose the endosperm for fermentation and digestion. If this is not done a significant amount of grain passes intact through the digestive tract. The only exception is oat grain which can be fed whole without reducing productivity. For the other grains a general rule of thumb is that if the cost of milling the grain is less than 30% of the cost of the grain then simple processing will be cost-effective. A more complex issue is the optimal particle size of processed grain. Opinion on this issue can vary from just cracking the grain using light pressure rolling through to fine grinding in a hammer mill. The particle size affects the rate and extent of fermentation in the rumen as the smaller particles are more fragile and accessible for digestion. Smaller particles are also likely to flow out of the rumen and absorbed intact from the small intestine therefore represents an increase in the efficiency of energy utilisation by around 30%. There may also be advantages to the animal in absorbing intact glucose and this is discussed later in the paper.
rumen more quickly than larger particles. The fact that these two aspects of particle size work in opposite directions may explain why there is relatively little difference in the effect of grinding compared to rolling on the proportion of dietary starch fermented in the rumen (Huntington 1994).

Table 2. The fermentation and digestion of starch from different cereal grains by ruminants (from 1 Nocek and Taminga, 1991 and 2 Huntington, 1994). The data refers to grains hammermilled or dry rolled.

<table>
<thead>
<tr>
<th></th>
<th>Maize</th>
<th>Sorghum</th>
<th>Barley</th>
<th>Wheat</th>
<th>Oats</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Starch content (%) of DM</strong></td>
<td>76</td>
<td>75</td>
<td>61</td>
<td>76</td>
<td>42</td>
</tr>
<tr>
<td><strong>Digestibility</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rumen (% of intake)</td>
<td>76</td>
<td>64</td>
<td>87</td>
<td>89</td>
<td>92</td>
</tr>
<tr>
<td>Post rumen (% of duodenal flow)</td>
<td>66</td>
<td>63</td>
<td>73</td>
<td>85</td>
<td>76</td>
</tr>
<tr>
<td>Whole tract (% of intake)</td>
<td>93</td>
<td>87</td>
<td>93</td>
<td>98</td>
<td>98</td>
</tr>
<tr>
<td><strong>Solubility (% loss from nylon bags)</strong></td>
<td>26</td>
<td>32</td>
<td>54</td>
<td>68</td>
<td>96</td>
</tr>
<tr>
<td><strong>For each kg DM consumed</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Starch intake (g/d)</td>
<td>760</td>
<td>750</td>
<td>610</td>
<td>760</td>
<td>420</td>
</tr>
<tr>
<td>Starch fermented in rumen (g/d)</td>
<td>578</td>
<td>480</td>
<td>531</td>
<td>676</td>
<td>386</td>
</tr>
<tr>
<td>Starch digested post ruminally (g/d)</td>
<td>120</td>
<td>169</td>
<td>58</td>
<td>71</td>
<td>26</td>
</tr>
<tr>
<td>Starch excreted in faeces (g/d)</td>
<td>57</td>
<td>97</td>
<td>40</td>
<td>14</td>
<td>7</td>
</tr>
</tbody>
</table>

While simple physical processing to crack the pericarp appears to be all that is needed to achieve optimal fermentation and digestion of wheat, there is evidence that steam treatment combined with rolling or flaking improves the utilisation of sorghum, maize and, to a lesser extent, barley. The digestibility of cereal starch is affected by the physical form of the starch and starch-protein associations. In the case of sorghum, steam and the physical forces of rolling are needed to disrupt the endosperm protein matrix to allow efficient fermentation and digestion. Steam flaking may increase the whole tract digestibility of sorghum by around 10 percentage units compared to dry rolling (from 87 to 98%) whereas the corresponding difference for maize is around six percentage units and for barley between two to five units (Huntington 1994; Zinn 1992). On the other hand steam processing of either wheat or oats gives no benefit over dry rolling or grinding (Huntington 1994; Zinn 1993). The effect of steam processing barley and wheat is summarised in Table 3. Steam treatment and thin flaking may actually be a disadvantage for barley and wheat as fermentation becomes so rapid as to cause acidic conditions in the rumen leading to subclinical acidosis and a rise in the incidence of liver abscesses (Zinn 1993; 1994).

III. ACIDOSIS AND ITS CONTROL IN RUMINANTS

(a) Problems of rapid starch fermentation in ruminants

Problems resulting from rapid fermentation of starch in the rumen include acidosis,
bloat and liver abscess. While all three are important, we only discuss acidosis and its control. The study of acidosis is made difficult by the variability between animals. In response to the same amount of carbohydrate, some animals will maintain a normal pattern of fermentation while others develop high levels of lactic acid in the rumen and/or severe scouring and a small proportion of animals may die (Aitchison et al. 1984). The exact factors contributing to this variation have never been studied or clearly identified. Most research on acidosis in ruminants has concentrated on changes in the rumen without any reference to possible problems of acidosis in the hindgut. In a number of studies in animals fed high levels of starch (eg Murray et al. 1990), there have been numerous cases of normal rumen fermentation in animals with severe scouring and therefore abnormalities in the hindgut. Lee (1986) and Godfrey et al. (1993) have reported high concentrations of lactic acid and more severe signs of acidosis in the hindgut than in the rumen of animals given high levels of starch. Still further evidence for the importance of the hindgut in acidosis is provided by the study of Ørskov et al. (1971) in which acidosis and watery faeces resulted from infusions of starch into the hindgut.

Table 3. Effect of steam processing barley or wheat grain on performance in cattle, fermentation in the rumen and digestion post-ruminally. (Zinn 1993; 1994)

<table>
<thead>
<tr>
<th></th>
<th>Dry rolled</th>
<th>Steam-rolled</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Coarse flake</td>
<td>Thin flake</td>
<td></td>
</tr>
<tr>
<td>Intake (kg DM/d)</td>
<td>7.50</td>
<td>7.30</td>
<td>7.0</td>
</tr>
<tr>
<td>Liveweight gain (kg/d)</td>
<td>1.31</td>
<td>1.29</td>
<td>1.28</td>
</tr>
<tr>
<td>Rumen pH</td>
<td>5.70</td>
<td>5.63</td>
<td>5.35</td>
</tr>
<tr>
<td>Rumen fermentation of starch (% of intake)</td>
<td>76</td>
<td>88</td>
<td>90</td>
</tr>
<tr>
<td>Post-ruminal digestion (% of duodenal flow)</td>
<td>79</td>
<td>81</td>
<td>87</td>
</tr>
<tr>
<td>Whole tract digestion (% of intake)</td>
<td>95</td>
<td>98</td>
<td>99</td>
</tr>
</tbody>
</table>

Barley grain (Zinn 1993)

<table>
<thead>
<tr>
<th></th>
<th>Intake (kg DM/d)</th>
<th>Liveweight gain (kg/d)</th>
<th>Rumen pH</th>
<th>Abscessed liver (%)</th>
<th>Rumen fermentation of starch (% of intake)</th>
<th>Post-ruminal digestion (% of duodenal flow)</th>
<th>Whole-tract digestion (% of intake)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dry rolled</td>
<td>7.30</td>
<td>0.89</td>
<td>5.30</td>
<td>4.3</td>
<td>83</td>
<td>79</td>
<td>97</td>
</tr>
<tr>
<td>Steam-rolled</td>
<td>6.70</td>
<td>1.02</td>
<td>5.47</td>
<td>4.3</td>
<td>90</td>
<td>83</td>
<td>99</td>
</tr>
<tr>
<td></td>
<td>6.60</td>
<td>1.00</td>
<td>5.27</td>
<td>12.7</td>
<td>86</td>
<td>91</td>
<td>99</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>0.48</td>
<td>8.0</td>
<td>5.2</td>
<td>4.5</td>
<td>0.9</td>
</tr>
<tr>
<td>SD</td>
<td>0.37</td>
<td>0.09</td>
<td>0.48</td>
<td>8.0</td>
<td>5.2</td>
<td>4.5</td>
<td>0.9</td>
</tr>
</tbody>
</table>

Wheat grain (Zinn 1994)

of fermentation while others develop high levels of lactic acid in the rumen and/or severe scouring and a small proportion of animals may die (Aitchison et al. 1984). The exact factors contributing to this variation have never been studied or clearly identified. Most research on acidosis in ruminants has concentrated on changes in the rumen without any reference to possible problems of acidosis in the hindgut. In a number of studies in animals fed high levels of starch (eg Murray et al. 1990), there have been numerous cases of normal rumen fermentation in animals with severe scouring and therefore abnormalities in the hindgut. Lee (1986) and Godfrey et al. (1993) have reported high concentrations of lactic acid and more severe signs of acidosis in the hindgut than in the rumen of animals given high levels of starch. Still further evidence for the importance of the hindgut in acidosis is provided by the study of Ørskov et al. (1971) in which acidosis and watery faeces resulted from infusions of starch into the hindgut.
The role of the hindgut in ruminants with grain-induced acidosis makes the task of manipulating starch fermentation and digestion even more difficult. It is not only a question of manipulating the proportion of starch fermented in the rumen compared to that digested post-ruminally. It is also essential to make sure that the overall level of starch reaching the hindgut is within the limits of this organ to ferment starch while maintaining normal conditions. Grains such as maize and sorghum are likely to deliver more starch to the hindgut than wheat, barley or oats (Table 2). It is also apparent from the studies by Mann and Ørskov (1973) that when starch is consumed in large discreet meals there is a greater effect on fermentation in the hindgut than when it is continuously available. Ørskov et al. (1971) estimated the capacity of the small intestine to absorb glucose in two sheep (Fig 1). These two sheep clearly showed a different capacity for glucose absorption and this variation between animals provides an additional explanation for some of the differences between animals in their susceptibility to acidosis.

There have been three types of additives used in attempts to reduce the adverse effects of rapid starch fermentation and/or problems with acidosis. These are: nutrients which facilitate balanced and efficient fermentation; buffers to maintain pH within physiological limits; and antibiotic feed additives which specifically target the bacteria which continue to produce lactic acid at low pH.

(b) Nutrients which facilitate efficient fermentation and digestion of starch

Urea and ammonium sulphate balance the supply of substrate for microbes during the rapid fermentation of starch in the rumen and improve the efficiency of microbial protein synthesis. Sources of soluble protein in the diet can also provide the nitrogen required to balance the nutrients required for the rapid fermentation. There is also evidence that protein may have a role in improving the efficiency of starch absorption from the small intestine. Taniguchi et al. (1992; 1993) showed increased absorption of glucose from the small intestine in response to increased protein entering the duodenum. It has been suggested that this is due to increased secretion of digestive enzymes from the pancreas in response to protein entering the intestine (Huntington 1994).
(c) Buffers and agents which slow down fermentation of starch

The most common buffer used is sodium bicarbonate. The effect of bicarbonate has been investigated in numerous metabolic studies and in various production trials. Xu (1994) concluded that the addition of buffers to the diets of dairy cows occasionally increased milk fat percentage without any measurable effect on rumen pH or VFA concentrations. Zinn and Borques (1993) similarly found no measurable effect of bicarbonate on rumen pH or on the site of starch digestion in feedlot steers. The use of bicarbonate has also been shown to be ineffective in reducing the proportion of animals with acidosis following administration of ground wheat into the rumen (Aitchison et al. 1987). It is therefore concluded that buffers such as bicarbonate offer little protection against acidosis when feeding rapidly fermentable carbohydrate to ruminants.

Formaldehyde has been tested as a means of reducing starch digestion in the rumen. The hypothesis is that formaldehyde would react with the protein matrix surrounding the starch granules and thereby prevent microbial attack and so slow fermentation of the rumen. While this works in vitro there is no evidence of efficacy in vivo (McAllister et al. 1992). A potential danger associated with this type of treatment is that it could increase the amount of starch reaching the hindgut and thereby increase the risk of acidosis.

The inclusion of fat in high-starch diets has been investigated as a way to slow down starch digestion and suggests that this strategy may reduce the risk of acidosis when feeding barley and wheat. Provided that fats can be included in the diet at a competitive price on the basis of their digestible energy the additional benefit in modifying starch digestion may be a worthwhile bonus.

(d) Antibiotic feed additives

Nagaraja et al. (1981) demonstrated that the ionophores monensin and lasalocid were effective in reducing the accumulation of lactic acid in fistulated steers given high levels of starch. There does not appear to be any effect of ionophores on the pattern of starch fermentation or digestion in cattle. We are also not aware of results of any studies on the use of ionophores to facilitate the safe feeding of cereal grain under radically different feeding systems. Work by Nagaraja et al. (1987) showed a wide range of antibiotic feed additives to be effective against lactic acid accumulation when incubating rumen fluid with glucose. These additives are all selectively active against Gram-positive bacteria including Streptococcus bovis and Lactobacillus sp. which are known to be important in the accumulation of lactic acid that leads to acidosis. Further screening work in Western Australia identified virginiamycin as a very effective compound for controlling lactic acid accumulation under conditions in vitro as well as in sheep (Rowe et al. 1989) and cattle (Thorniley et al. 1994). In addition to controlling lactic acid accumulation in the rumen in animals fed high levels of grain, studies by Godfrey et al. (1993a) showed the control of acidosis in the hindgut with virginiamycin.

The use of virginiamycin has now been tested under conditions of pen feeding and in grazing animals fed supplements of cereal grain and there is comprehensive evidence that it reduces the risk of acidosis to the point where cereal grains can be fed in a similar way to lupins (Rowe and Zorrilla-Rios 1992). This is illustrated in Fig. 2 which summarises the data of Godfrey et al. (1993b) comparing feeding intervals and animal performance of sheep fed lupins or barley (± virginiamycin). This shows that even when 2.8 kg of barley with virginiamycin is fed at fortnightly intervals, liveweight gain and feed intake are similar to when lupins are fed. When barley was fed alone, liveweight gain was reduced at feeding intervals of once or twice per week and there were signs of subclinical acidosis and scouring among sheep in these treatment groups. Because of the risk of acidosis, fortnightly feeding of barley without virginiamycin would not be considered practical or ethical.
Fig. 2. Responses in liveweight gain when lupin (o), barley (Δ) or barley with virginiamycin (●) were fed as a supplement to sheep with access to oat chaff. The grain was fed daily, twice weekly, weekly or fortnightly to provide the equivalent of 200 g/d. Bars show standard error of difference. (Godfrey et al. 1993b).

In feeding trials with cattle to supplements of cereal grain and virginiamycin fed at weekly intervals gave similar responses to those achieved with daily feeding (see Fig. 3). The efficiency of conversion of grain to liveweight is approx. 6.5 which is not quite as good as for fully mixed feedlot diets but it creates new opportunities to finish cattle using grain supplements without the costs of the expensive infrastructure involved in feed lots. This approach has other advantages in relation to animal health and welfare, as well as to the environmental impact of intensive animal production in feedlots.

IV. METABOLIC EFFECTS OF INCREASING GLUCOSE ABSORPTION

(a) Glucose: a regulatory nutrient for ruminant production

The additional safety with which starch can be fed with virginiamycin opens up the possibility of giving grain in discreet meals to increase the flow of starch from the rumen and its absorption as glucose from the small intestine.

The metabolic effects of an increased glucose supply have either been determined directly by provision of extra glucose or more commonly by varying the ratio of propionate: acetate + butyrate. An increased availability of propionate has been assumed to lead to increases in glucose availability via acting as a gluconeogenic precursor. This does not appear to be the case since increased propionate production, due to the use of an ionophore, only increased the proportion of glucose derived from propionate with no increase in glucose entry rate (Casson et al. 1986). The conclusions of Lindsay (1970) that glucose entry rate is mainly influenced by digestible energy intake appear to hold true in the light of a wide range of more recent data. In considering the role of glucose as a nutrient for ruminants, it is therefore essential to also take account of total digestible energy intake.
In dry animals (non-lactating and non-pregnant) fed to maintenance there is little evidence that glucose limits any aspect of metabolism. The fact that 50% of the oxidative energy requirements of skeletal muscle are provided by glucose indicates little pressure on carbohydrate metabolism (Pethick et al. 1987). Preston and Leng (1987) argued that glucose was a limiting nutrient for many productive ruminants. This suggestion was based on studies by Leng and coworkers (Leng et al. 1978; Kempton et al. 1978) in which glucose was administered to growing lambs and increased growth rate. Unfortunately these experiments are difficult to interpret since there they were not designed in an isojoulic manner; i.e. glucose infusion represented extra energy.

(b) Lipid synthesis

Traditionally ruminants are thought to synthesise fat substantially from acetate using glucose only as a source of glycerol and reducing equivalents (Vernon 1981; Van der Walt 1984). However there is also evidence for some synthesis from glucose, especially via lactate (Prior, 1978). Indeed Smith and Crouse (1984) suggested that adipocytes associated with intramuscular fat (marbling) are more responsive to glucose and/or lactate as a substrate than they are to acetate. Smith et al. (1992) showed a massive increase in the citrate cleavage pathway of subcutaneous fat in cattle fed a maize-based diet as the level of feeding increased from 0.8 to 2.0 times maintenance. In addition, the total capacity for fat biosynthesis as judged by the activity of acetylCoA carboxylase increased dramatically. It is probable that, given the diets used, maize supplied some starch for digestion post-ruminally and so this could be construed as a special dietary situation. Nevertheless, it suggests that fat biosynthesis from...
both glucose and acetate can be up-regulated by an increased availability of glucose.

Recently, we have examined the influence of glucose infusion on lipid biosynthesis. We found the enzymes of the citrate cleavage pathway within adipose tissue increased as the intake of a lupin-based diet (20% straw: 80% lupin) increased from 0.8 to 1.7 times maintenance (Fig. 4). Clearly as energy intake increases even on a diet containing virtually no starch the supply of glucose from gluconeogenesis is sufficient to allow the induction of the citrate cleavage pathway for the synthesis of fat. The inclusion of glucose via jugular infusion under an isojoulic design further increased the citrate cleavage pathway.

![Graph showing the effect of glucose infusion on ATP citrate lyase activity](image)

**Fig. 4.** The effect of glucose infusion (2g/kg body wt.) and level of nutrition on the activity of ATP citrate lyase in subcutaneous fat. * indicates significantly different to control, P<0.05.

In a second experiment sheep were fed at 1.5 times maintenance and infused with a similar level of glucose; infusion increased the total capacity for fat synthesis as measured by acetylCoA carboxylase activity. This work clearly illustrates the role of glucose availability in determining the rate of lipid biosynthesis and suggests that the primary mechanism is for increased capacity of lipogenic enzymes rather than the provision of a limiting precursor (i.e. glucose) as suggested by Preston and Leng (1987). The mechanism whereby glucose can increase the lipogenic enzymes most probably involves the insulin axis.

(c) Glycogen levels

Glycogen in muscle is an important metabolite for homeostatic and production purposes. The level of glycogen in muscle tissue is responsive to carbohydrate in the diet of nonruminant animals (Sherman 1991). There is little work on increasing glycogen levels in the ruminant animal although there is some evidence of a general nutritional effect (Pethick et al. 1994; McVeigh and Tarrant 1982). Repletion of glycogen level in ruminant animals is very slow, taking three to eleven days (Tarrant 1989) and it is assumed that this is associated with low glucose availability. It would seem that further work is needed to test the role of glucose availability on stimulating glycogen metabolism. The new methods of feeding grain described in this paper offer exciting prospects for manipulating glycogen repletion.

A final example is the high-yielding, lactating dairy ruminant where there is a clear advantage in increasing the availability of propionate and/or glucose. This stems from the close link between glucose availability and lactose synthesis; the latter being the major determinant of milk production. Thus to maximise milk yield and minimise the risk of bovine ketosis, relatively high grain diets (55-65%) are recommended to assure high levels of propionate and glucose via intestinal absorption. In dairy cows fed high levels of grain there is considerably more post-ruminal starch digestion than in steers consuming lesser amounts (Table 4). This is clearly linked to the level of intake and the effect on flow rate through the rumen as well as
grain type but illustrates that the amount of glucose absorbed by dairy cattle may be far higher than in steers fed grain ad libitum. When available, appropriately-processed sorghum or maize should represent excellent energy sources due to increased levels of starch reaching the small intestine (Lean et al. 1992). Although production studies yield no clear evidence that increasing starch digestion post ruminally increases milk production (Nocek 1990) there is evidence that production of milk protein can be increased in response to grain treatment which increases starch digestion (Huntington 1994).

Table 4. Differences between steers and lactating dairy cows in the amount of digested post-ruminally.

<table>
<thead>
<tr>
<th></th>
<th>Lactating cows¹</th>
<th></th>
<th>Steers²</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Maize</td>
<td>Barley</td>
<td>SEM</td>
<td>Maize</td>
</tr>
<tr>
<td>Total feed intake (kg DM/d)</td>
<td>23.3</td>
<td>20.5</td>
<td>0.7</td>
<td>6.44</td>
</tr>
<tr>
<td>Rumen pH</td>
<td>5.96</td>
<td>5.62</td>
<td>0.04</td>
<td>5.56</td>
</tr>
<tr>
<td>Intake (kg starch/d)</td>
<td>10.3</td>
<td>8.2</td>
<td>0.3</td>
<td>2.33</td>
</tr>
<tr>
<td>Rumen digestion (% of intake)</td>
<td>52</td>
<td>76</td>
<td>2.1</td>
<td>84</td>
</tr>
<tr>
<td>Post rumen digestion (% of duodenal flow)</td>
<td>84</td>
<td>83</td>
<td>1.8</td>
<td>89</td>
</tr>
<tr>
<td>Post rumen digestion (kg starch/d)</td>
<td>4.2</td>
<td>1.6</td>
<td>0.3</td>
<td>0.3</td>
</tr>
<tr>
<td>Whole tract (% of intake)</td>
<td>93</td>
<td>97</td>
<td>0.7</td>
<td>98</td>
</tr>
</tbody>
</table>

¹ McCarthy et al. (1989)  ² Zinn (1992)

VI. CONCLUSIONS

The development of methods which make it safer to feed cereal grain to ruminants creates the opportunity to re-explore carbohydrate digestion and utilisation in ruminant animals. There is evidence that post-ruminal digestion of starch and absorption of glucose may be advantageous for some aspects of production. The apparent effects of glucose on lipid synthesis in rapidly growing animals, in high producing dairy cows and in the maintenance of glycogen levels in muscle justify further research in the field of carbohydrate digestion and metabolism in ruminants.

REFERENCES


SHERMAN, W.M. (1991). In 'Perspectives in exercise science and sports medicine Vol. 4: Ergogenics - enhancement of physical performance in sport and exercise.', pp1-34, eds. D.R.Lamb and M.H. Williams (Brown and Benchmark; Michigan)


