Beefing up starch digestion

A.F. Channon[1] and J.B. Rowe[2]

[1]Cooperative Research Centre for Cattle and Beef Quality, Animal Science, University of New England, Armidale NSW 2351
[2]Australian Sheep Industry CRC, Locked Bag 1, Armidale NSW 2350   achanno2@metz.une.edu.au

Summary

Any improvements in starch digestion in cattle would undoubtedly be of great benefit to the feedlot industry. There are numerous factors that are likely to vary between animals that may affect both the efficiency and site of starch digestion. The benefits of starch digestion in the small intestine, as opposed to in the rumen, include a higher energetic efficiency, and a reduced risk of acidosis provided that high levels of starch do not reach the hindgut. Recent research has identified genetic differences between similar cattle in their ability to digest starch. The evidence is provided by differences between progeny groups of steers in the level of fermentation occurring in the hindgut. We have also found between–animal differences in total tract starch digestibility that are consistent across diets.

Keywords: starch, digestion, fermentation, faeces, genetic variation, cattle, hindgut

Introduction

Profitable beef production in feedlots relies heavily on efficient grain–starch digestion. For this reason, the opportunity of being able to identify and select for cattle that are more efficient at digesting starch is of great potential importance to the industry. Aside from economic and environmental benefits, identification of animals that are more efficient at starch digestion may also improve the safety of grain feeding.

Our interest in the concept of genetic variation in starch digestion has been stimulated by the relatively recent finding that genetic variation in feed conversion efficiency exists between animals of the same breed (Archer *et al*. 1999). It is not known exactly why some animals are more efficient; differences in the ability to digest feed may be one of the biological mechanisms involved (Oddy and Herd 2000). This paper develops the idea that variation in the efficiency of starch digestion exists throughout the gastrointestinal tract and shows that this variation may be an important factor influencing feed efficiency in intensive grain–feeding systems.

The importance of site of digestion

There are three sites of importance: the rumen, small intestine, and hindgut (large intestine–caecum and colon) (see Figure 1). The rumen is the major site of starch digestion (Huntington 1997). Microorganisms ferment substrate entering the rumen to short–chain steam–volatile fatty acids (VFA), methane (CH_4) and carbon dioxide (CO_2). CH_4 is of no use to either the microbes or the host animal and, coupled with the heat of fermentation, represents a loss of energy. The host animal absorbs and utilises VFA as the major source of energy and carbon (Wolin 1981) and microbial materials (carbohydrate, lipid and protein) pass into the small intestine for subsequent digestion and absorption. A similar pattern of fermentation also occurs in the hindgut. Unfortunately, microbial peptides and amino acids produced here cannot be absorbed and are lost in the faeces (Ørskov *et al*. 1970b). Fermentation in the hindgut also suffers from the same sort of energetic losses as those that occur in the rumen.

Acidosis can arise when microbial populations in the rumen (Nocek 1997) or hindgut (Zust *et al*. 2000) rapidly ferment starch. The deleterious effects of clinical acidosis have been widely documented (Al Jassim and Rowe 1999; Owens *et al*. 1998). It is now understood that sub–clinical acidosis may be an even more widespread and costly problem in grain–fed cattle than the clinical condition (Beauchemin 2000; Rowe 1999). In this situation, animals appear to be healthy but the acid concentration in the rumen is unusually high (greater than 120 mM; Goad *et al*. 1998) and pH is typically between 5.0 and 5.8. This is below optimal for fibre fermentation (Russell and Wilson 1996). It can be seen that there is a conflict between avoiding acidosis and extensively processing grain to maximize digestibility in the rumen.
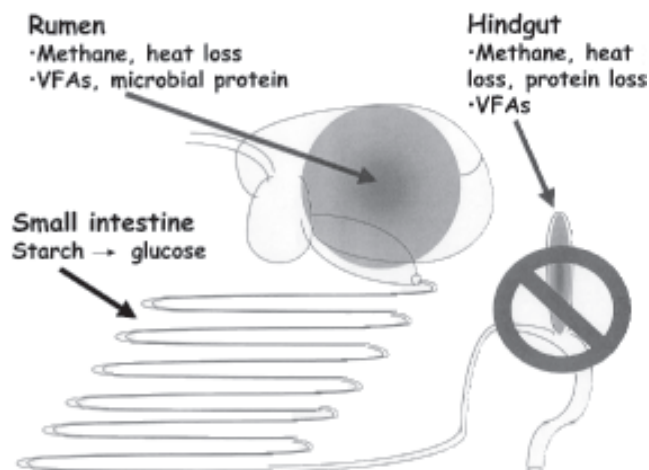
Figure 1 The ruminant digestive tract. From an energetic perspective, the small intestine is the most desirable site of starch digestion and the hindgut is the least desirable.

In contrast to the two sites of fermentation, the small intestine contains the animal's own digestive enzymes that break down starch to glucose for absorption (Bauer *et al*. 1995; Harmon 1993). The small intestine does host a relatively small microbial population (Allison 1993) and there is some evidence that microbial metabolism may make a small contribution to small intestinal starch disappearance (Kreikemeier *et al*. 1991).

In a summary of experimental findings and theoretical calculations, Harmon and McLeod (2001) concluded that starch fermentation was 25–30% less energetically efficient than starch digestion. This is because of the losses associated with fermentation (methane and heat) and with differences in partial efficiencies of the absorbed substrates. It appears that for the energetic benefits of starch digestion and glucose assimilation in the small intestine to be fully realised, starch digestion must be sufficiently complete to minimise the amount of starch reaching, and subsequently being fermented in, the hindgut (Harmon and McLeod 2001). Fermentation in the hindgut would be even less energetically efficient than rumen fermentation given that the energy incorporated into the microbial biomass is lost in the faeces (Knowlton *et al*. 1998; Ørskov *et al*. 1970b; Ørskov *et al*. 1972). The hindgut is the least desirable site of starch digestion.

Given this information, we can hypothesize that an animal should theoretically be more efficient if it can maximise starch digestion in the rumen and, in particular, in the small intestine. Experiments to test this hypothesis are described later in this paper.

Why is variation in starch digestion likely to exist in cattle?

There is variation in any biological system and differences will always occur between animals. The process of natural and human selection of ruminants has traditionally occurred under grazing conditions based largely on pasture and/or supplements of hay or silage. Therefore, it is not surprising that the digestive tract of ruminants is ideally suited to utilizing low quality fibrous material and is not particularly well adapted to processing cereal grain. The pancreatic and duodenal digestive enzyme systems and the absorptive mechanisms of the small intestine have never needed to evolve to handle high levels of starch.

There has been no direct genetic selection for efficient starch digestion in cattle. This is despite the fact that more than 700 000 were being fed in Australian feedlots in December 2002 (ALFA 2003). The fact that a feedlot steer still spends over half of its life in a paddock may have contributed to the lack of interest in this area of selection. Breeding females must also still perform on a forage diet.

Conversely, poultry and pigs have been much more intensively selected for efficient intestinal starch digestion on the basis of performance on grain–based diets. Despite this selection pressure, high phenotypic variability in starch digestibility has been shown to exist in young broilers eating wheat–based diets (Rogel 1985). In that instance there was no difference in weight gain between birds because poor starch digesters ate much more to compensate for poor energy utilisation. Svihus (2003) also reported that poor starch digestibility was a problem for a small percentage of birds and suggested that digestion in these birds was impaired due to a high feed intake and passage rate. Evidence of variation in starch digestion in these species gives reason to believe that it would exist in cattle.

Likely mechanisms behind variation in starch digestion

There are numerous factors likely to vary between animals that may have an effect on the site, rate, and extent of starch digestion throughout the gastrointestinal

tract. Animal factors that could possibly be under genetic control include a number discussed in this section.

Feeding and intake

Feeding behaviour, voluntary feed intake, dentition, and the quantity and composition of saliva production (Slyter 1976) may all vary between animals. The level of mastication/rumination influences feed particle size and saliva production. Ruminants eating grain–based diets are particularly dependent on the buffering capacity that saliva provides in the rumen (Argenzio 1993d; Beauchemin 2000). This is needed because of the rapid rate of acid production from the fermentation of starch, compared to forage. The efficiency of microbial growth and overall animal health strongly depends on their capacity to maintain a normal rumen pH (Russell and Wilson 1996; Slyter 1976).

Feed intake is dependent on animal, environmental and dietary factors. It has been shown that sheep selected for clean fleece weight have a higher dry matter intake (DMI) than sheep selected against fleece weight (Kahn *et al*. 2000; Thompson *et al*. 1989). Eating rate has also been reported to be highly variable between animals (Frisch and Vercoe 1977). Eating rate is negatively related to whole tract digesta retention time and positively related to DMI. It has been shown that steers selected for high feed efficiency (low residual feed intake; RFI) had a lower DMI and ate less often during the day than low feed efficiency (high RFI) steers (Richardson *et al*. 2000). The implications of this feeding behaviour on digestive function and starch digestion are unclear. However it is likely that certain animals will ingest grain in a way that will ensure a pattern of fermentation where the rate of acid removal can match the rate of acid production. In contrast, other animals with rapid feed consumption may be more likely to experience acidosis–related problems.

Rumen

The frequency and efficiency of rumination, rumen motility and residence time of particles may differ between similar individuals given the same diet (Hegarty 2000). Differences in digesta turnover rate may affect starch digestion in a number of ways:

- changes in the microbial species within the rumen;

- changes in the pattern of VFA and methane production;

- changes in microbial efficiency;

- changes in the amount of undegraded starch and dietary protein supplied to the small intestine.

There is evidence that selection for and against wool growth in Merino sheep has resulted in concomitant changes in rumen function. Kahn (1996) discovered that the sheep selected for high wool yield produced significantly more microbial protein per kg of DMI, than sheep selected for low wool yield. Selection for wool yield had evidently caused changes in the rumen environment that were more favourable to microbial growth. This would most likely be a change in the rumen dilution rate. Variation between sheep selection lines in the retention time of digesta in the rumen was also reported by Thompson *et al.* (1989) and Smuts *et al.* (1995). Ørskov *et al.* (1971a) reported large differences in digestion between two sheep fed a diet containing 93% pelleted corn. Whilst around 97% of the available starch was fermented in the rumen of one sheep, only 57% of the available starch was fermented in the rumen of the other. This second sheep produced much less microbial protein in the rumen and much more starch was delivered to the small intestine and hindgut. The authors attributed these differences to variation in rumen outflow rate between the sheep. Very importantly, Smuts *et al.* (1995) demonstrated that the retention time of digesta in the rumen was a heritable trait in sheep (heritability of 0.45–0.6). This is likely to be similar for cattle. Variation in rumen outflow rate in cattle was reported by Ørskov *et al.* (1988). They found that differences in rumen outflow rates between cows persisted with both *ad libitum* and restricted intakes of high and low roughage diets. The consistency in the differences between cows under controlled experimental conditions indicates that rumen outflow rate is under genetic control.

There are unlikely to be inherent, measurable differences in the rumen microbial populations of cattle. The microbial composition of the rumen varies between different layers of digesta (Hungate 1966). Furthermore, a single animal on a constant ration will exhibit fluctuations in rumen characteristics over time (Hungate 1966). Any between–animal differences in the rumen microbial population are likely to be downstream effects of variation in diet composition and rumen dilution rate (Hegarty 2000).

Oesophageal (reticular) groove physiology and activation stimuli (Ørskov *et al*. 1970a) are other factors that may influence the efficiency of starch digestion in the rumen. However, the usefulness of this mechanism in mature ruminants remains dubious. There may also be physiological differences in the structural integrity of the rumen, small intestine and hindgut wall. For example, considerable variation in the rate of ruminal parakeratosis development has been demonstrated in a group of similar steers fed pelleted lucerne (Hinders and Owen 1965).

Abomasum

Residence time and rate of HCl secretion in the abomasum may vary between animals. Protein digestion is initiated in the abomasum with the secretion of pepsinogen (Argenzio 1993d). Pepsinogen is converted to its active form, pepsin, in the presence of acid in the lumen. Similarly, the pancreas secretes inactive trypsinogen into the small intestine. In the intestinal lumen, trypsinogen is then activated to the protease,

trypsin (Argenzio 1993d). Trypsin then activates the remaining trypsinogen as well as the other proteolytic proenzymes, chymotrypsin and elastase (Argenzio 1993a). Proteases are important in breaking down cell walls and structural protein and the extent of starch–protein interactions in cereal grain are known to affect starch digestibility (Rooney and Pflugfelder 1986). The speculative implication of this association is that animals that are more efficient at digesting protein may indirectly be more efficient at starch digestion.

Small intestine

The ruminant has the capacity to adapt to diets delivering more starch to the small intestine by increasing the output of pancreatic α–amylase (Clary *et al*. 1969; Owens *et al*. 1986; Russell *et al*. 1981) and glucose absorption capacity (Bauer *et al*. 1995; Shirazi–Beechey *et al*. 1991). This ability to adapt to high–starch diets may vary between individuals. For example, Ørskov *et al.* (1971b) demonstrated considerable variation between two sheep in the capacity to absorb glucose from the small intestine. This variation is depicted in Figure 2.

It could be assumed that an animal with more starch or free glucose leaving the small intestine would be more susceptible to hindgut acidosis. In this example, an increased supply of glucose to the hindgut resulted in watery faeces and reduced faecal pH. This sort of variation may help to explain the differences between animals in their susceptibility to acidosis.

The physiological mechanisms controlling pancreatic function in ruminants are not well understood but are likely to involve the central nervous system, gastrointestinal hormones (cholecystokinin and secretin) and possibly VFA concentration (Argenzio 1993c; Croom *et al*. 1992). Metabolizable energy intake also appears to exert a major influence on pancreatic α–amylase concentration (Harmon 1992). A better understanding of this regulation may lead to methods of improving digestion in the small intestine. Taniguchi *et al.* (1995) speculated that protein/peptide entry into the small intestine stimulated an increase in α–amylase production and glucose absorption. If this is true, starch digestion in the duodenum is likely to be increased by the outflow of microbial and bypass protein from the rumen.

Small intestinal motility may vary between individuals. This influences the time that substrate is available for enzymatic digestion. Digesta are moved through the small intestine by peristaltic (propulsion) and segmentation (mixing) reflexes (Argenzio 1993b). On average, digesta spend less than 3 h in the small intestine of steers (Zinn and Owens 1980, cited by Owens *et al.* 1986). A slow rate of passage through the small intestine is ideal to ensure more complete digestion of carbohydrate before it reaches the hindgut.

Hindgut

Factors affecting the ability of microorganisms in the hindgut to ferment starch will be similar to those influencing fermentation in the rumen. Digesta intermittently fills and empties from the caecum with the flow being influenced by the type of diet and DMI (Grovum and Hecker 1973; Ulyatt *et al*. 1975). An increase in the proportion of grain in the diet typically delivers more starch to the hindgut (DeGregorio *et al*. 1982; Siciliano–Jones and Murphy 1989a; Siciliano–Jones and Murphy 1989b). The microbial population of the hindgut readily responds to substrate changes in a similar fashion to that of the rumen (Mann and Ørskov 1973; Ørskov *et al*. 1970b). The efficiency of digestion in the rumen and small intestine will indirectly affect the quantity and quality of digesta reaching the hindgut.

Evidence of genetic variation in starch digestion

We have now established that site of starch digestion is important and there are reasons to expect between–animal differences that may be physiologically important. Unfortunately, there appears to have been
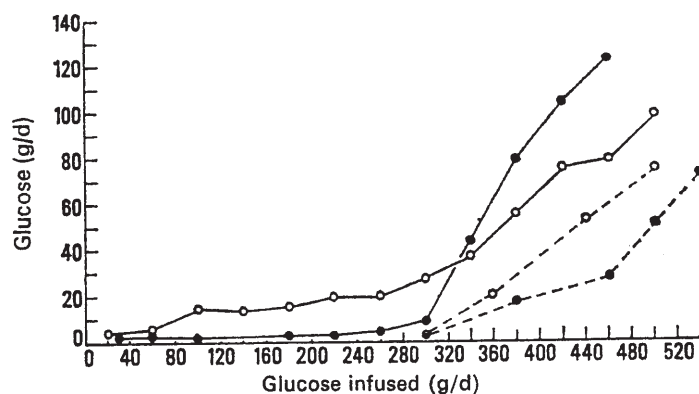
Figure 2 Effect of the level of glucose infused into the abomasum on glucose passing the terminal ileum (—) and excreted in faeces (– – –) of sheep 1 (●) and sheep 2 (o). Adapted from Ørskov *et al.* (1971b).

very little research directly designed to identify genetic variation in starch digestion in cattle. It is important to point out that this is a discussion of the possibility that cattle may vary in their capacity to digest starch as distinct from their ability to convert starch–based feeds into liveweight gain. We already know that overall feed efficiency in cattle has genetic variation (Herd *et al*. 1997; Richardson *et al*. 1998). We could expect feed conversion ratio (FCR) to be associated with the efficiency of starch digestion but the two do not necessarily correlate. For example, two animals might have a similar capacity to digest feed but other factors (e.g. metabolism, maintenance requirements or activity levels) may cause one animal to exhibit a better FCR. Much of the available information concerns variation in animal performance and total tract dry matter (DM) digestibility without directly quantifying any differences that exist in starch digestion. Nonetheless, this information does help to build the argument that genetic variation in the ability to digest starch does exist in cattle.

In terms of between–breed differences, it is difficult to conclude if *Bos indicus* content influences starch digestibility. Warwick and Cobb (1975) reviewed genetic variation in cattle in the ability to digest nutrients but did not focus on starch. These researchers reported inconsistent results but reached the general conclusion that cattle with *B. indicus* content were slightly more efficient than their *B. taurus* counterparts in digesting DM and crude protein. For starch–based diets, it has been reported that there are no differences in DMI, ADG and FCR between *B. indicus* crossbred and *B. taurus* cattle (Boyles and Riley 1991; Krehbiel *et al*. 2000). Beaver *et al*. (1989) fed a finishing corn silage–whole shelled corn–based diet to Angus and Brangus steers over two years. The Angus cattle had a greater DMI for the first year but they were no more efficient than the Brangus steers. In the second year, the Angus steers

had higher DM and starch digestibilities than the Brangus. This indicates that *B. indicus* cattle did not increase their starch digestibility, as did the *B. taurus* animals. This suggests that there may be genetic differences in long–term adaptation to high–starch diets.

Richardson *et al*. (1996) reported small but significant differences in DM digestibility between cattle of high and low RFI. Cattle with high net feed conversion efficiency had a one–percentage unit higher DM digestibility than cattle with low net feed conversion efficiency (fed a pelleted 70% lucerne: 30% wheat mixture). Likewise, low RFI (high efficiency) Angus steers tended to digest about two–percentage units more DM from a feedlot ration than high RFI (low efficiency) Angus steers (calculated DM digestibility = 78%; R.M. Herd *et al.* unpublished data).

Meissner *et al*. (1996) observed substantial differences between corn–fed steers in non–ammonia nitrogen and starch availability in the duodenum. The data are shown in Table 1.

Organic matter digestibility in the rumen (OMD_R) was significantly negatively associated with NAN ($r^2 = 0.37$) and starch ($r^2 = 0.77$) passage to the duodenum (Meissner *et al*. 1996). The effect of the variation in OMD_R meant that some animals had more than twice the amount of NAN and starch entering the duodenum (Meissner *et al*. 1996). OMD_R is known to be associated with rumen retention time, which in turn, is usually correlated with feed intake. There was a very poor relationship between feed intake and OMD_R in this experiment. Consequently, this meant that the observed variation in OMD_R and the passage of starch and non–ammonia nitrogen to the small intestine was the result of inherent variability in rumen retention time.

In the feedlot perhaps the most obvious sign that animals vary in their capacity to efficiently and safely digest starch is the noticeable variation in faecal

Table 1 Variation between individual steers in the proportion of OM fermented in the rumen (OMD_R) and its relationship with non–ammonia nitrogen (NAN) and starch passage to the duodenum (average for 4 corn–based diets fed to each animal where treatment differences were mainly not significant). Adapted from Meissner *et al*. (1996).

Steer	OMD_R (%)	Flow to duodenum (g/day)	
		NAN	Starch
1	85.0[c]	51.7[ab]	340[a]
2	80.5[bc]	37.4[a]	490[ab]
3	76.1[abc]	44.0[a]	550[abc]
4	72.7[abc]	70.1[bc]	790[bc]
5	72.1[abc]	65.2[bc]	670[abc]
6	71.8[abc]	90.8[d]	1000[c]
7	70.7[a]	67.7[bc]	840[bc]
8	66.4[a]	78.4[cd]	960[c]
Average	74.4	63.2	705
SD	1.43	2.26	50

Values in the same column with different superscripts differ significantly (*P*<0.05)

consistency and pH. It is very hard to predict which animals will be susceptible to acidosis upon entry into the feedlot and the variability between animals has made it quite difficult to study the condition (Rowe and Pethick 1994; Slyter 1976). Considerable variation in the ability of animals to cope with a 'carbohydrate challenge' has been reported by Brown *et al*. (2000) and Dougherty *et al*. (1975). In the latter study, 70 g of grain (75:25 whole corn:whole oats)/kg of body weight was administered directly into the rumen of 3 steers. Whilst the rumen pH in one steer did not fall below 5.5, the other 2 steers experienced acute acidosis. One of these animals had to be euthanased.

The question is whilst some animals experience acute acidosis, how do other individuals maintain good health and feed intake when fed a diet high in fermentable starch? The reasons for this variation are not clear but could involve differences in salivary buffering, the microbial population (before and after exposure to a large amount of fermentable carbohydrate), varying digestive efficiency throughout the gastrointestinal tract, differences in the immune response to tissue damage/disease or variable changes in the gut wall characteristics and the extent of inflammation and leakage. The ability to efficiently and safely digest starch is certainly likely to be involved and there may be scope for genetic selection for 'resistance to acidosis' on this basis. In particular, if an animal has the ability to extensively digest starch in the small intestine, there is less chance of delivering starch to be fermented in the hindgut.

New findings

Some relevant new work (Channon *et al.* in press, 2003) has provided good evidence that genetic differences in starch digestion do exist. Steer progeny of lines selected for either low RFI (high efficiency) or high RFI (low efficiency) were finished in a feedlot on a 75% barley ration. Measurements of feed intake, liveweight gain and faecal parameters were combined to investigate associations between starch digestion and feed efficiency. Faecal pH, DM and nitrogen (N) content were used as indirect indicators of the amount of starch being fermented in the hindgut. The results are presented in Tables 2, 3 and 4.

Table 2 shows that there were significant differences between sire progeny groups in faecal pH and faecal DM content indicating genetic differences in these parameters. This variation was occurring even after results were corrected by covariance for differences in DMI. That these faecal parameters are likely to reflect the extent of starch fermentation in the hindgut (low pH and DM content indicating more fermentation), provides evidence of genetic variation in the amount of starch reaching the hindgut.

Table 2 Differences between sire progeny groups in faecal parameters.

Sire	Progeny	pH	DM %	N %
Q002	17	6.85^a	14.61^a	2.30
Q072	13	6.90^{ab}	15.54^{abc}	2.35
Q018	14	6.91^{ab}	15.97^{bcd}	2.21
Q048	12	6.91^{ab}	15.68^{abc}	2.25
Q312	12	6.94^{abc}	14.73^{ae}	2.41
Q106	11	6.96^{abc}	15.83^{bcde}	2.25
Q006	10	6.98^{bc}	16.36^{bc}	2.20
Q167	14	7.00^{bc}	14.99^{ad}	2.26
Q198	19	7.04^c	15.75^{bde}	2.22

Means within a column with different superscripts differ significantly (*P*<0.05)

Table 3 Phenotypic associations between dry matter intake, kg/d, and residual feed intake, kg DM/d, with faecal parameters.

Repeated measures	DMI	RFI
Faecal pH	0.02*	0.01
Faecal DM (%)	−0.20*	−0.47**
Faecal N (%)	0.02	−0.02

*P<0.05, **P<0.01; indicate that the regression coefficient (b value) is significantly different from zero

Table 4 The genetic association between faecal parameters in progeny and mid–parent estimated breeding value (EBV) for residual feed intake, kg DM/d.

Repeated measures	RFI
Faecal pH	−0.07*
Faecal DM (%)	−0.80**
Faecal N (%)	0.03

*P<0.05), **P<0.01; indicate that the regression coefficient (b value) is significantly different from zero

Table 3 shows that in these feedlot animals, low faecal DM content was associated with higher RFI (i.e. lower efficiency). Therefore, those animals that were more efficient in the feedlot (lower RFI) tended to have firmer faeces (indicating less hindgut fermentation).

Table 4 shows that there was a significant association between faecal pH and DM content and mid–parent Estimated Breeding Values (EBV) for RFI. This means that high efficiency parents (selected for low RFI) generally produced progeny that had a higher faecal pH and faecal DM content than the progeny of low efficiency sires (selected for high RFI) when fed high–starch diets. This was confirmation of an association between parameters believed to describe starch digestion and the genetic variation in an important production trait. This means that there could be an opportunity to identify and select for animals, within a breed, that are more efficient at rumen + small intestinal starch digestion.

We have also identified between–animal variation in starch digestion in a recent grain–feeding trial (Channon and Rowe 2003, unpublished). Six crossbred cows (Low–Line x Angus, 28 months old, 398 kg liveweight) were used in a crossover design and fed diets based on dry–rolled wheat, poorly flaked wheat (coarse steam–flaked) and well flaked wheat (thin steam–flaked). Chromic oxide was used as a digestibility marker. Spot faecal samples were taken and the marker ratio technique was used to calculate a value for total tract starch digestibility for each cow–diet combination. The results are shown in Table 5.

The consistency of ranking of cows for total tract starch digestibility of diets differing in grain processing method, determined by coefficient of concordance, was significant ($P<0.01$). This is a non–parametric statistic that is used for ranking results by ignoring the actual values (Moroney 1968). Animal 1 appears to have the highest capacity for starch digestion whereas animal 6 tends to have the poorest capacity. That the environment, treatment and feeding of these animals has been the same for most of their lives suggests that there is a genetic component to these between–animal differences in starch digestion. The mechanisms behind these differences are unknown but are likely to involve the factors discussed earlier in this paper.

It was interesting to see that the between–animal differences are greatest for the diet of the lowest average digestibility, the dry rolled wheat diet. The highly digestible, well flaked wheat diet enabled the poorer animals to attain starch digestibility values comparable to the best animals. Similarly, the variability in starch digestibility in chickens is greater for poorly digestible wheat diets compared to relatively well digested corn diets (Rogel 1985).

The cows also had similar rankings for faecal starch percentage ($P<0.01$), and faecal starch was very closely correlated to starch digestibility ($r^2 = 0.94$; $P<0.01$). This is very consistent with the results of Zinn (1994) and Zinn *et al.* (2002). This result suggests that faecal starch could be a useful tool for assessing the efficiency of grain processing and for identifying between–animal differences.

Future

Identification of cattle that are more efficient at starch digestion may provide an important opportunity to improve the profitability of our grain–feeding systems. There is a need to explore fully the extent of genetic variation in starch digestion to see if it is large enough in magnitude to be of practical significance. If the variability is low, the rate of genetic improvement would be small.

In future trials, it would be useful to relate total tract starch digestibility to faecal pH and DM content as well as faecal VFA and lactate levels. An easily obtained faecal measurement such as pH would make it easier to estimate variation in starch digestion in a larger number of cattle and thereby enable estimations of genetic parameters. The use of a relatively poorly digestible grain such as sorghum may be useful in attempts to clearly identify those individuals that have the greatest capacity for starch digestion.

Traditionally, feedlotters have put considerable effort into diet preparation for feedlot cattle in order to

Table 5 Ranking of animals by their total tract starch digestibility for three wheat–based feedlot rations.

Dry rolled		Poorly flaked		Well flaked	
Animal	**Digestibility**	**Animal**	**Digestibility**	**Animal**	**Digestibility**
6	95.6	6	96.9	3	98.5
2	96.7	2	97.6	2	98.5
3	97.1	3	98.7	6	98.6
4	97.2	4	98.7	5	98.9
5	97.3	5	99.0	1	98.9
1	98.5	1	99.2	4	99.
Average	97.07		98.36		98.75

increase starch digestibility. Whilst there is no denying that starch digestibility can be significantly improved using processing techniques such as steam flaking, perhaps we should now start thinking about feeding this costly and well–prepared grain to those animals that can digest the starch most efficiently?

Acknowledgements

References

Al Jassim, R.A.M. and Rowe, J.B. (1999). Better understanding of acidosis and its control. *Recent Advances in Animal Nutrition in Australia* 12, 91–97.

ALFA (2003). Feedlot industry in a state of flux. In: *Lotfeeding; Official Journal of the Australian Lot Feeders Association*, pp.18–19.

Allison, M.J. (1993). Microbiology of the rumen and small and large intestines. In: *Dukes Physiology of Domestic Animals,* pp. 417–427 (eds. M.J. Swenson and W.O. Reece). Comstock Publishing Associates, London, England.

Archer, J.A., Richardson, E.C., Herd, R.M. and Arthur, P.F. (1999). Potential for selection to improve efficiency of feed use in beef cattle: a review. *Australian Journal of Agricultural Research* 50, 147–161.

Argenzio, R.A. (1993a). Digestion and absorption of carbohydrate, fat, and protein. In: *Dukes Physiology of Domestic Animals,* pp. 362–375 (eds. M.J. Swenson and W.O. Reece). Comstock Publishing Associates, London, England.

Argenzio, R.A. (1993b). Gastrointestinal motility. In: *Dukes Physiology of Domestic Animals,* pp. 336–348. (eds. M. J. Swenson and W. O. Reece). Comstock Publishing Associates, London, England.

Argenzio, R.A. (1993c). General functions of the gastrointestinal tract and their control and integration. In: *Dukes Physiology of Domestic Animals,* pp. 325–335 (eds. M.J. Swenson and W.O. Reece). Comstock Publishing Associates, London, England.

Argenzio, R.A. (1993d). Secretory functions of the gastrointestinal tract. In: *Dukes Physiology of Domestic Animals,* pp. 349–361 (eds. M.J. Swenson and W.O. Reece). Comstock Publishing Associates, London, England.

Bauer, M.L., Harmon, D.L., McLeod, K.R. and Huntington, G.B. (1995). Adaptation to small intestinal starch assimilation and glucose transport in ruminants. *Journal of Animal Science* 73, 1828–1838.

Beauchemin, K.A. (2000). Managing rumen fermentation in barley–based diets: balance between high production and acidosis. *Advances in Dairy Technology* 12, 109–125.

Beaver, E.E., Williams, J.E., Miller, S.J., Hancock, D.L., Hannah, S.M. and O'Conner, D.L. (1989). Influence of breed and diet on growth, nutrient digestibility, body composition and plasma hormones of Brangus and Angus steers. *Journal of Animal Science* 67, 2415–2425.

Boyles, S.L. and Riley, J.G. (1991). Feedlot performance of Brahman x Angus versus Angus steers during cold weather. *Journal of Animal Science* 69, 2677–2684.

Brown, M.S., Krehbiel, C.R., Galyean, M.L., Remmenga, M.D., Peters, J.P., Hibbard, B., Robinson, J. and Moseley, W.M. (2000). Evaluation of models of acute acidosis and subacute acidosis on dry matter intake, ruminal fermentation, blood chemistry, and endocrine profiles of beef steers. *Journal of Animal Science* 78, 3155–3168.

Clary, J.J., Mitchell Jr, G.E., Little, C.O. and Bradley, N.W. (1969). Pancreatic amylase activity from ruminants fed different rations. *Canadian Journal of Physiology and Pharmacology* 47, 161–164.

Croom Jr, W.J., Bull, L.S. and Taylor, I.L. (1992). Regulation of pancreatic exocrine secretion in ruminants: a review. *Journal of Nutrition* 122, 191–202.

DeGregorio, R.M., Tucker, R.E., Mitchell Jr, G.E. and Gill, W.W. (1982). Carbohydrate fermentation in the large intestine of lambs. *Journal of Animal Science* 54, 855–862.

Dougherty, R.W., Riley, J.L., Baetz, A.L., Cook, H.M. and Coburn, K.S. (1975). Physiologic studies of experimentally grain–engorged cattle and sheep. *American Journal of Veterinary Research* 36, 833–835.

Frisch, J.E. and Vercoe, J.E. (1977). Food intake, eating rate, weight gains, metabolic rate and efficiency of feed utilisation in *Bos taurus* and *Bos indicus* crossbred cattle. *Animal Production* 25, 343–358.

Goad, D.W., Goad, C.L. and Nagaraja, T.G. (1998). Ruminal microbial and fermentative changes associated with experimentally induced subacute acidosis in steers. *Journal of Animal Science* 76, 234–241.

Grovum, W.L. and Hecker, J.F. (1973). Rate of passage of digesta in sheep. 2. The effect of level of food intake on digesta retention times and on water and electrolyte absorption in the large intestine. *British Journal of Nutrition* 30, 221–230.

Harmon, D.L. (1992). Dietary influences on carbohydrases and small intestinal starch hydrolysis capacity in ruminants. *Journal of Nutrition* 122, 203–210.

Harmon, D.L. (1993). Nutritional regulation of postruminal digestive enzymes in ruminants. *Journal of Dairy Science* 76, 2102–2111.

Harmon, D.L. and McLeod, K.R. (2001). Glucose uptake and regulation by intestinal tissues: implications and whole–body energetics. *Journal of Animal Science* 79, 59–72.

Hegarty, R.S. (2000). Genetic diversity in function and microbial metabolism of the rumen. In: *Proceedings of the Feed Efficiency Workshop,* pp. 63–68. (eds. J. A.

Archer, R. M. Herd and P. F. Arthur), CRC for Cattle and Beef Quality, Armidale, Australia.

Herd, R.M., Archer, J.A., Arthur, P.F., Richardson, E.C., Wright, J.H., Dibley, K.C.P. and Burton, D.A. (1997). Performance of progeny of high vs low net feed conversion efficiency cattle. *Association for the Advancement of Animal Breeding and Genetics* 12, 742–745.

Hinders, R.G. and Owen, F.G. (1965). Relation of ruminal parakeratosis development to volatile fatty acid absorption. *Journal of Dairy Science* 48, 1069–1075.

Hungate, R.E. (1966). *The Rumen and its Microbes.* Academic Press, New York.

Huntington, G.B. (1997). Starch utilisation by ruminants: from basics to the bunk. *Journal of Animal Science* 75, 852–867.

Kahn, L.P. (1996). Differences between Merino selection lines in microbial yield from the rumen and utilisation of protein for wool growth. PhD Thesis, University of New England, Armidale, Australia.

Kahn, L.P., Leng, R.A. and Piper, L.R. (2000). Rumen microbial yield from sheep genetically different for fleece weight. *Asian–Australasian Journal of Animal Sciences 13, July Supplement Volume C*, 137.

Knowlton, K.F., Glenn, B.P. and Erdman, R.A. (1998). Performance, ruminal fermentation, and site of starch digestion in early lactation cows fed corn grain harvested and processed differently. *Journal of Dairy Science* 81, 1972–1984.

Krehbiel, C.R., Kreikemeier, K.K. and Ferrell, C.L. (2000). Influence of *Bos indicus* crossbreeding and cattle age on apparent utilisation of a high–grain diet. *Journal of Animal Science* 78, 1641–1647.

Kreikemeier, K.K., Harmon, D.L., Brandt Jr, R.T., Avery, T.B. and Johnson, D.E. (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. *Journal of Animal Science* 69, 328–338.

Mann, S.O. and Ørskov, E.R. (1973). The effect of rumen and post–rumen feeding of carbohydrates on the caecal microflora of sheep. *Journal of Applied Bacteriology* 36, 475–484.

Meissner, H.H., Paulsmeier, D.V., Leeuw, K.–J. and Coetzer, C.M. (1996). Ruminal and postruminal digestion of dietary protein and starch in steers: 2. Multivariate model prediction of non–ammonia nitrogen and starch passage and digestibility. *South African Journal of Animal Science* 26, 66–74.

Moroney, M.J. (1968). *Facts from Figures*. Pelican, Penguin Books Ltd., Harmondsworth, Middlesex, England.

Nocek, J.E. (1997). Bovine acidosis: implications on laminitis. *Journal of Dairy Science* 80, 1005–1028.

Oddy, V.H. and Herd, R.M. (2000). Potential mechanisms for variation in efficiency of feed utilisation in ruminants. In: *Proceedings of the Feed Efficiency Workshop,* pp. 30–34 (eds. J.A. Archer, R.M. Herd and

P.F. Arthur), CRC for Cattle and Beef Quality, Armidale, Australia.

Ørskov, E.R., Benzie, D. and Kay, R.N.B. (1970a). The effects of feeding procedure on closure of the oesophageal groove in young sheep. *British Journal of Nutrition* 24, 785–794.

Ørskov, E.R., Fraser, C., Mason, V.C. and Mann, S.O. (1970b). Influence of starch digestion in the large intestine of sheep on caecal fermentation, caecal microflora and faecal nitrogen excretion. *British Journal of Nutrition* 24, 671–682.

Ørskov, E.R., Fraser, C. and McDonald, I. (1971a). Digestion of concentrates in sheep. 3. Effect of rumen fermentation of barley and maize diets on protein digestion. *British Journal of Nutrition* 26, 477–486.

Ørskov, E.R., Mayes, R.W. and Penn, A. (1971b). The capacity for the removal of glucose from the small intestine by mature sheep. *Proceedings of the Nutrition Society* 30, 43A.

Ørskov, E.R., Mayes, R.W. and Mann, S.O. (1972). Postruminal digestion of sucrose in sheep. *British Journal of Nutrition* 28, 425–432.

Ørskov, E.R., Ojwang, I. and Reid, G.W. (1988). A study on consistency of differences between cows in rumen outflow rate of fibrous particles and other substrates and consequences for digestibility and intake of roughages. *Animal Production* 47, 45–51.

Owens, F.N., Secrist, D.S., Hill, W.J. and Gill, D.R. (1998). Acidosis in cattle: a review. *Journal of Animal Science* 76, 275–286.

Owens, F.N., Zinn, R.A. and Kim, Y.K. (1986). Limits to starch digestion in the ruminant small intestine. *Journal of Animal Science* 63, 1634–1648.

Richardson, E.C., Herd, R.M., Archer, J.A., Woodgate, R.T. and Arthur, P.F. (1998). Steers bred for improved net feed efficiency eat less for the same feedlot performance. *Animal Production in Australia* 22, 213–216.

Richardson, E.C., Herd, R.M., Arthur, P.F., Wright, J., Xu, G., Dibley, K. and Oddy, V.H. (1996). Possible physiological indicators for net feed conversion efficiency in beef cattle. *Animal Production in Australia* 21, 103–116.

Richardson, E.C., Herd, R.M. and Oddy, V.H. (2000). Variation in body composition, activity and other physiological processes and their associations with feed efficiency. In: *Proceedings of the Feed Efficiency Workshop,* pp. 46–50 (eds. J.A. Archer, R.M. Herd and P.F. Arthur). CRC for Cattle and Beef Quality, Armidale, Australia.

Rogel, A.M. (1985). The digestion of wheat starch in broiler chickens. PhD Thesis, University of Sydney, Sydney, Australia.

Rooney, L.W. and Pflugfelder, R.L. (1986). Factors affecting starch digestibility with special emphasis on sorghum and corn. *Journal of Animal Science* 63, 1607–1623.

Rowe, J.B. (1999). How much acid in the gut is too much? *Recent Advances in Animal Nutrition in Australia* 12, 81–89.

Rowe, J.B. and Pethick, D.W. (1994). Starch digestion in ruminants—problems, solutions and opportunities. *Proceedings of the Nutrition Society of Australia* 18, 40–52.

Russell, J.B. and Wilson, D.B. (1996). Why are ruminal cellulolytic bacteria unable to digest cellulose at low pH? *Journal of Dairy Science* 79, 1503–1509.

Russell, J.R., Young, A.W. and Jorgensen, N.A. (1981). Effect of dietary corn starch intake on pancreatic amylase and intestinal maltase and pH in cattle. *Journal of Animal Science* 52, 1177–1182.

Shirazi–Beechey, S.P., Hirayama, B.A., Wang, Y., Scott, D., Smith, M.W. and Wright, E.M. (1991). Ontogenic development of lamb intestinal sodium–glucose co–transporter is regulated by diet. *Journal of Physiology* 437, 699–708.

Siciliano–Jones, J. and Murphy, M.R. (1989a). Nutrient digestion in the large intestine as influenced by forage to concentrate ratio and forage physical form. *Journal of Dairy Science* 72, 471–484.

Siciliano–Jones, J. and Murphy, M.R. (1989b). Production of volatile fatty acids in the rumen and caecum–colon of steers as affected by forage:concentrate and forage physical form. *Journal of Dairy Science* 72, 485–492.

Slyter, L.L. (1976). Influence of acidosis on rumen function. *Journal of Animal Science* 43, 910–929.

Smuts, M., Meissner, H.H. and Cronje, P.B. (1995). Retention time of digesta in the rumen: its repeatability and relationship with wool production of Merino rams. *Journal of Animal Science* 73, 206–210.

Svihus, B. (2003). Physiological and chemical constraints to starch digestion and glucose absorption in broilers. In: *Proceedings of the Australian Poultry Science Symposium* 15, 17–25. Sydney University, Sydney, Australia.

Taniguchi, K., Huntington, G.B. and Glenn, B.P. (1995). Net nutrient flux by visceral tissues of beef steers given abomasal and ruminal infusions of casein and starch. *Journal of Animal Science* 73, 236–249.

Thompson, B.C., Dellow, D.W. and Barry, T.N. (1989). The effect of selection for fleece weight upon urea metabolism and digestive function in Romney sheep. *Australian Journal of Agricultural Research* 40, 1065–1074.

Ulyatt, M.J., Dellow, D.W., Reid, S.W. and Bauchop, T. (1975). Structure and function of the large intestine of ruminants. In: *Digestion and Metabolism in the Ruminant. Proceedings of the IV International Symposium on Ruminant Physiology,* pp. 119–133 (eds. I.W. McDonald and A.C.I. Warner). University of New England, Armidale, Australia.

Warwick, E.J. and Cobb, E.H. (1975). Genetic variation in nutrition of cattle for meat production. In: *The Effect of Genetic Variance on Nutritional Requirements of Animals,* pp. 3–18. National Academy of Sciences, Maryland, USA.

Wolin, M.J. (1981). Fermentation in the rumen and human large intestine. *Science* 213, 1463–1468.

Zinn, R.A. (1994). Influence of flake thickness on the feeding value of steam–rolled wheat for feedlot cattle. *Journal of Animal Science* 72, 21–28.

Zinn, R.A., Owens, F.N. and Ware, R.A. (2002). Flaking corn: Processing mechanics, quality standards, and impacts on energy availability and performance of feedlot cattle. *Journal of Animal Science* 80, 1145–1156.

Zust, J., Pestevsek, U. and Vengust, A. (2000). Impact of lactic acid fermentation of carbohydrates in the large intestine on the pathogenesis of acute lactic acidosis of cattle. *Deutsche Tierärztliche Wochenschrift* 107, 359–363.