

Abomasal glucose, maize starch and maize dextrin infusions in cattle: small-intestinal disappearance, net portal glucose flux and ileal oligosaccharide flow

BY K. K. KREIKEMEIER

U.S. Department of Agriculture, Agricultural Research Service, Roman L. Hruska U.S. Meat Animal Research Center, Clay Center, Nebraska 68933, USA

AND D. L. HARMON

Department of Animal Sciences, University of Kentucky, Lexington, 40546-1027, Kentucky, USA

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Three castrated male Holstein cattle (423 (SD 19) kg live weight) fitted with elevated carotid artery, portal, and mesenteric venous catheters, and abomasal and ileal cannulas were used to study small-intestinal starch digestion. The cattle were infused abomasally with water (275 ml/h), glucose (66 g/h), maize dextrin (66 g/h) or maize starch (66 g/h) in an incomplete Latin square design, with eight infusion periods. Infusion with carbohydrate resulted in higher arterial glucose concentrations and greater net portal glucose flux than when cattle were infused with water. Arterial glucose concentration and net portal glucose flux were highest when glucose was infused. In the small intestine, 85% of abomasally-infused glucose, 78% of infused dextrin, and 66% of infused starch disappeared. Of the carbohydrate that disappeared in the small intestine, that which could be accounted for as net portal glucose flux was 73% for glucose, 60% for dextrin, and 57% for starch. Ileal digesta contained unpolymerized glucose, and short-chain soluble α -glucoside. Of the infused dextrin flowing past the ileum (14 g/h), 0.3 g/h was glucose, 6.2 g/h was soluble α -glucoside, and 7.5 g/h was insoluble α -glucoside. Of the infused starch flowing at the ileum (22.2 g/h), 0.9 g/h was glucose, 5.3 g/h was soluble α -glucoside, and 15.9 g/h was insoluble α -glucoside. The average chain lengths of the soluble α -glucosides in ileal digesta were 2.07 and 2.36 for dextrin and starch infusions respectively, indicating mostly di- and to a lesser extent trisaccharides. We conclude that (1) when 66 g raw starch is presented to the small intestine per h, about half of the intestinal disappearance appears as glucose in the portal vasculature, and (2) α -1,4 glucosidase (EC 3.2.1.20) activity at the brush border is the rate-limiting step to small-intestinal starch digestion in cattle.

Cattle: Starch digestion: Small intestine

Starch in the diet of ruminants is not completely fermented in the rumen and flow to the small intestine varies. When flow of maize starch or wheat starch to the small intestine was less than 600 g/d, apparent starch disappearance in the small intestine exceeded 90% of duodenal starch flow in 300 kg cattle (Axe *et al.* 1987; Zinn, 1990; Kreikemeier *et al.* 1991). As maize starch flow to the duodenum increased to 900 g/d, starch disappearance decreased to between 53 and 67% (Zinn, 1990; Kreikemeier *et al.* 1991). With sorghum-grain feeding, duodenal starch flows of 1300 g/d have been reported in cattle (Axe *et al.* 1987; Streeter *et al.* 1991), and 3500 g/d in lactating cows (Poore *et al.* 1993). In four recent studies with sorghum-grain feeding, Streeter *et al.* (1989, 1990a, b, 1991) reported that 20 to 40% of duodenal starch flow disappeared before the ileum.

In the present experiment the objectives were (1) to evaluate the effect of abomasally infused maize starch, maize dextrin, and glucose on small-intestinal carbohydrate

disappearance and net portal glucose flux, and (2) to determine the profile of infused carbohydrate escaping small-intestinal digestion.

MATERIALS AND METHODS

Animals and design

Three castrated male Holstein cattle (423 (SD 19) kg live weight) were surgically prepared with permanent portal and mesenteric venous catheters, an elevated carotid artery, an ileal cannula (0.6 to 0.9 m anterior to the ileo-caecal junction), and a catheter (Bard Urological Division, size 36 FR., C. R. Bard, Inc., Murray Hill, NJ 07974, USA) which was fitted in the mid-portion of the abomasum and exteriorized through the adjacent body wall as described previously (Kreikemeier *et al.* 1991).

In an incomplete Latin-square design consisting of eight infusion periods, the three cattle were continuously infused with either water (control), maize starch (66 g glucose/h), maize dextrin (66 g glucose/h), or glucose (66 g/h; U.S. Biochemical Corporation, Cleveland, OH 44128, USA) into the abomasum. Infusion rates are expressed on a glucose basis assuming that the molecular weight of unpolymerized glucose is 180 and that of polymerized glucose is 162.

Maize dextrin was prepared commercially under the following conditions. Roasting temperature was 138 to 140°, roasting time was 3.0 to 6.5 h, HCl served as the catalyst, and the pH was 1.9 to 2.0 (U.S. Biochemical Corporation).

Animal management

Cattle were fed on chopped lucerne (*Medicago sativa*) hay (181 g crude protein (CP)/kg) at 15 g/kg live weight (LW) (dry matter basis) in two equal meals (08.00 and 17.00 hours). Fresh water and a trace-mineralized salt block (containing not less than 2 g Mn, 1 g Mg, 0.5 g S, 0.25 g Cu, 0.1 g Co, 0.08 g Zn and 0.07 g I/kg salt) were available continuously. Any feed refusals were collected, weighed, and discarded daily.

The cattle were housed in a partly controlled environment. Temperature varied from approximately 18 to 28°. The building was ventilated continuously with outside air and there was a combination of natural (06.00 to 21.00 hours) and supplemental (08.00 to 17.00 hours) fluorescent lighting provided. Cattle were tethered in tie stalls (1.5 m wide) containing a rubber mat. Stalls were cleaned and cattle were washed daily.

Experimental

For the 10 h infusion period, cattle were infused with 275 ml solution/h, consisting of Cr-EDTA (50 ml/l; Binnerts *et al.* 1968), the appropriate carbohydrate and tap water. Maize starch and maize dextrin were kept suspended in solution using an automatic stirrer during the infusion periods. The solutions were infused with a peristaltic pump (Harvard Apparatus Model 1200, South Natick, MS 01760, USA) fitted with Tygon® pump tubing (internal diameter 2.79 mm).

From 3 to 10 hours of abomasal infusion, eight ileal digesta samples were collected at approximately 1 h intervals (100–200 g). Ileal pH was recorded, and 10 M-NaOH was added (0.5 ml NaOH:100 g digesta) to inactivate any residual carbohydrase activity in the digesta. This raised the pH above 10. The samples were mixed and frozen (–20°) for later analysis.

When digesta was thawed it was divided into three portions. One portion was analysed for dry matter (DM) (48 h at 65°). Another portion was centrifuged (20000 g) and the supernatant fluid was harvested. That fluid was analysed for Cr (atomic absorption spectroscopy), glucose (Gochman & Schmitz, 1972), and volatile fatty acids (VFA;

Harmon *et al.* 1988). A third portion was analysed for starch (MacRae & Armstrong, 1968), and oligosaccharide chain length (described later). Digesta flow at the ileum was calculated as follows:

$$\text{fluid flow (g/h)} = \frac{\text{Cr concentration in abomasal infusate (ppm)}}{\text{Cr concentration in ileal fluid (ppm)}} \times \text{abomasal fluid infusion rate (g/h)},$$

$$\text{total digesta flow (g/h)} = \frac{\text{fluid flow (g/h)}}{(1 - \text{digesta DM})},$$

$$\text{DM flow} = \text{total digesta flow} - \text{fluid flow}.$$

Ileal flows of glucose, ethanol-soluble oligosaccharides, and VFA were calculated as fluid flow multiplied by nutrient concentration. Ileal flows of starch and ethanol-insoluble oligosaccharide were calculated as DM flow multiplied by the nutrient concentration.

At 2.5 h after the start of abomasal infusion, cattle were infused into the mesenteric venous catheter with a primed (15 ml), continuous infusion (0.7 ml/min) of para-aminohippuric acid (PAH; 100 g/l). From 3 to 9 hours of infusion, 10 ml arterial and portal venous blood were collected simultaneously into heparinized syringes at 1.5 h intervals (five sets of samples). Blood was transferred into 50 ml centrifuge tubes containing 30 mg NaF and put on ice. At the end of blood sampling the blood was centrifuged (20000 g), and the plasma was harvested and frozen (-20°). Later the plasma was thawed and it was analysed for PAH (Harvey & Brothers, 1962) and glucose (Gochman & Schmitz, 1972). Portal plasma flow was calculated as follows:

$$\text{plasma flow (ml/min)} = \frac{\text{PAH concentration in mesenteric infusate (ppm)}}{\text{PAH concentration in portal plasma (ppm)}} \times \text{mesenteric infusion rate (ml/min)}.$$

Portal glucose flux was calculated by subtracting glucose concentration in arterial plasma from the glucose concentration in portal plasma and then multiplying that value by the portal plasma flow.

The experiment took 11 d to complete. The eight infusion periods (10 h/infusion) were conducted on consecutive days with a 3 d break between period four and period five. It was assumed that steady-state conditions occurred during the sampling periods and that no carryover effects from the previous infusion occurred (Kreikemeier *et al.* 1991).

Oligosaccharide chain length

We determined the average chain length (also called degree of polymerization) of the ethanol-soluble oligosaccharides using procedures outlined by Robyt & French (1967). Anhydrous ethanol (10 ml) and 5 g raw ileal digesta were mixed in a glass test-tube and allowed to stand overnight at 4°. The tube was then centrifuged (3000 g), and after pouring off the supernatant fraction, the pellet was resuspended with 5 ml anhydrous ethanol and centrifuged. This washing procedure was conducted three times, always saving the supernatant fluid in a separate test-tube. Maltodecaose is the largest oligosaccharide in the ethanol supernatant fraction (Robyt & French, 1967). Ethanol was evaporated and the residue was rehydrated with acetate buffer (0.2 M, pH 4.5). Glucose in the rehydrated residue was then determined using glucose oxidase (EC 1.1.3.4) (Gochman & Schmitz,

1972) and reducing sugars were determined using alkaline ferricyanide (Kidder *et al.* 1972). The α -linked glucose polymers were hydrolysed using amyloglucosidase (*EC* 3.2.1.3; MacRae & Armstrong, 1968) and glucose concentration was again determined. Average chain length was then calculated as follows:

$$\text{chain length} = \frac{\left(\begin{array}{c} \text{glucose concentration} \\ \text{after } \alpha\text{-hydrolysis} \end{array} \right) - \left(\begin{array}{c} \text{glucose concentration} \\ \text{before } \alpha\text{-hydrolysis} \end{array} \right)}{\left(\begin{array}{c} \text{reducing sugar concentration} \\ \text{before } \alpha\text{-hydrolysis} \end{array} \right) - \left(\begin{array}{c} \text{glucose concentration} \\ \text{before } \alpha\text{-hydrolysis} \end{array} \right)}$$

Characterization of maize starch and maize dextrin

To characterize maize starch and maize dextrin as to their apparent differences in enzyme accessibility, their rates of hydrolysis were determined with an α -glucosidase. Portions of maize starch and maize dextrin were weighed in quadruplicate for each of three incubation times with amyloglucosidase; 0, 30 and 60 min. These samples were incubated under standard conditions (MacRae & Armstrong, 1968) except that the carbohydrates were not gelatinized. Incubation was stopped by adding NaOH to raise the pH to greater than 12 and placing in an ice-water bath. The incubation medium was centrifuged (20000 g, 15 min), the supernatant fraction was analysed for glucose as described above and the amounts of glucose hydrolysed from maize starch and maize dextrin were calculated.

Statistical analysis

Means were calculated for each animal within sampling period by averaging values obtained from the five blood samples. pH, VFA and Cr were determined for each sample of ileal digesta. For those samples containing Cr, their values were averaged as just described. Ileal digesta samples that contained Cr were composited (equal weight basis) by animal within period and analysed for glucose, starch, reducing sugars, carbohydrate fractions and dry matter. Data were analysed using the general linear models procedures of SAS (1985); the model included animal, infusion period, and carbohydrate type. There were six observations per treatment. Single degree of freedom orthogonal contrasts were used to test for treatment effects. They were (1) water *v.* (glucose + dextrin + starch), (2) glucose *v.* (dextrin + starch), and (3) dextrin *v.* starch.

Data on glucose release from starch and dextrin due to hydrolysis by amyloglucosidase were analysed as a completely random design having a 2 \times 3 factorial arrangement. Main effects were substrate (starch *v.* dextrin) and incubation time (0, 30, and 60 min). The model included substrate, incubation time, and substrate \times incubation time interaction. There were four replications per treatment.

RESULTS

Intake was not affected by treatment and cattle consumed 6.4 kg lucerne hay daily during the infusion periods (Table 1). Cattle infused with carbohydrate had higher ($P < 0.01$) arterial glucose concentrations, increased ($P < 0.01$) net portal glucose flux, and higher ($P < 0.01$) ileal digesta DM than cattle infused with water. Within carbohydrate sources, cattle infused with glucose had a higher arterial glucose concentration ($P < 0.01$) and net portal glucose flux ($P < 0.05$). Ileal digesta DM and starch content were highest when starch or dextrin were infused ($P < 0.01$). Glucose concentration in ileal digesta was highest when glucose was infused ($P < 0.01$). The molar proportion of acetate accounted for over 99% of ileal fluid VFA concentration (results not shown) and VFA concentration was

Table 1. Effect of abomasally infused water, glucose, maize dextrin and maize starch on net portal glucose absorption, small-intestinal disappearance, and α -glucoside in ileal digesta of cattle§

(Mean values with their pooled standard error)

Variable	Abomasal infusion				SE
	Water	Glucose	Maize dextrin	Maize starch	
Dry matter intake (kg)	6.4	6.3	6.6	6.3	0.4
Arterial glucose (mm)	3.96*	4.51†	4.25	4.22	0.08
Portal plasma flow (l/h)	898	823	731	730	80
Portal glucose flux (g/h)	-15.2*	26.0†	16.1	9.9	4.7
Ileal digesta					
pH	7.87	7.41	7.68	7.72	0.11
Dry matter (g/kg)	68.0*	70.7†	91.6	93.2	4.1
Starch (g/kg)	0.2*	0†	75.6	108.5	16.2
Total VFA (mm)	24.4	21.5	25.9	27.8	1.7
Glucose (mm)	0*	39.17†	2.45	1.86	1.88
EtOH-soluble RS (mm)	1.2*	0†	10.3	7.3	1.4
EtOH-insoluble RS (mm)	0.1*	0†	3.7	2.7	0.5
EtOH-soluble RS, CL	0.03*	0.01†	2.07	2.36	0.11
Ileal flow					
Glucose (g/h)	0*	10.71†	0.27	0.95	0.39
EtOH-soluble α -glucoside (g/h)	0.25*	0†	6.18	5.33	0.67
EtOH-insoluble α -glucoside (g/h)	0.06*	0†	7.52†	15.92	1.9
Total glucoside (g/h)	0.01*	9.77†	13.98†	22.22	2.17
Dry matter (g/h)	150	124†	161	218	22
Fluid (g/h)	1854	1523	1559	2141	242
Total VFA (mmol/h)	43.5	34.8	44.3	56.1	6.8

VFA, volatile fatty acids; EtOH, ethanol; RS, reducing sugars; CL, chain length.

* Mean values were significantly different from those for (glucose + dextrin + starch), $P < 0.05$.

† Mean values were significantly different from those for (dextrin + starch), $P < 0.05$.

‡ Mean values were significantly different from those for starch, $P < 0.05$.

§ For details of procedures, see pp. 764–766.

greater ($P < 0.05$) when starch or dextrin were infused compared with when glucose was infused. The concentration of reducing sugars in both the ethanol-soluble and -insoluble fractions was greatest when starch or dextrin were infused ($P < 0.01$). The average chain length of ethanol-soluble oligosaccharides in ileal digesta was 2.07 when dextrin was infused and 2.36 when starch was infused. Glucose flowed past the ileum when carbohydrates were infused ($P < 0.01$) and was highest during glucose infusions ($P < 0.01$). Ethanol-soluble oligosaccharide flow was greatest when starch or dextrin were infused ($P < 0.01$). For the insoluble fraction, flow was greatest when starch was infused ($P < 0.01$). Total glucose plus glucoside flow at the ileum was in the order, starch > dextrin > glucose > water.

A comparison of the degradability of the carbohydrate sources *in vitro* is presented in Table 2. Amyloglucosidase hydrolysed more maize dextrin than maize starch at 30 (52 v. 5%) and 60 (64 v. 9%) min of incubation ($P < 0.01$).

Table 2. *Effect of incubation time with amyloglucosidase (EC 3.2.1.3) on α -hydrolysis of maize starch and maize dextrin**

Variable	Incubation time (min)			SE
	0	30	60	
Maize starch hydrolysis (%)	0.2	5.0	8.6	1.0
Maize dextrin hydrolysis (%)	0.6	51.6	64.3	—

* Substrate by incubation time interaction was significant ($P < 0.01$). At 0 min, extents of starch and dextrin hydrolysis were similar ($P = 0.78$) and at 30 and 60 min they were different ($P < 0.01$).

DISCUSSION

Maize starch v. maize dextrin

According to Kennedy & Fischer (1984), dry-roasting causes both depolymerization of starch and condensation of starch fragments. The result is a more highly branched molecule with a lower molecular weight than the parent starch had. During condensation, α -1,6 bonds predominate (Dr Dave Skogberg, Grain Processing Corporation, Muscatine, Iowa, USA, personal communication).

The maize dextrin we infused had low solubility and was white in colour. We assayed it in our laboratory and found it to contain less than 1% free glucose and less than 1% ethanol-soluble oligosaccharide. Additionally, amyloglucosidase hydrolysed maize dextrin eight to ten times more rapidly than it hydrolysed maize starch (Table 2). Because amyloglucosidase hydrolyses both α -1,4 and α -1,6 bonds (Robyt, 1984), we expect that the maize dextrin was available for hydrolysis in the small intestine.

Pancreatic and small-intestinal carbohydrases are still required for dextrin hydrolysis. Therefore, the comparison between starch and dextrin should allow us to evaluate whether starch granular characteristics affect digestion of starch, presumably by limiting accessibility of carbohydrases to the polymerized glucose.

Small-intestinal disappearance and net portal glucose flux

The apparent disappearance of infused carbohydrate in the small intestine (infused minus ileal glucoside flow) was 56.2, 52.0 and 43.8 g/h for glucose, maize dextrin and maize starch respectively. Because significantly more carbohydrate disappeared from the small intestine when glucose was infused compared with when dextrin or starch was infused, it can be inferred that the potential for glucose absorption by the small intestine is greater than starch hydrolysis coupled with glucose absorption. That small-intestinal dextrin disappearance was greater than starch disappearance could be due to two reasons. First, the granular structure of starch may partly limit carbohydrase availability. Second, the molecular rearrangement of the starch fragments (glucose polymers) that occurs during dextrinization may differ significantly from the parent starch, whereby the polymerized glucose in dextrin is more easily hydrolysed by α -glucosidases.

Net portal glucose flux was negative when water was infused; assuming no glucose was available from the diet, glucose flux during water infusion represented glucose used by the gut for metabolic purposes. Although glucose use by the gut may have differed when water was infused compared with when carbohydrate was infused, we calculated net portal glucose flux during carbohydrate infusion by subtracting the rate arising from the water infusion from those for the other treatments. Therefore, 'adjusted' net portal glucose fluxes were 41.2, 31.3 and 25.1 g/h for glucose, dextrin and starch respectively. That net portal

glucose flux was greatest when glucose was infused was probably the result of a greater amount of infused carbohydrate disappearing within the small intestine when glucose was infused. The small numerical difference between dextrin and starch was consistent with differences in small-intestinal carbohydrate disappearance but it was not significant.

Of the infused carbohydrate disappearing from the small intestine, that which resulted in net glucose absorption was 73.3% for glucose, 60% for dextrin, and 57% for starch. In an earlier report (Kreikemeier *et al.* 1991) the infusion of 60 g glucose/h into the abomasum resulted in 90% of small-intestinal disappearance being accounted for as increased net portal glucose flux, whereas only 38% of starch and 29% of dextrin disappearance could be accounted for in net portal glucose flux. Although this accountability of infused carbohydrate is less with glucose and greater with maize starch and maize dextrin, the relative ranking is the same (glucose > starch = dextrin). The higher accountability of infused starch being absorbed as glucose in the present study (60%) agrees with Seal *et al.* (1993) who found that 84% of infused starch resulted in net portal glucose flux.

Some factors that might affect the poor accountability of small-intestinal starch disappearance have already been discussed (Kreikemeier *et al.* 1991). Cappelli *et al.* (1993) reported that infusing glucose either into the duodenum or the jugular vein in sheep increased whole-body glucose turnover rate by 58% and portal glucose use by 40%. Because carbohydrate infusions increased the metabolic glucose supply, it is probable that glucose turnover and portal glucose use increased during the carbohydrate infusions in the present study as well. Because we assumed that portal glucose use remained constant during carbohydrate infusions (equal to our water infusion), it is likely that we underestimated net portal glucose flux, and consequently, underestimated small-intestinal carbohydrate disappearance that results in net portal glucose flux.

Glucose and oligosaccharides at the ileum

Of the infused dextrin or starch flowing past the ileum, 2–4% was free glucose. This compares with 9 and 7% of the infused carbohydrate passing the ileum as free glucose when dextrin and starch were infused at 60 g/h (Kreikemeier *et al.* 1991). Although glucose can be liberated from starch by α -amylase (EC 3.2.1.1) *in vitro* (Taravel *et al.* 1983), this has not been found *in vivo* (Robyt, 1984). Glucose in luminal fluid could arise from two sources. First, traces of α -1,4 glucosidase (EC 3.2.1.20) activity could occur in the luminal fluid of the small intestine (Gray, 1975). A small amount could be pancreatic in origin (glucoamylase; Kreikemeier *et al.* 1990b) and the rest probably arises from sloughed mucosa. The second possible source of glucose in ileal fluid seems to be from brush border oligosaccharide hydrolysis, leaching out of the unstirred water layer into the luminal liquid phase.

There were 6 g soluble α -glucoside flowing past the ileum when dextrin was infused and 5 g when starch was infused. The average chain lengths of the soluble α -glucosides were 2.1 and 2.4 glucose units for dextrin and starch respectively, indicating a high proportion of di- and, to a lesser extent, trisaccharides. When Mayes & Ørskov (1974) infused gelatinized maize starch into the abomasum of sheep of various ages they reported that infused carbohydrate flowing past the ileum consisted of 12% glucose, 17% maltose, 17% maltotriose, 18% maltotetraose, 16% higher order soluble α -glucoside and 20% insoluble α -glucoside. Therefore, the two data sets are in disagreement. Our study suggests that the soluble oligosaccharide flowing at the ileum is a disaccharide, whereas Mayes & Ørskov (1974) suggest that the soluble oligosaccharide is composed of a mixture consisting of maltotriose to maltodecaose.

Other results that agree with the present study include: (1) after exhaustive hydrolysis of

amylpectin with salivary α -amylase, no glucose was present, 72% was converted to maltose, and the α -limit dextrins had a degree of polymerization of 8.9 (Roberts & Whelan, 1960); and (2) in the caecum of mice fed on a 57% starch diet, glucose was the major hydrolysis product found, followed by traces of maltose and maltotriose without any intermediary between maltotriose and long-chain malto-oligosaccharides (Andrieux *et al.* 1992).

Perhaps our results differed from those of Mayes & Ørskov (1974) because the hydrolysis mechanism by α -amylase on the starch substrate may have differed between the two studies. We used native starch and the other study used gelatinized starch. In a single attack mechanism, α -amylase catalyses the hydrolysis of only one bond per enzyme-substrate complex formed. Conversely, in the multiple attack mechanism, once the enzyme-substrate complex is formed the enzyme catalyses the hydrolysis of several bonds (liberating maltose, maltotriose and maltotetraose) before it dissociates and forms a new enzyme-substrate complex (Robyt, 1984). At optimal pH (6.9), porcine pancreatic α -amylase hydrolysed six bonds per encounter in a multiple attack mechanism. This compares with less than one (0.7) at pH 10.5, similar to a single attack mechanism (Robyt & French, 1967). Therefore, differences in ileal oligosaccharide flow between the present study and that of Mayes & Ørskov (1974) may be due to differences in the type of attack by α -amylase on native starch used in our study *v.* gelatinized starch used in the other study. If the hydrolysis mechanism of α -amylase on native starch is more characteristic of multiple attack, then one would expect the ethanol-soluble α -glucoside to contain a greater proportion of di- and trisaccharides.

Limitations to small-intestinal starch digestion

Factors that may be rate-limiting to small-intestinal starch digestion in cattle include starch granular structure, pancreatic α -amylase activity, intestinal disaccharidase activity, and glucose absorptive capacity of the small intestine.

In the comparison of starch *v.* dextrin, a greater amount of intestinal disappearance suggests that starch granule characteristics may partly limit intestinal digestion. However, based on the similarities in arterial glucose concentration, net portal glucose flux, and ileal flow of glucose and ethanol-soluble α -glucoside, any argument about granular characteristics limiting enzyme accessibility loses credibility.

Two pieces of evidence suggest that α -amylase is limiting. First, large amounts of ethanol-insoluble α -glucoside flowing past the ileum when starch or dextrin were infused suggest that more pancreatic α -amylase was required to solubilize the starch granule. Second, 14-d-old pigs (Kreikemeier *et al.* 1990*a*) have 500 times more pancreatic α -amylase activity (per g pancreatic tissue) than yearling cattle (Kreikemeier *et al.* 1990*b*). However, there were large amounts of disaccharide flowing past the ileum when starch and dextrin were infused (5–6 g/h). Because maltose and isomaltose are endproducts of α -amylase hydrolysis, this suggests that there was more potential for solubilization of the starch granule by α -amylase than for the conversion of disaccharide to glucose. Another interesting observation is that the concentration of ethanol-soluble α -glucoside in the luminal fluid (digesta) was 7–10 mM. It raises the possibility of endproduct inhibition, that is the high concentration of disaccharide reduces the hydrolytic activity of α -amylase on starch.

Two pieces of evidence suggest that mucosal disaccharidase activity in the small intestine of cattle is limiting. First, in the present study, large amounts of short-chain α -glucoside flowing past the ileum (6 g/h) indicate that either α -1,4 or α -1,6 glucosidase activity was limiting. Second, Andrieux *et al.* (1992) reported that in rats fed on starch, hydrolysis products in the caecum included mostly glucose and only traces of maltose and maltotriose.

Previously, Kreikemeier *et al.* (1991) proposed that glucose transport across the small intestine may be limiting small-intestinal starch digestion. Krehbiel & Britton (1993) have also provided evidence in support of this from a study on the distal segments of the small intestine. However, in the present study there are two pieces of evidence that do not support this argument. First, small-intestinal disappearance of the infused carbohydrate and net portal glucose flux were greater when glucose was infused compared with when dextrin or starch were infused. Second, when dextrin or starch were infused the concentration of glucose in luminal fluid (digesta) and the amount of glucose flowing at the ileum were much less than for the ethanol-soluble α -glucoside.

If disaccharidase activity at the brush border is the rate-limiting step to small-intestinal starch digestion of cattle, then one question remains: is it α -1,4 or α -1,6 glucosidase activity that is rate limiting? Because we determined only the average chain length of the ethanol-soluble α -glucoside and did not determine the composition (e.g. maltose and isomaltose) we can only speculate. As mentioned at the start of the discussion, the maize dextrin we infused was most probably of lower molecular weight, and was more highly branched, containing a greater number of α -1,6 bonds than native maize starch. In terms of intestinal disappearance and net portal glucose flux, the dextrin appeared to be similar to or even slightly more digestible than starch. Because adding α -1,6 bonds to the starch substrate did not lower small-intestinal digestion, it would appear that α -1,4 glucosidase activity is the rate-limiting step in small-intestinal starch digestion in cattle.

Portions of this work were completed by DLH while on faculty at Kansas State University, Manhattan.

REFERENCES

- Andrieux, C., Pacheco, E. D., Bouchet, B., Gallant, D. & Szylił, O. (1992). Contribution of the digestive tract microflora to amylo maize starch degradation in the rat. *British Journal of Nutrition* **67**, 489–499.
- Axe, D. E., Bolson, K. K., Harmon, D. L., Lee, R. W., Milliken, G. A. & Avery, T. B. (1987). Effect of wheat and high moisture sorghum grain fed singly and in combination on ruminal fermentation, solid and liquid flow, site and extent of digestion and feeding performance of cattle. *Journal of Animal Science* **64**, 897–906.
- Binnerts, W. T., Van't Klooster, A. T. & Frens, A. M. (1968). Soluble chromium indicator measured by atomic absorption in digestion experiments. *Veterinary Record* **81**, 470.
- Cappelli, F. P., Seal, C. J. & Parker, D. S. (1993). Portal glucose absorption and utilization in sheep receiving exogenous glucose intravascularly or intraduodenally. *Journal of Animal Science* **70**, Suppl. 1, 279 (Abstr.).
- Gochman, N. & Schmitz, J. M. (1972). Application of a new peroxide indicator reaction to the specific automated determination of glucose with glucose oxidase. *Clinical Chemistry* **18**, 943–950.
- Gray, G. M. (1975). Oligosaccharidases of the small intestinal brush border. In *Physiological Effects of Food Carbohydrates*, pp. 181–190 [J. Allene and J. Hodge, editors]. Washington D.C.: American Chemical Society.
- Harmon, D. L., Avery, T. B., Huntington, G. B. & Reynolds, P. J. (1988). Influence of ionophore addition to roughage and high-concentrate diets on portal blood flow and net nutrient flux in cattle. *Canadian Journal of Animal Science* **68**, 419.
- Harvey, R. B. & Brothers, A. J. (1962). Renal extraction of para-aminohippurate and creatinine measured by continuous *in vivo* sampling of arterial and renal-vein blood. *Annals of the New York Academy of Sciences* **102**, 46–54.
- Kennedy, H. M. & Fischer, A. C. Jr (1984). Starch and dextrans in prepared adhesives. In *Starch: Chemistry and Technology*, 2nd ed., pp. 593–610 [R. L. Whistler, J. N. BeMiller and E. F. Paschall, editors]. Orlando, Florida: Academic Press.
- Kidder, D. E., Hill, F. W. G. & Stevens, J. A. (1972). Automatic measurement of some mucosal carbohydrases. *Clinica Chimica Acta* **37**, 491–501.
- Krehbiel, C. & Britton, R. (1993). Glucose absorption in the small intestine in steers. *Nebraska Beef Cattle Report MP: 59-A*, 66–67.
- Kreikemeier, K. K., Harmon, D. L., Brandt, R. T. Jr, Avery, T. B. & 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.
- Kreikemeier, K. K., Harmon, D. L. & Nelssen, J. L. (1990a). Influence of hydrocortisone acetate on pancreas and mucosal weight, amylase and disaccharidase activities in 14-day-old pigs. *Comparative Biochemistry and Physiology* **97A**, 45–50.

- Kreikemeier, K. K., Harmon, D. L., Peters, J. P., Gross, K. L., Armendariz, C. K. & Krehbiel, C. R. (1990*b*). Influence of dietary forage and feed intake on carbohydrase activities and small intestinal morphology of calves. *Journal of Animal Science* **68**, 2916–2929.
- MacRae, J. C. & Armstrong, D. G. (1968). Enzyme methods for determination of alpha-linked glucose polymers in biological materials. *Journal of the Science of Food and Agriculture* **19**, 578–581.
- Mayes, R. W. & Ørskov, E. R. (1974). The utilization of gelled maize starch in the small intestine of sheep. *British Journal of Nutrition* **32**, 143–153.
- Poore, M. H., Moore, J. A., Eck, T. P., Swingle, R. S. & Theurer, C. B. (1993). Effect of fiber source and ruminal starch degradability on site and extent of digestion in dairy cows. *Journal of Dairy Science* **76**, 2244–2253.
- Roberts, P. J. P. & Whelan, W. J. (1960). The mechanism of carbohydrase action. 5. Action of human salivary alpha-amylase on amylopectin and glycogen. *Biochemical Journal* **76**, 246–253.
- Roby, J. F. (1984). Enzymes in the hydrolysis and synthesis of starch. In *Starch: Chemistry and Technology*, 2nd ed., pp. 87–123 [R. L. Whistler, J. N. BeMiller and E. F. Paschall, editors]. Orlando, Florida: Academic Press.
- Roby, J. F. & French, D. (1967). Multiple attack hypothesis of alpha-amylase action: action of porcine pancreatic, human salivary, and aspergillus oryzae alpha-amylases. *Archives of Biochemistry and Biophysics* **122**, 8–16.
- SAS (1985). *SAS Users' Guide: Statistics*. Cary, NC: SAS Institute Inc.
- Seal, C. J., Parker, D. S. & Lobley, G. E. (1993). Effect of intraduodenal starch infusion on glucose metabolism of growing steers fed alfalfa. *Journal of Animal Science* **70**, Suppl. 1, 279 (Abstr.).
- Streeter, M. N., Wagner, D. G., Hibberd, C. A. & Owens, F. N. (1990*a*). The effect of sorghum grain variety on site and extent of digestion in beef heifers. *Journal of Animal Science* **68**, 1121–1132.
- Streeter, M. N., Wagner, D. G., Hibberd, C. A. & Owens, F. N. (1990*b*). Comparison of corn with four sorghum grain hybrids: site and extent of digestion in steers. *Journal of Animal Science* **68**, 3429–3440.
- Streeter, M. N., Wagner, D. G., Owens, F. N. & Hibberd, C. A. (1989). Combinations of high-moisture harvested sorghum grain and dry-rolled corn: effects on site and extent of digestion in beef heifers. *Journal of Animal Science* **67**, 1623–1633.
- Streeter, M. N., Wagner, D. G., Owens, F. N. & Hibberd, C. A. (1991). The effect of pure and partial yellow endosperm sorghum grain hybrids on site and extent of digestion in beef steers. *Journal of Animal Science* **69**, 2571–2584.
- Taravel, F. R., Datema, R., Woloszczuk, W., Marshall, J. J. & Whelan, W. J. (1983). Purification and characterization of a pig intestinal α -limit dextrinase. *European Journal of Biochemistry* **130**, 147–153.
- Zinn, R. A. (1990). Influence of steaming time on site of digestion of flaked corn in steers. *Journal of Animal Science* **68**, 776–781.