Small intestinal fermentation contributes substantially to starch disappearance in milk-fed calves

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Introduction

Calf milk replacers commonly contain 40-50% lactose. For economic reasons, starch is of interest as a lactose replacer. The low ileal digestibility of starch (60%) compared to lactose (97%) in calves (Coombe and Smith, 1974), indicates that enzyme activity required for the hydrolysis of starch to glucose is limited. Which enzyme system is limiting starch digestion in milk-fed calves is unknown. In steers, portal glucose appearance was only 57% of small intestinal starch disappearance (Kreikemeier and Harmon, 1995). This gap includes starch fermentation and glucose use by portal drained viscera. Abomasal infusion of a starch hydrolysate resulted in a linear decrease in ileal pH (Branco et al., 1999), illustrating that fermentation may be an important contributor to small intestinal starch disappearance. The objectives were therefore 1) to determine the rate-limiting enzyme for hydrolysis and disappearance of starch from the intestinal lumen and 2) to quantify starch fermentation in milk-fed calves.

Material and methods

Forty male calves (224 ± 2.0 kg BW) were fed milk replacer containing either lactose as only source of carbohydrate (control) or 18% of one of 4 corn starch products included at the expense of lactose. The 4 corn starch products differed in the enzymes required for their complete hydrolysis to glucose: gelatinized starch (α-amylase and maltase); maltodextrin (α-amylase and maltase); maltodextrin with a high degree of α-1,6-branching (α-amylase, maltase and isomaltase) and maltose (maltase). Calves were adapted to the diets for 15 weeks before the start of the measurements. All diets included Co-EDTA as an indigestible marker. The corn starch products (1.093 atom% ^{13}C) differed in natural ^{13}C enrichment from lactose (1.073 atom% ^{13}C) and the remainder of the diet (1.078 atom% ^{13}C).
Feces were collected quantitatively during 4 days to measure apparent total tract disappearance of the starch products and to calculate total tract starch fermentation based on fecal ^{13}C excretion (Gerrits et al., 2012). Blood samples were taken at -30, 30, 60, 120, 180, 240 and 360 min after feeding to measure ^{13}C enrichment in plasma glucose. On the day of blood sampling only, control calves received ^{13}C enriched lactose (1.092 atom% ^{13}C). Calves were sacrificed 4 h after feeding and ileal digesta were collected to measure apparent ileal disappearance of starch products. Variables were analyzed for treatment effects by ANOVA.

Results and Discussion

Apparent total tract (99.1 ± 0.4%) and ileal (61.7 ± 6.3%) starch disappearance did not differ between starch products. Total tract starch fermentation, estimated from increased fecal ^{13}C excretion, was not affected by treatment and averaged 376 ± 39 g/d, corresponding to 81% of starch intake (Table 1). Starch-fed calves produced more feces (+70 g DM/d) than control calves ($P < 0.001$), which consisted of 5.0 g starch, 0 g fat and 0 g ash per day. This leaves 65 g/d unaccounted for, which is hypothesized to be increased undigested microbial mass resulting from starch fermentation. Assuming a ratio of 4.54 gram starch fermented for each g of fecal microbial output (Livesey et al., 1991), this would require 295 g/d starch to be fermented, corresponding to 63% of starch intake. In the control calves,

^{13}C enrichment in plasma glucose increased from 1.083 to 1.094 atom% at 3h after feeding. In starch-fed calves, ^{13}C enrichment in plasma glucose did not increase relative to baseline (1.084 atom%). Hence, absorption of starch-derived glucose was not sufficient to lead to a measurable increase in ^{13}C enrichment in plasma glucose.

The combination of the 4 starch products would lead us to deduce the rate-limiting enzyme for starch digestion in milk-fed calves. Ileal starch digestibility did not differ between starch products, suggesting that maltase activity limits starch digestion in milk-fed calves. Two methods were used to quantify starch fermentation; one based on increased fecal DM output and the other on increased fecal ^{13}C excretion. Based on these methods, starch fermentation was 63 to 81% of the starch intake in milk-fed calves. This is in agreement with the absence of a postprandial response in ^{13}C enrichment of plasma glucose to feeding corn starch products that are characterized by a relatively high natural ^{13}C enrichment. Starch fermentation in the colon (i.e. the difference between total tract and ileal disappearance) averaged 37%. Therefore, an additional 26 to 44% of the starch intake is fermented before the colon. Overall, this study shows that small intestinal fermentation contributes substantially to starch disappearance and that maltase limits starch digestion in milk-fed calves.

Table 1: Fecal characteristics of calves fed a milk replacer containing lactose as only source of carbohydrate (CON) or 18% of naturally ^{13}C enriched starch products (GS, gelatinized starch; MD, maltodextrin; MDB, maltodextrin with a high degree of branching; MT, maltose).

Treatment	**CON**	**GS**	**MD**	**MDB**	**MT**		
			Mean			Pooled SEM	*P*-value[1]
Number of calves	7	8	7	8	7		
Fecal ^{13}C enrichment, atom%	1.0776[a]	1.0829[b]	1.0832[b]	1.0825[b]	1.0828[b]	0.0004	<.001
Fecal dry matter output, g/d	168[a]	259[b]	245[b]	222[ab]	226[ab]	16	0.002
Fermentation[2], g/d	-	406	410	349	339	39	0.574
Fermentation[2], % of intake	-	80	82	78	82	8	0.925

[1] *P*-value for differences between treatments. When no value for the CON treatment is shown, the *P*-value applies for differences between the starch product treatments only.

[2] Estimated fermentation of starch products.

[ab] Means with different superscripts in the same row differ significantly ($P < 0.05$).

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