Animal (2016), **10:8**, pp 1296–1302 © The Animal Consortium 2016
doi:10.1017/S1751731116000252

animal

The effect of replacing lactose by starch on protein and fat digestion in milk-fed veal calves

A. M. Pluschke[1,2†], M. S. Gilbert[2], B. A. Williams[1], J. J. G. C. van den Borne[2], H. A. Schols[3] and W. J. J. Gerrits[2]

[1]*ARC Centre of Excellence in Plant Cell Walls, Queensland Alliance for Agriculture and Food Innovation, Centre for Nutrition and Food Sciences, The University of Queensland, St Lucia Brisbane, QLD 4072, Australia;* [2]*Animal Nutrition Group, Wageningen University, PO Box 338, 6700 AH Wageningen, The Netherlands;* [3]*Laboratory of Food Chemistry, Wageningen University, PO Box 17, 6700 AA Wageningen, The Netherlands*

(Received 13 August 2015; Accepted 24 January 2016; First published online 1 March 2016)

Replacing dairy components from milk replacer (MR) with vegetable products has been previously associated with decreased protein and fat digestibility in milk-fed calves resulting in lower live weight gain. In this experiment, the major carbohydrate source in MR, lactose, was partly replaced with gelatinized corn starch (GCS) to determine the effect on protein and fat digestibility in milk-fed calves. In total, 16 male Holstein-Friesian calves received either MR with lactose as the carbohydrate source (control) or 18% GCS at the expense of lactose. In the adaptation period, calves were exposed to an increasing dose of GCS for 14 weeks. The indigestible marker cobalt ethylenediaminetetraacetic acid was incorporated into the MR for calculating apparent nutrient digestibility, whereas a pulse dose of chromium (Cr) chloride was fed with the last MR meal 4 h before slaughter as an indicator of passage rates. The calves were anesthetized and exsanguinated at 30 weeks of age. The small intestine was divided in three; small intestine 1 and 2 (SI1 and SI2, respectively) and the terminal ileum (last ~100 cm of small intestine) and samples of digesta were collected. Small intestinal digesta was analysed for α-amylase, lipase and trypsin activity. Digestibility of protein was determined for SI1, SI2, ileum and total tract, whereas digestibility of fat was determined for SI1, SI2 and total tract. Apparent protein digestibility in the small intestine did not differ between treatments but was higher in control calves at total tract level. Apparent crude fat digestibility tended to be increased in SI1 and SI2 for GCS calves, but no difference was found at total tract level. Activity of α-amylase in SI2 and lipase in both SI1 and SI2 was higher in GCS calves. Activity of trypsin tended to be higher in control calves and was higher in SI1 compared with SI2. A lower recovery of Cr in SI2 and a higher recovery of Cr in the large intestine suggest an increased rate of passage for GCS calves. Including 18% of GCS in a milk replacer at the expense of lactose increased passage rate and decreased apparent total tract protein digestibility. In the small intestine, protein digestion did not decrease when feeding GCS and fat digestion even tended to increase. Overall, effects on digestion might be levelled when partially replacing lactose with GCS, because starch digestion is lower than that of lactose but fat digestion may be slightly increased when feeding GCS.

Keywords: milk-fed calf, starch, α-amylase, lipase, trypsin

Implication

In the present study, 18% of GSC was included in the milk replacer at the expense of lactose and the impact on protein and fat digestion was measured. Protein digestion in the small intestine was unaffected, whereas fat digestion tended to increase. Passage rates in gelatinized corn starch (GCS) milk-fed calves increased likely related to fermentation of a major portion of the starch. Hence, 18% of GSC could be included in milk replacer at the expense of lactose without negatively affecting digestion.

† E-mail: a.pluschke@uq.edu.au

Introduction

Milk replacers (MR) are generally formulated from dairy products, together with animal fats or vegetable oils plus added vitamins and minerals (Heinrichs *et al*., 1995). The ingredients that are required to formulate MR are increasingly expensive. The replacement of dairy proteins (in part) by proteins of vegetable origin has proved to be successful (Verdonk *et al*., 2002). Replacing dairy carbohydrates such as lactose with a cheaper alternative is desirable as well.

However, replacing key components of MR with vegetable substitutes has been shown to change the composition and therefore subsequent digestion of nutrients (Huber and Slade, 1967). Replacing skimmed-milk protein by soya protein resulted in a lower protein and fat digestion in veal calves (Xu *et al*., 1997). Replacing dairy proteins with proteins such as soyabean and fish flour in MR has been shown to reduce fat digestibility (Huber and Slade, 1967; Akinyele and Harshbarger, 1983). Flipse *et al*. (1950) observed that MR containing glucose and corn syrup compared with MR containing lactose decreased growth performance of calves.

It has been documented that as little as 2% starch (food grade corn starch or partially hydrolysed starch based from corn) in MR is enough to depress growth by decreased digestion of nutrients (Natrajan *et al*., 1972; Soliman *et al*., 1979). Liang *et al*. (1967) suggested that milk-fed calves are able to utilize starch as a source of energy by microbial degradation. Including starch into MR has been previously reported to reduce daily gains in Holstein calves (Huber *et al*., 1968; Nitsan *et al*., 1990). The calves had reduced daily gains irrespective of the amount of amylopectin or corn starch in the MR: however, this was measured in calves of 3 weeks of age. Blaxter and Mitchell (1948) suggested that indigestible residues of nutrients other than protein have a marked effect on apparent digestibility of protein, due to increased passage of metabolic or endogenous secretion of nitrogen. Including a considerable portion of starch in the diet likely affects passage rates, with unknown effects on enzyme activities and thereby on digestion of the other nutrients. However, in Huber *et al*. (1961) and Le Huerou-Luron *et al*. (1992a and 1992b) little starch was fed with the milk replacer while in Morrill *et al*. (1970) and Toofanian *et al*. (1973) no starch was fed with the milk replacer and therefore, effects of starch on protein-degrading enzyme activities are not known. In exclusively milk-fed pre-ruminant calves from 2 to 119 days, the enzyme activities for chymotrypsin, elastase, carboxypeptidases A and B, ribonuclease and α-amylase increased with age. The enzyme activities for chymosin, lysozyme and colipase decreased, however, there was no change in the case of pepsin, trypsin, lipase and phospholipase A2 enzyme activities when compared with animals at birth (Le Huerou-Luron *et al*., 1992a and 1992b).

Lactose is readily digested with an apparent total tract disappearance of 98% to 100% (Van den Borne *et al*., 2006) and apparent ileal disappearance of 97% (Blaxter and Mitchell, 1948; Coombe and Smith, 1974). Starch digestion (or disappearance) is much lower, with an apparent total tract disappearance of 79% for amylopectin and corn starch (Blaxter and Mitchell, 1948) and an apparent ileal disappearance of 60% for partial acid-hydrolyzed starch (Coombe and Smith, 1974). It is not known how replacing lactose, which typically makes up 40% to 50% of the MR, with gelatinized corn starch (GCS) will affect protein and fat digestibility.

This study aims to determine the effect of replacing lactose with GCS on the digestibility of protein and fat in milk-fed calves from 13 to 30 weeks of age. We hypothesized that replacing lactose with a pre-GCS in the milk replacer would, due to limited capacity for starch digestion in calves, increase digesta passage rates and thereby reduce small intestinal digestion of protein and fat. The effects on starch digestion are presented elsewhere (Gilbert *et al*., 2015a).

Material and methods

Experimental design, animals and housing

The experiment was reviewed and approved by the Animal Care and Use Committee of Wageningen University, Wageningen, The Netherlands. In total, 16 male Holstein-Friesian calves of 13 weeks of age (103.2 ± 0.72 kg) received one of two MR treatments varying in carbohydrate source. The control treatment contained lactose (527 g/kg) as the only source of carbohydrate. The other MR contained 180 g GCS and 347 g lactose/kg MR. An industrial GCS product was selected (Tate & Lyle Europe, Boleraz, Slovakia). The GCS was analysed by high-performance size exclusion chromatography and by high-performance anion exchange chromatography as described by Gilbert *et al*. (2015b) and these analyses showed that GCS only contained polymers, and no low-molecular weight fractions. The experiment consisted of an adaptation and an experimental period. In the adaptation period, calves were exposed to the dietary treatments for 14 weeks. During these 14 weeks, the GCS calves were step-wise exposed to an increasing dose of GCS (3%/week) to allow maximal adaptation of all enzyme systems involved (Gilbert *et al*., 2015b). The exchange ratio between GCS and lactose was determined based on the titration during the adaption phase, monitoring faecal dry matter (DM) and pH. The experimental period started at 27 weeks of age (212.1 ± 4.26 kg) and lasted 3 weeks (until 30 weeks of age; 230.3 ± 4.82 kg). During the experimental period, small intestinal, ileal and total tract digestibility, enzyme activities and rate of passage were measured to determine the effects of replacing lactose by GCS on protein and fat digestion. The calves were housed on wooden, slatted floors in pairs (except during faeces collection). During the collection of faeces, calves were housed individually for 8 consecutive days, they could change posture freely but could not turn around, facilitating the collection of faeces. Per calf, 2.7 m^2 was available. Lights were on from 0600 to 1800 h. The stable was mechanically ventilated.

Diet and feeding

Calves were fed individually according to their metabolic weight at twice the metabolizable energy requirements for maintenance (ME_m). Feeding rates were adjusted weekly. ME_m was assumed at 460 kJ/kg$^{0.75}$ per day (Van Es *et al*., 1969). MR was provided in buckets. Solid feed was not provided as this would lead to difficulties in estimating starch flow and α-amylase activity in the intestinal tract. Lactose was exchanged for GCS on a weight basis. Ingredient and nutrient compositions have been described elsewhere (Gilbert *et al*., 2015b). In brief, milk replacer was composed of 375.0 g/kg lactose, 285.4 g/kg delactosed whey powder, 123.2 g/kg whey protein concentrate, 46.2 g/kg palmstearin, 45.0 g/kg soya oil, 37.5 g/kg palm-kernel oil, 30.0 g/kg palm oil, 11.4 g/kg lecithin, 2.4 g/kg emulsifier, 14.8 g/kg calcium formiate, 8.0 g/kg premix, 7.2 g/kg L-lysine HCl, 6.2 g/kg mono ammonium phosphate, 5.7 g/kg methionine, 1.4 g/kg threonine and 0.6 g/kg citric acid. Milk replacer contained 171 g/kg CP, 176 g/kg crude fat, 63 g/kg crude ash, 21 g/kg moisture and 522 g/kg lactose for the control treatment. For the GCS treatment, 180 g lactose/kg was exchanged for GCS on a wt/wt basis. MR was mixed with water to obtain a concentration of 154 g/kg and was supplied to the calves at a temperature of ~42°C at 0600 and 1600 h in two equal portions. All diets included cobalt ethylenediaminetetraacetic acid (EDTA) as an indigestibly maker (1.3 g Co-EDTA/kg MR). A pulse dose of chromium chloride (7.69 g of $CrCl_3$ hexahydrate) was provided with the last MR meal 4 h before slaughter. Water was available *ad libitum*.

Sample collection and measurements

Until 13 weeks of age, calves were fed a commercial MR and crushed barley from 3 to 8 weeks of age. When the calves reached 13 weeks of age, they were adapted to the control diet in 4 days, which all calves received thereafter for a week. Following this week, calves were assigned to the dietary treatments. Calves were weighed each week in order to adapt feeding level to their metabolic weight. Calves were first habituated to individual housing for 4 days before starting faeces collection. Faeces were collected from the buckets under the slatted floor twice a day for 4 consecutive days and were weighed, homogenized, sampled and stored at −20°C until analysis. As faeces were collected semi-quantitatively in trays underneath the slatted floor, no clean urine samples could be collected.

At 30 weeks of age, calves were anesthetized 4 h after feeding by pentobarbital injection. Calves were lifted by the forelegs to prevent reflux of MR from the abomasum into the rumen. Calves were subsequently exsanguinated. After opening the abdominal cavity, the digestive tract was ligated at five points to prevent digesta from flowing between gastrointestinal (GIT) sections. The small intestine was separated from the other parts of the GIT and divided into small intestine 1 and small intestine 2 (SI1 and SI2, respectively) and terminal ileum (defined as the last metre). The entire intestinal tract was removed from the calf, thereafter SI1 and SI2 were separated based on equal length of the small intestine excluding the ileum. Digesta samples were collected from each compartment (after collecting and weighing all digesta and homogenization) and were stored at −20°C (from SI1, SI2 and ileum for enzyme analyses and from all compartments; reticulorumen, abomasum, SI1, SI2, ileum and large intestine (colon + caecum) for Cr analysis to determine passage rates. This process was finished within 20 min/calf.

Analytical procedures

Samples of MR and GCS were collected weekly, pooled and analysed for DM, CP, crude fat and total glucose (Total starch kit from Megazyme International Ireland Ltd, Co., Wicklow, Ireland; Association of Analytical Communities 996.11). Diets, GIT digesta and faeces were analysed in duplicate for content of DM (ISO 1999a and 1999b), CP (Kjeldahl method (ISO 2005)) for SI1 and SI2 samples and Dumas combustion method for ileal samples due to a small amount of digesta. (AOAC 990.03, using a Thermo Quest NA 2100 Nitrogen and Protein analyzer of Interscience, Troy, NY, USA) and crude fat with acid hydrolysis for faeces and without hydrolysis for SI1 and SI2 (ISO 1999a and 1999b). Cobalt (faeces and ileal digesta) and chromium (GIT samples) were measured by atomic absorption spectrophotometry using a SpectrAA300 (Varian, B.V., Middelburg, the Netherlands).

Digestibility (%) was calculated using the following equation:

$$\text{Digestion } (\% = 100 - (100 \times (\text{Co}_{\text{feed}}/\text{Co}_{\text{digesta}}) \times (\text{Nutrient}_{\text{digesta}}/\text{Nutrient}_{\text{feed}}))$$

where Co_{feed} is the cobalt concentration in the milk replacer (mg/kg DM), $\text{Co}_{\text{digesta}}$ the cobalt concentration in the faeces or digesta (mg/kg DM), $\text{Nutrient}_{\text{digesta}}$ the nutrient concentration in the faeces or digesta (g/kg DM) and $\text{Nutrient}_{\text{feed}}$ the nutrient concentration in the milk replacer (g/kg DM).

Quantifying enzyme activity

Intestinal digesta from SI1 and SI2 were thawed and analysed using an α-amylase activity assay kit (BioVision K711-100, Milpitas, CA, USA), a lipase activity assay kit (BioVision 723-100) and a trypsin activity assay kit (BioVision K771-100) using an colorimeter TECAN Infinite F500 spectrophotometer (Grödig, Austria). Activity was corrected for the dilution factor between sample and buffer. One unit (U) of enzyme activity was defined as the amount of enzyme that hydrolysed 1 μmol substrate/minute at pH 7.20 and 25°C for trypsin and α-amylase and 37°C for lipase. Activity was expressed against the Co concentration present in the small intestine section, thereby correcting for changes in enzyme activity related to the disappearance of nutrients along the digestive tract. Each assay was performed in duplicate.

Statistical methods

All statistical analyses were performed using SAS 9.3 (SAS Institute Inc., Cary, NC, USA). Apparent total tract digestibility was analysed for treatment effects by ANOVA using the GLM procedure. Apparent SI digestibility, enzyme activities and recovery of Cr were analysed on treatment, GIT and treatment × GIT effects using the MIXED procedure, using GIT as a repeated measure, with calf as subject. One calf with a Cr recovery in the rumen >50% was excluded from the analysis, as this high recovery is evidence of ruminal drinking (Labussière *et al*., 2014). After an interaction effect was found, treatment effects per segment were analysed using the slice statement in the MIXED procedure. Total tract crude fat digestibility, apparent ileal N digestibility and α-amylase activity were log transformed to obtain homogeneity of variance. Differences were considered significant when $P < 0.05$ and tendencies were noted when $0.10 > P > 0.05$. Results are expressed as non-transformed means ± SEM.

Results

One calf from the control treatment was identified as a ruminal drinker; this calf was excluded from the analyses.

Control calves had higher α-amylase activity in SI1 than GCS calves (Table 1). Whereas α-amylase activity was higher in SI2 for GCS calves (treatment × GIT, $P = 0.025$). Lipase activity was higher for GCS calves ($P = 0.023$). The large SEM for lipase activity is due to large variation observed from the GCS calves. Trypsin activity was higher in SI1 compared with SI2 ($P = 0.017$) and tended to be greater for control calves ($P = 0.087$).

Apparent small intestinal protein digestibility did not differ between treatments ($P = 0.386$) (Table 2). Apparent total tract protein digestibility was decreased in GSC calves ($P = 0.035$). Apparent crude fat digestibility tended to be increased by 4.8% in SI1 and 3.0% in SI2 for GCS calves compared with control calves. However, total tract fat digestibility did not differ between treatments ($P = 0.24$).

Apparent disappearance of GCS was 64.0 ± 9.94% of intake at the ileum and 99.0 ± 0.51% of intake at total tract, indicating that 35% of the GCS intake was fermented in the large intestine. In addition, total tract fermentation of GCS was quantified, which averaged 447 ± 27 g/day, corresponding to 89% of intake. By difference, this indicated that 54% of the GCS intake was fermented before the terminal ileum (Gilbert *et al.*, 2015a).

Total recovery of Cr averaged 87 ± 1% and did not differ between treatments ($P = 0.924$). Chromium recoveries per compartment of milk-fed calves (13 to 30 weeks) are presented in Table 3. There was an interaction between treatment and GIT ($P = 0.037$). Less Cr was recovered in SI2 ($P = 0.042$) and more in the large intestine ($P = 0.047$) for GCS calves compared with control calves.

Table 1 *Luminal α-amylase, lipase and trypsin activity in small intestinal segments of calves fed a milk replacer containing lactose as only carbohydrate source (control) or 18% of gelatinized corn starch (GCS) at the expense of lactose*[1]

	Treatments			*P*-value		
Digestive enzyme activity (U/mg Co)	Control	GCS	SEM	GIT	Treatment	Treatment × GIT
α-amylase[2]						
SI1	3.9	1.9	2.3	Ns	**	**
SI2	0.0	5.2	1.5			
Lipase[2]						
SI1	16.2	95.7	34.8	Ns	**	Ns
SI2	18.9	53.2	21.9			
Trypsin[2]						
SI1	5.9	4.4	1.8	***	†	Ns
SI2	2.3	1.7	0.6			

GIT = gastrointestinal; SI = small intestine; Ns = not significant.
[1]Values represent means ± SEM and ($n = 15$, control = 7, GCS = 8).
[2]All enzyme activities are expressed per gram of indigestible marker cobalt (Co). †$P < 0.10$, **$P < 0.05$, ***$P < 0.001$.

Table 2 *Apparent total tract, ileal and small intestinal (SI) protein and fat digestibility of calves fed a milk replacer containing lactose as only carbohydrate source (control) or 18% of gelatinized corn starch at the expense of lactose*

		Treatments			*P*-value		
Apparent digestibility (%)	*n*	Control	Starch	SEM	GIT	Treatment	Treatment × GIT
Protein							
SI1	14	77.9	77.4	2.8	***	Ns	Ns
SI2	14	94.1	93.8	0.7			
Ileal	12	83.1	83.6	0.9			
Total tract[1]	15	86.1	79.8	1.8		**	
Fat							
SI1	14	21.5	26.3	7.1	***	†	Ns
SI2	14	94.7	97.7	0.6			
Total tract	15	91.0	93.6	1.6		Ns	

GIT = gastrointestinal; Ns = not significant.
Values represent means ± SEM.
[1]Total tract digestibility was analysed separately as the faeces was not collected at the same time as small intestinal digesta. †$P < 0.10$, ***$P < 0.001$, **$P < 0.05$.

Table 3 *Recovery of chromium (Cr) per gastrointestinal (GIT) compartment in calves fed a pulse dose of chromium chloride hexahydrate with the milk replacer containing lactose as only carbohydrate source (control) or 18% of gelatinized corn starch at the expense of lactose*[1]

	Treatments			*P*-value		
Cr per compartment (% of intake)	Control	Starch	SEM	GIT	Treatment	Treatment × GIT
Rumen	7.4	4.3	2.2		Ns	
Abomasum	12.9	21.0	3.8			
SI1	11.9	11.7	1.0			
SI2	48.3	35.2	4.4	***		*
Ileal	2.5	1.1	0.6			
Large intestine	4.9	14.8	3.2			
Total	88.1	86.4	2.5		Ns	

Ns = not significant.
[1]Values represent means ± SEM and $n = 14$. *$P < 0.05$, ***$P < 0.001$.

The average lengths of small intestine excluding the ileum for the control and starch treatments were 26.8 ± 1.1 m and 28.0 ± 1.5 m, respectively, and did not differ between treatments.

Discussion

This experiment was conducted to determine the effects of replacing one-third of the lactose with GCS on the digestibility of protein and fat in milk-fed calves (13 to 30 weeks).

Milk-fed calves were fed a pulse dose of chromium before they were euthanized providing an indication of passage rates. Calves fed MR with GCS had increased passage rates as indicated by a higher recovery of chromium in the large intestine and a lower recovery in the small intestine, which have been previously associated with increased fermentation of starch occurring along the GIT. DM content and pH has been found to decrease when feeding starch to calves (13 to 27 weeks old) (Gilbert *et al.*, 2015b) and sheep (lambs from 4 to 17 weeks and mature sheep from 2 to 3 years) (Mayes and Ørskov, 1974), and diarrhoea was observed after feeding increasing concentration of starch to cattle of various ages (Huber *et al.*, 1961). A decrease in ileal pH after abomasal infusion of increasing amounts of starch has been found in steers (Kreikemeier *et al.*, 1991).

Apparent protein digestibility in the small intestinal tract did not differ between treatments, whereas trypsin activity tended to be higher in control calves. A decrease in trypsin activity was found after abomasal infusion of starch hydrolysate in steers (Swanson *et al.*, 2002). Trypsin activity was highest in SI1. This is in agreement with a loss of protease activity along the small intestinal tract (Layer *et al.*, 1986). GCS calves had decreased apparent total tract protein digestibility. This is probably due to increased endogenous secretions of nitrogen or an influx of urea occurring in the later parts of the GIT, because apparent ileal digestibility did not differ between treatments.

Passage rate was increased in GSC calves, which was probably the result of starch being (partly) undigested in these calves, resulting in water being drawn into the lumen. As a result of less starch digestion, it is likely that the starch becomes substrate for microbial fermentation in the large intestine causing an influx of urea nitrogen into the large intestine (Gerrits *et al.*, 2012). Substantial starch fermentation was observed in milk-fed calves (13 to 30 weeks), with 37% of the ingested starch fermented in the colon and an additional 41% of the ingested starch fermented in the small intestine (Gilbert *et al.*, 2015a). Although the inclusion level of GCS was not fixed, GCS-fed calves had a reduction in growth as a result of fermentation of GCS instead of digestion. Increasing the number of calves would improve the reliability of the growth rates. The estimated daily gain of control calves was 1169 ± 26 g and was 1130 ± 31 g for GCS calves. Apparently, the increase in passage rate did not affect protein digestion in the small intestine, which could be because it is already very high in SI1, corresponding with the enzyme activities.

GCS calves had higher lipase activity throughout the small intestine when compared with control calves, which correlates well with the higher small intestinal fat digestibility. Lipase activity determined in small intestinal luminal contents has been positively correlated with the concentration of lipase secreted from the pancreas (Sternby *et al.*, 1991). Pancreatic lipase secretions are readily influenced by the amount of fat in the diet (Mu and Hoy, 2004). However, neither the fat content nor the fat source differed between treatments. Adding GCS into the MR might improve the ability of the secreted bile salts to emulsify the luminal contents sufficiently as reviewed by Radostits and Bell (1970) or reduce the binding affinity of lipase to the lipids (Lairon *et al.*, 1978). A reduced affinity of lipase to its substrate may result in an increase in the hydrolysis of added substrate and therefore be recorded as increased activity. The decreased apparent total tract protein digestibility and increased passage rate when feeding GSC suggest that starch was fermented, and starch fermentation in both the large and small intestine was indeed confirmed by Gilbert *et al.* (2015a). From the current study, replacing lactose with GCS in the MR increased α-amylase activity, potentially by adaptation to the starch as reviewed by Brannon (1990) and Mosenthin and Sauer (1993) or by inducing microbial amylase activity (Cummings and Macfarlane, 1991). This is in contrast to the findings of Walker and Harmon (1995) who determined that abomasal infusion of partially hydrolysed starch in steers decreased pancreatic α-amylase activity in both pancreatic tissue and secreta. In our study, increased amylase activity was measured in the second part of the small intestine in GCS-fed calves. We speculate this increase to be either of microbial origin. The increased passage rate could also have resulted in active pancreatic α-amylase being transported with digesta to distal sections of the small intestine. Although the capacity for starch digestion in milk-fed calves is limited, additional negative effects on digestion of other nutrients were not demonstrated. Thus, the economic incentive of replacing lactose in calf milk replacers by starch is a trade-off between the digestive yield of these energy sources and ingredient prices.

Conclusions

Including 18% of GCS in milk replacer at the expense of lactose increased passage rate and decreased apparent total tract protein digestibility, most likely as a result of starch fermentation. However, in the small intestine, protein digestion did not decrease when feeding GCS and fat digestion tended to increase, which was also reflected in increased lipase activity in the small intestine of calves fed GCS. Overall, effects on digestion might be levelled when partially replacing lactose with GCS, because starch digestion is lower than that of lactose but fat digestion may be slightly increased when feeding GCS.

Acknowledgements

A. P. was supported by the Wageningen Institute of Animal Sciences and by the ARC Centre of Excellence for Plant Cell Walls. Technical assistance was provided by Saskia van Laar and Erika Beukers-van Laar (Animal Nutrition Group, Wageningen University) and Edwin Bakx (Laboratory of Food Chemistry, Wageningen University). This project is jointly financed by the European Union, European Regional Development Fund and the Ministry of Economic Affairs, Agriculture and Innovation, Peaks in the Delta, the Municipality of Groningen, the Province of Groningen as well as the Dutch Carbohydrate Competence Center (CCC2 WP21), and by Tereos Syral, VanDrie Group and Wageningen University.

References

Akinyele IO and Harshbarger KE 1983. Performance of young calves fed soybean protein replacers. Journal of Dairy Science 4, 825–832.

Blaxter KL and Mitchell HH 1948. The factorization of the protein requirements of ruminants and of the protein values of feeds, with particular reference to the significance of the metabolic nitrogen. Journal of Animal Science 3, 351–372.

Brannon PM 1990. Adaptation of the exocrine pancreas to diet. Annual Review of Nutrition 1, 85–105.

Coombe NB and Smith RH 1974. Digestion and absorption of starch, maltose and lactose by the preruminant calf. British Journal of Nutrition 31, 227–235.

Cummings JH and Macfarlane GT 1991. The control and consequences of bacterial fermentation in the human colon. Journal of Applied Bacteriology 6, 443–459.

Flipse RJ, Huffman CF, Webster HD and Duncan CW 1950. Carbohydrate utilization in the young calf. I. Nutritive value of glucose, corn syrup and lactose as carbohydrate sources in synthetic milk. Journal of Dairy Science 8, 548–556.

Gerrits WJJ, Bosch MW and Van den Borne JJGC 2012. Quantifying resistant starch using novel, in vivo methodology and the energetic utilization of fermented starch in pigs. The Journal of Nutrition 2, 238–244.

Gilbert MS, Pantophlet AJ, Berends H, Pluschke AM, Van den Borne JJGC, Hendriks WH, Schols HA and Gerrits WJJ 2015a. Fermentation in the small intestine contributes substantially to intestinal starch disappearance in calves. The Journal of Nutrition 145, 1147–1155.

Gilbert MS, Van den Borne JJGC, Berends H, Pantophlet AJ, Schols HA and Gerrits WJJ 2015b. A titration approach to identify the capacity for starch digestion in milk-fed calves. Animal 2, 249–257.

Heinrichs AJ, Wells SJ and Losinger WC 1995. A study of the use of milk replacers for dairy calves in the United States. Journal of Dairy Science 12, 2831–2837.

Huber JT, Jacobson NL, Allen RS and Hartman PA 1961. Digestive enzyme activities in the young calf. Journal of Dairy Science 8, 1494–1501.

Huber JT, Jacobson NL, McGilliard AD and Allen RS 1961. Utilization of carbohydrates introduced directly into the omaso-abomasal area of the stomach of cattle of various ages. Journal of Dairy Science 2, 321–330.

Huber JT, Natrajan S and Polan CE 1968. Varying levels of starch in calf milk replacers. Journal of Dairy Science 7, 1081–1084.

Huber JT and Slade LM 1967. Fish flour as a protein source in calf milk replacers. Journal of Dairy Science 8, 1296–1300.

ISO 1999a. Animal feeding stuffs – determination of fat content. International Organization for Standardization, Geneva, Switzerland.

ISO 1999b. Animal feeding stuffs – determination of moisture and other volatile matter content. International Organization for Standardization, Geneva, Switzerland.

ISO 2005. Animal feeding stuffs – determination of nitrogen content and calculation of crude protein content. International Organization for Standardization, Geneva, Switzerland.

Kreikemeier KK, Harmon DL, Brandt RT, Avery TB and Johnson DE 1991. Small intestinal starch digestion in steers – effect of various levels of abomasal glucose, corn starch and corn dextrin infusion on small intestinal disappearance and net glucose absorption. Journal of Animal Science 1, 328–338.

Labussière E, Berends H, Gilbert MS, Van den Borne JJGC and Gerrits WJJ 2014. Estimation of milk leakage into the rumen of milk-fed calves through an indirect and repeatable method. Animal 10, 1643–1652.

Lairon D, Nalbone G, Lafont H, Leonardi J, Domingo N, Hauton JC and Verger R 1978. Inhibition of lipase adsorption at interfaces. Role of bile salt micelles and colipase. Biochemistry 2, 205–208.

Layer P, Liang V, Go W and Dimagno EP 1986. Fate of pancreatic enzymes during small intestinal aboral transit in humans. American Journal of Physiology 4, 475–480.

Le Huerou-Luron I, Guilloteau P, Wicker-Planquart C, Chayvialle J-A, Burton J, Mouats A, Toullec R and Puigserver A 1992a. Gastric and pancreatic enzyme activities and their relationship with some gut regulatory peptides during postnatal development and weaning in calves. The Journal of Nutrition 7, 1434–1445.

Le Huerou-Luron I, Guilloteau P, Wicker C, Mouats A, Chayvialle J-A, Bernard C, Burton J, Toullec R and Puigserver A 1992b. Activity distribution of seven digestive enzymes along small intestine in calves during development and weaning. Digestive Diseases and Sciences 1, 40–46.

Liang YT, Morrill JL and Noordsy JL 1967. Absorption and utilization of volatile fatty acids by the young calf. Journal of Dairy Science 7, 1153–1157.

Mayes RW and Ørskov ER 1974. The utilization of gelled maize starch in the small intestine of sheep. British Journal of Nutrition 1, 143–153.

Morrill JL, Stewart WE, McCormick RJ and Fryer HC 1970. Pancreatic amylase secretion by young calves. Journal of Dairy Science 1, 72–78.

Mosenthin R and Sauer WC 1993. Exocrine pancreatic secretions in pigs as influenced by the source of carbohydrate in the diet. Zeitschrift Fur Ernahrungswissenschaft 2, 152–155.

Mu HL and Hoy CE 2004. The digestion of dietary triacylglycerols. Progress in Lipid Research 2, 105–133.

Natrajan S, Chandler PT, Huber JT, Polan CE and Jahn E 1972. Ruminal and post-ruminal utilization of starch in young bovine. Journal of Dairy Science 2, 238–244.

Nitsan Z, Ben-Asher A, Nir I and Zoref Z 1990. Utilization of raw or heat-treated starch fed in liquid diet to pre-ruminants. 1. Calves. Reproduction Nutrition Development 30, 507–514.

Radostits OM and Bell JM 1970. Nutrition of the pre-ruminant dairy calf with special reference to the digestion and absorption of nutrients: a review. Canadian Journal of Animal Science 3, 405–452.

Soliman HS, Orskov ER, Atkinson T and Smart RI 1979. Utilization of partially hydrolysed starch in milk replacers by the newborn lamb. The Journal of Agricultural Science 92, 343–349.

Sternby B, Nilsson Å, Melin T and Borgström B 1991. Pancreatic lipolytic enzymes in human duodenal contents radioimmunoassay compared with enzyme activity. Scandinavian Journal of Gastroenterology 8, 859–866.

Swanson KC, Matthews JC, Woods CA and Harmon DL 2002. Postruminal administration of partially hydrolyzed starch and casein influences pancreatic α-amylase expression in calves. The Journal of Nutrition 3, 376–381.

Toofanian F, Hill FWG and Kidder DE 1973. The mucosal disaccharidases in the small intestine of the calf. Annales De Recherches Veterinaires 4, 57–69.

Van den Borne JJGC, Verstegen MWA, Alferink SJJ, Giebels RMM and Gerrits WJJ 2006. Effects of feeding frequency and feeding level on nutrient utilization in heavy preruminant calves. Journal of Dairy Science 9, 3578–3586.

Van Es AJH, Nijkamp HJ, Van Weerden EJ and Van Hellemond KK 1969. Energy, carbon and nitrogen balance experiments with veal calves. In Energy metabolism of farm animals (ed. KL Blaxter, J Kielanowski and G Thorbek), vol. 12, pp. 197–201. Oriel Press, Newcastle upon Tyne, UK.

Verdonk JMAJ, Gerrits WJJ, Beynen AC and Blok MC 2002. Replacement of milk protein by vegetable protein in milk replacer diets for veal calves: digestion in relation to intestinal health. In Nutrition and health of the gastrointestinal tract (ed. MC Blok, HA Vahl, L De Lange, AE Van de Braak, G Hemke and M Hessing), pp. 183–198. Wageningen Academic Publishers, Wageningen, The Netherlands.

Walker JA and Harmon DL 1995. Influence of ruminal or abomasal starch hydrolysate infusion on pancreatic exocrine secretion and blood glucose and insulin concentrations in steers. Journal of Animal Science 73, 3766–3774.

Xu C, Wensing T, Van der Meer R and Beynen AC 1997. Mechanism explaining why dietary soya protein vs. skim-milk protein lowers fat digestion in veal calves. Livestock Production Science 3, 219–227.