

Potato and high-amylose maize starches are not equivalent producers of butyrate for the colonic mucosa

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Portal appearance of short-chain fatty acids (SCFA) produced from fermentation of three different resistant starch (RS) sources (raw potato starch, high-amylose maize starch and retrograded high-amylose maize starch) was investigated in pigs. The catheterization technique coupled with determination of portal blood flow was used to estimate SCFA uptake by the colonic mucosa. Our hypothesis was that these three RS were not equivalent butyrate providers for the colonic mucosa and that butyrate uptake would therefore be different after *in vivo* fermentation of each starch. The starches induced different patterns of appearance of SCFA in the portal blood; raw potato starch was the only RS source to show a significant appearance of butyrate in the portal blood. Thus, uptake of butyrate by the colonic mucosa apparently differed between starches. This finding suggests that butyrate uptake does not only depend on the flow of butyrate appearing in the lumen. Indeed, for unexplained reasons, utilization of butyrate by the colonic mucosa appeared to be less efficient when the butyrate was produced from fermentation of potato starch than when it was produced from fermentation of the other RS sources.

Resistant starch: Butyrate: Pig: Portal appearance: Colonic mucosa uptake

Resistant starches (RS) are defined as: ‘the sum of starch and products of starch degradation not absorbed in the small intestine of healthy subjects’ (Asp, 1992). They undergo bacterial fermentation in the colon (Cummings & Englyst, 1987) producing short-chain fatty acids (SCFA), particularly butyrate in the hindgut (Annisson & Topping, 1994). Butyrate is the major fuel of colonocytes (Darcy-Vrillon *et al.* 1996), and its positive effect on the treatment or prevention of colonic cancer is now widely recognised (Hague *et al.* 1997). RS are therefore claimed to be beneficial in reducing the risk of colon cancer (Bingham, 1990). However, it remains uncertain as to whether RS inhibits colonic carcinogenesis. Results from previous studies indicate that some starches are protective against tumour development (Thorup *et al.* 1995; Caderni *et al.* 1996; Kristiansen *et al.* 1996; Perrin *et al.* 2000) whereas other starches fail to protect and may enhance tumourigenesis (Calvert *et al.* 1989; Sakamoto *et al.* 1996; Young *et al.* 1996). There are numerous sources of RS which differ widely in their characteristics (e.g. different structure of

starch granules and different food processing procedures). Uncooked potato starch may exhibit some deleterious effects on the colonic mucosa, but the exact mechanism remains unknown (Young *et al.* 1996).

Thus we can consider whether these different sources of RS are equivalent butyrate providers for the colonocytes, and whether the kind of RS could have an impact on butyrate uptake by the colonic mucosa. However, these questions are difficult to solve in human subjects as invasive investigations would need to be performed. We therefore used the pig as an animal model for man. The pig is an omnivore with a gut physiology close to that of man (Topping *et al.* 1985). Moreover, Bach Knudsen (1991) determined that digestive transit time is similar for pigs and human subjects. We measured the rate of appearance in the portal vein of the butyrate produced from the fermentation of three different starches: raw potato starch (PoS), high-amylose maize starch (HS) and retrograded high-amylose maize starch (RHS). We used the catheterization technique coupled with determination of portal blood flow to estimate

Abbreviations: HS, high-amylose maize starch; PoS, raw potato starch; RHS, retrograded high-amylose maize starch; RS, resistant starch; SCFA, short-chain fatty acids.

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uptake by the colonic mucosa. We hypothesised that the flow of acetate appearing in the portal vein reflected the hindgut production of acetate from colonic fermentation of the starches. Indeed, only a small proportion of acetate is metabolised by the colonic mucosa (Roediger, 1995). We estimated the flow of butyrate metabolised by the colonic mucosa from the concentration of acetate appearing in the portal vein and the *in vitro* ratio of SCFA for the same starches previously determined using pig inocula by Martin *et al.* (1998).

Experimental methods

Animals

Four female pigs with an initial body weight of 35 (SD 1.5) kg were used. The pigs were fed on a body-weight basis (1200 kJ metabolizable energy/kg metabolic weight 0.75). Water was provided *ad libitum*. Throughout the study (adaptation and test periods) pigs were housed individually in metabolism cages in a room with a controlled temperature of 20°C. Animals were fed a meal twice daily at 07.30 hours and 15.00 hours. The experimental diet was mixed with water immediately before feeding (1:2, w/v). Animal welfare was always in accordance with French legislation.

Diets

Three RS sources, PoS (Roquette, Lestrem, France), HS (National Starch, Bridgewater, NJ, USA) or RHS (Cerestar, Vilvoorde, Belgium) were included in three different diets. The compositions of the experimental diets are shown in Table 1. The metabolizable energy content (kJ/kg DM) was 17 200, 17 130 and 17 150 for the PoS, HS and RHS diets respectively. The diets were formulated to provide 30 g indigestible carbohydrate/d during the adaptation period. The RS were the only source of indigestible material in the diets of the pigs. The amount of RS ingested on the day of the experiment was 0.9 mg RS/kJ which corresponds with the estimated human consumption reported by Brighenti *et al.* (1998).

Table 1. Composition of the experimental diets (g/kg)*

Diet...	PoS	HS	RHS
Pregelatinised potato starch	544.6	514.8	440.2
Meat meal	124.0	124.0	124.0
Skimmed-milk powder	82.0	82.0	82.0
Maize oil	46.0	46.0	46.0
Lard	96.0	96.0	96.0
Beet sugar	54.0	54.0	54.0
PoS [†]	53.4	–	–
HS [‡]	–	83.2	–
RHS [§]	–	–	157.8
Metabolizable energy (kJ/kg DM)	17 200	17 130	17 150

PoS, raw potato starch; HS, high-amylose maize starch; RHS, retrograded high-amylose maize starch.

* Vitamin and mineral mix (vitabiose[®]; Schering-Plough, Segre, France) was included at 15 g/d per animal.

† Roquette, Lestrem, France.

‡ National Starch, Bridgewater, USA.

§ Cerestar, Vilvoorde, Belgium.

al. (1998). Each pig received each of the three diets at random for 5 d (adaptation period) before sampling.

Experimental procedure

Each animal was anaesthetised by inhalation of a mixture of halothane (Belamont, Paris, France), nitrogen protoxide and O₂ via a mask (with 4 % (v/v) halothane for induction and 2 % (v/v) for anaesthesia, and O₂ and nitrogen protoxide each at 1.5 l/min). Pigs were fitted with a 14 mm Transonic[®] blood-flow probe (Transonic Systems Ltd, Ithaca, NY, USA) around the portal vein. Indwelling catheters were used in the portal vein, left jugular vein and left carotid artery. The catheter site in the portal vein was chosen to prevent interference with the measurement of blood flow. The portal-vein catheter and the probe flex were exteriorized through the body wall on the right flank, and the jugular and carotid catheters were exteriorized between the shoulder blades. The catheters were flushed daily with a solution of heparinized (50 IU/ml) physiological saline (9 g NaCl/l) solution. The jugular catheter was only used to perfuse lactate Ringer solution to the animals for the post-operative recovery (24 h). It was not used for blood collection.

Animals were adapted to each diet for 5 d and then fasted for 16 h on day 6. On day 7 at 07.30 hours each pig was fed its morning meal, containing 15 g RS. A painless blood sample (5 ml blood per vessel) was taken from the conscious animal before mealtime (–15 min) and hourly for the next 14 h. Samples were immediately centrifuged (3500 g; 4°C). Portal blood flow (ml/kg per min) was recorded continuously during the experimental trial. Plasma samples were kept at –80°C before analysis. The SCFA analyses were performed using the procedure described by Brighenti (1997).

Calculations and statistics

The ultrasonic blood-flow probe was directly linked to a computer (Acer 760C, Amsterdam, The Netherlands) which recorded instantaneous data and produced a value for the integrated flow rate.

The plasma samples obtained from the hepatic portal vein and carotid artery were analysed for acetate, propionate, and butyrate. The appearance of SCFA in the portal circulation was calculated according to the formula of Rérat *et al.* (1980). This method is based on the quantitative determination of the increase in nutrients within intestinal blood flow after a meal according to the formula:

$$\int_{t_0}^{t_1} dQ = \int_{t_0}^{t_1} (c_p(t) - c_a(t)) \times D(t) \times dt,$$

where $\int dQ$ (mmol) is the quantity absorbed during the experimental period, c_p ($\mu\text{mol/l}$) is the concentration of nutrients in the hepatic portal vein, c_a ($\mu\text{mol/l}$) is the concentration in arterial blood and $D(t)$ (l/min) is the portal-blood flow rate during the short period of time dt .

The colonic uptake of butyrate was estimated hourly

using the following formula:

$$y = \int dq \times (\%C_4 \text{ in vitro}) / (\%C_2 \text{ in vitro}),$$

where $\int dq$ (mmol/h) is the quantity of acetate absorbed in 1 h, $\%C_4 \text{ in vitro}$ is the butyrate- \sum SCFA measured *in vitro* and $\%C_2 \text{ in vitro}$ is the acetate- \sum SCFA measured *in vitro*.

In order to take into account the possible effect of the adaptation of the colonic flora, the 'pre-treatment' factor was added to the statistical analysis (Van der Meulen *et al.* 1997). Data were analysed by ANOVA with diet, animal and pre-treatment as main factors. No pre-treatment effect was apparent for any variables. When the effect of the diet was significant (F test, $P < 0.05$), the differences in mean values between diets were assessed by the Fisher's least significant difference test (matrix of pairwise comparison probabilities). The total amounts of SCFA and butyrate (diet PoS *v.* diets HS and RHS) that appeared in the portal vein were assessed by contrast analysis. $P < 0.05$ was considered to be significant. The differences between the regression coefficients, calculated to estimate butyrate colonocyte uptake, were assessed by the ANCOVA analysis. All statistics were performed using SuperANOVA™ Software (version 1.1, 1989; Abacus Concepts Inc., Berkeley, CA, USA).

Results

All pigs ate the three diets rapidly and remained in good health throughout the 21 d experiment. The mean quantities of starch consumed on the experimental days were 27.5, 41.0 and 82.6 g/d, corresponding to 15.4 (SEM 1.8), 14.8 (SEM 1.1) and 15.7 (SEM 1.1) g RS/d for the PoS, HS and RHS diets respectively. The values were not significantly different between trials.

Portal-blood flow rate

Throughout the 14 h trial, the average portal-blood flow rate was slightly higher ($P = 0.01$) after the RHS meal than after the other meals (Table 2). Regardless of the RS used,

an increase in the portal-blood flow rate was detectable immediately after the morning meal. The values began to decrease 3–4 h after the meal, with the lowest flow rate occurring at the end of the measurement (between 11 and 14 h after the meal).

Arterial and portal short-chain fatty acid concentrations

Only acetate was found in peripheral blood (carotid artery), regardless of the diet used (Table 2). Mean arterial concentrations (fifteen values per pig and per diet for four pigs) were significantly higher with the RHS diet than with the HS and PoS diets ($P < 0.001$).

The mean portal concentrations were higher than the corresponding arterial concentrations, and all three SCFA appeared in the portal blood, regardless of the starch used in the diet (Table 2). The highest mean SCFA concentration in portal blood was measured with RHS ($P < 0.001$). The mean concentration of acetate was also significantly ($P < 0.001$) higher after consumption of diet RHS than after consumption of the other diets. However, significantly higher concentrations of propionate ($P = 0.001$) and butyrate ($P < 0.001$) were measured in the portal vein after consumption of PoS starch. As described by several authors (Giusi-Périer *et al.* 1989; Rérat, 1996) for other sources of fermentable carbohydrates, SCFA concentrations decreased during the first 3 h and then increased during the remaining 11 h of the experimental period after PoS or HS ingestion. For RHS, small variations were observed during the whole postprandial period.

Amounts of short-chain fatty acids in portal blood

The quantities of SCFA appearing in the portal vein after ingestion of the PoS and HS meals decreased during the first 4 h of the experimental period and then increased. However, after ingestion of RHS, a high rate of SCFA absorption in the portal blood was observed in the early phase of the measurement, with relatively small variations in SCFA concentration thereafter. Thus, to avoid any carry-over fermentation effects from RS in previous meals, data

Table 2. Portal blood-flow rate and short-chain fatty acid (SCFA) concentrations in pigs during a 14 h period following consumption of a meal containing raw potato starch (PoS), high-amylose maize starch (HS) or retrograded high-amylose maize starch (RHS)†
(Mean values with their standard errors for four pigs)

Dietary starch...	PoS		HS		RHS		Statistical significance of difference between treatments: <i>P</i>
	Mean	SE	Mean	SE	Mean	SE	
Portal blood-flow rate (ml/kg per min)	24.3	0.6	24.5	0.6	25.0**	0.7	
Arterial concentration (μmol/l)							
Acetate	121.1 ^a	3.4	134.3 ^b	3.7	149.4 ^c	9.5	<0.001
Propionate	nd		nd		nd		
Butyrate	nd		nd		nd		
Portal concentration (μmol/l)							
Acetate	236.5 ^a	9.6	206.4 ^a	10.2	321.5 ^b	11.1	<0.001
Propionate	47.4 ^a	2.3	34.1 ^b	2.5	38.8 ^b	2.7	0.001
Butyrate	21.5 ^a	1.5	1.5 ^b	1.6	2.6 ^b	1.7	<0.001
Total SCFA	305.4 ^a	12.5	242.0 ^b	13.3	363.0 ^c	14.5	<0.001

nd, not detected.

^{a,b,c}Mean values within a row with unlike superscript letters were significantly different at the levels indicated.

Mean values were significantly higher than that for PoS and HS: ** $P = 0.01$.

† For details of diets and procedures, see Table 1 and p. 690.

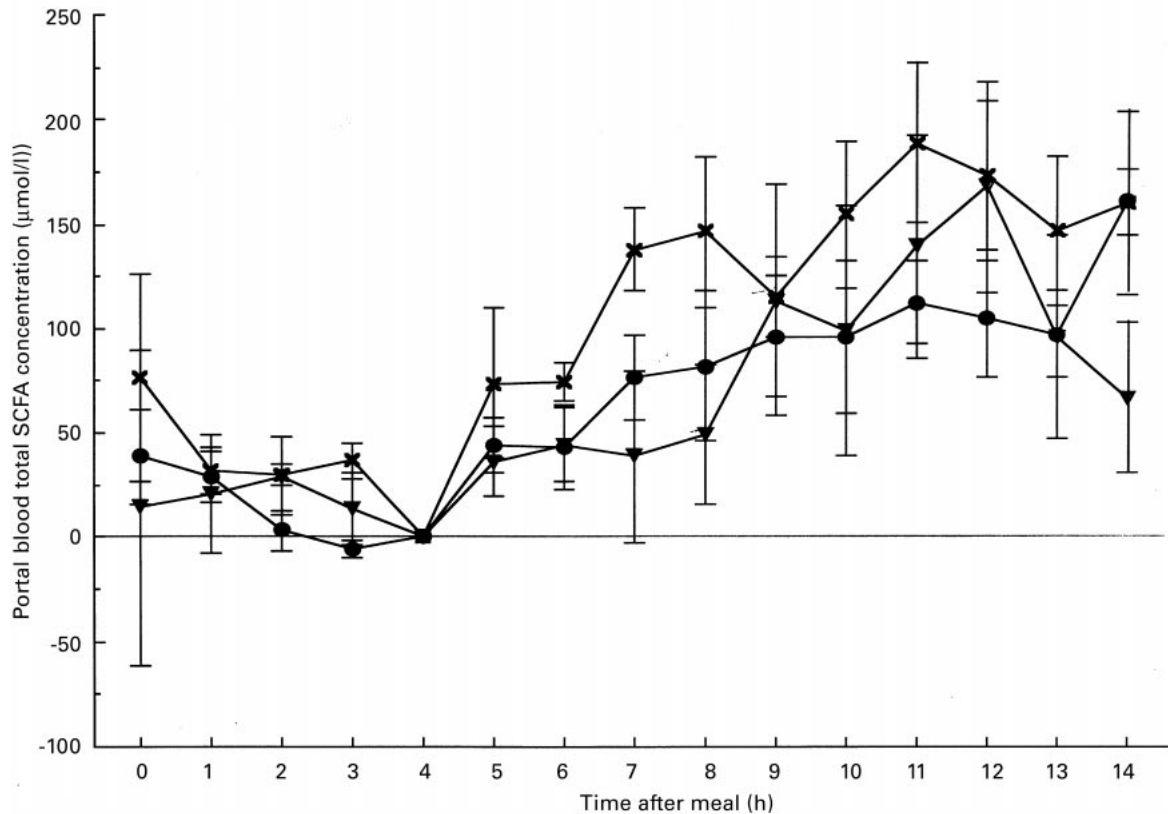


Fig. 1. Appearance of total short-chain fatty acids (SCFA) in the portal blood of pigs during a 14 h test period following consumption of a morning meal containing raw potato starch (×), high-amylose maize starch (●) or retrograded high-amylose maize starch (▼). Data are presented with SCFA concentrations at 4 h as the base value to avoid any carry-over fermentation effects from resistant starch in previous meals. Values were calculated according to the following formula: $(C_p - C_a) - (C_{p4h} - C_{a4h})$, where C_p and C_a are the total SCFA concentrations in the portal blood and carotid artery respectively, and C_{p4h} and C_{a4h} are the SCFA concentrations in the portal blood and carotid artery at 4 h respectively. Values are raw means with their standard errors represented by vertical bars for four pigs. For details of diets and procedures, see Table 1 and p. 690.

were recalculated with concentrations of SCFA at 4 h as the basal value (Figs. 1 and 2). According to this calculation, the total amount of SCFA measured postprandially in the portal vein during 14 h was significantly higher ($P = 0.04$) with the PoS (75.7 mmol) than with the HS (42.8 mmol) and RHS (44.4 mmol) diets.

The comparison between the quantities of SCFA appearing in portal blood during three different periods of postprandial absorption (0–4 h, 4–8 h and 8–14 h (Table 3)) showed differences with the time elapsed for PoS ($P = 0.020$) and HS ($P = 0.023$). The highest appearance of SCFA in the portal blood for PoS and HS starches was observed at 8–14 h. For RHS, SCFA appearing in the portal vein showed the lowest variations ($P > 0.05$), although they increased slightly throughout the experimental period.

The most noteworthy result concerned the amount of butyrate appearing in the portal vein (Fig. 2). PoS induced a much greater ($P < 0.001$) appearance of butyrate (11.9 mmol) than either RHS (3.8 mmol) or HS (0.0 mmol). After consumption of PoS and RHS, the amounts of butyrate appearing in the portal vein decreased during the first 4 h of the experimental period and then increased (Fig. 2). The appearance of butyrate increased progressively from 5 to 14 h after PoS ingestion but after

RHS ingestion butyrate reached a plateau between 10 and 12 h and then decreased. With HS, very little butyrate was detectable in the portal vein.

We estimated the theoretical flow of butyrate produced from starch fermentation (Table 3) using the *in vitro* data of Martin *et al.* (1998). A regression analysis was carried out between the theoretical flow of butyrate and the estimated uptake by the colonic mucosa (theoretical flow – flow in the portal blood) (Fig. 3). For the PoS, the following equation was calculated: $y = -0.436 + 0.678x$ (r^2 0.515; $P = 0.0086$), and for the two maize starches: $y = 0.022 + 0.926x$ (r^2 0.979; $P < 0.001$). The ANCOVA analysis revealed that the uptake of butyrate by the colonic mucosa differed between starches ($P = 0.0001$), although the slopes of the equations did not differ significantly ($P = 0.1106$).

Discussion

Many studies have investigated the role of RS in colonic functions, especially tumorigenesis. RS, by stimulating digestive fermentation, especially butyrate production, is considered to provide protection against colonic cancer (Hylla *et al.* 1998). Nevertheless, the exact amounts of SCFA produced in the digestive tract after ingestion of

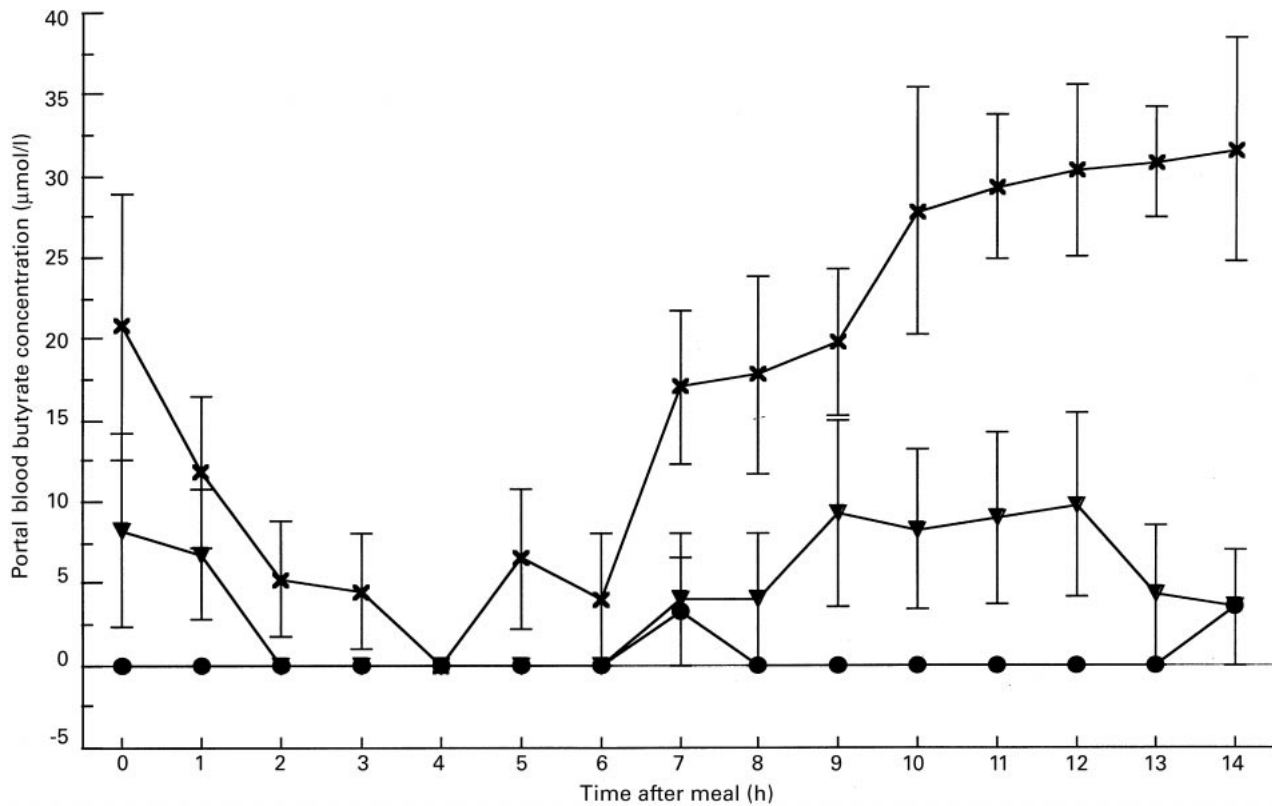


Fig. 2. Appearance of butyrate in the portal blood of pigs during a 14 h test period following consumption of a morning meal containing raw potato starch (x), high-amylose maize starch (●) or retrograded high-amylose maize starch (▼). Data are presented with butyrate concentrations at 4 h as the base value to avoid any carry-over fermentation effects from resistant starch in previous meals. Values were calculated according to the following formula: $(C_p - C_{p_{4h}})$, where C_p is the butyrate concentration in the portal blood and $C_{p_{4h}}$ is the butyrate concentration in the portal blood at 4 h. Values are raw means with their standard errors represented by vertical bars for four pigs. For details of diets and procedures, see Table 1 and p. 690.

Table 3. Amount of short-chain fatty acids (SCFA; mmol/h) appearing in the portal vein in 1 h after a morning meal and estimated theoretical flow of butyrate, in pigs during three different time periods following consumption of a morning meal containing raw potato starch (PoS), high-amylose maize starch (HS) or retrograded high-amylose maize starch (RHS)*

(Mean values with their standard errors for four pigs)

Dietary starch...	PoS		HS		RHS		Statistical significance of difference between treatments: <i>P</i>
	Mean	SE	Mean	SE	Mean	SE	
Acetate							
T1	3.72 ^a	0.588	2.79 ^a	0.677	8.68 ^b	1.49	0.005
T2	5.97 ^{ab}	0.49	4.25 ^a	0.21	8.86 ^b	1.56	0.022
T3	6.89 ^{ab}	0.79	5.58 ^a	0.55	9.77 ^b	1.45	0.044
Butyrate							
T1	0.78 ^a	0.76	0.00 ^a	0.00	0.18 ^a	0.11	0.091
T2	0.75 ^a	0.224	0.04 ^b	0.04	0.08 ^b	0.08	0.009
T3	1.57 ^a	0.09	0.01 ^a	0.01	0.36 ^b	0.18	0.000
Total SCFA							
T1	6.60 ^a	0.96	4.04 ^a	1.07	10.97 ^b	1.64	0.011
T2	9.24 ^a	0.88	5.90 ^b	0.11	10.99 ^a	1.54	0.019
T3	11.38 ^a	1.04	7.55 ^b	0.66	12.55 ^a	1.50	0.028
Theoretical flow of butyrate produced from starch fermentation [†]							
T1	0.87 ^a	0.27	0.65 ^a	0.16	1.80 ^b	0.31	0.010
T2	2.18 ^a	0.18	1.12 ^b	0.05	2.73 ^a	0.48	0.012
T3	2.52 ^a	0.29	1.47 ^b	0.14	3.00 ^a	0.45	0.021

T1, 0–4 h after consumption of the morning meal; T2, 4–8 h after consumption of the morning meal; T3, 8–14 h after consumption of the morning meal.

^{a,b,c}Mean, values within a row with unlike superscript letters were significantly different at the levels indicated.

* For details of diets and procedures, see Table 1 and p. 690.

[†] Calculated from the mean hourly amount of acetate appearing in the period vein in the present study and the *in vitro* SCFA ratio previously determined by Martin *et al.* (1998).

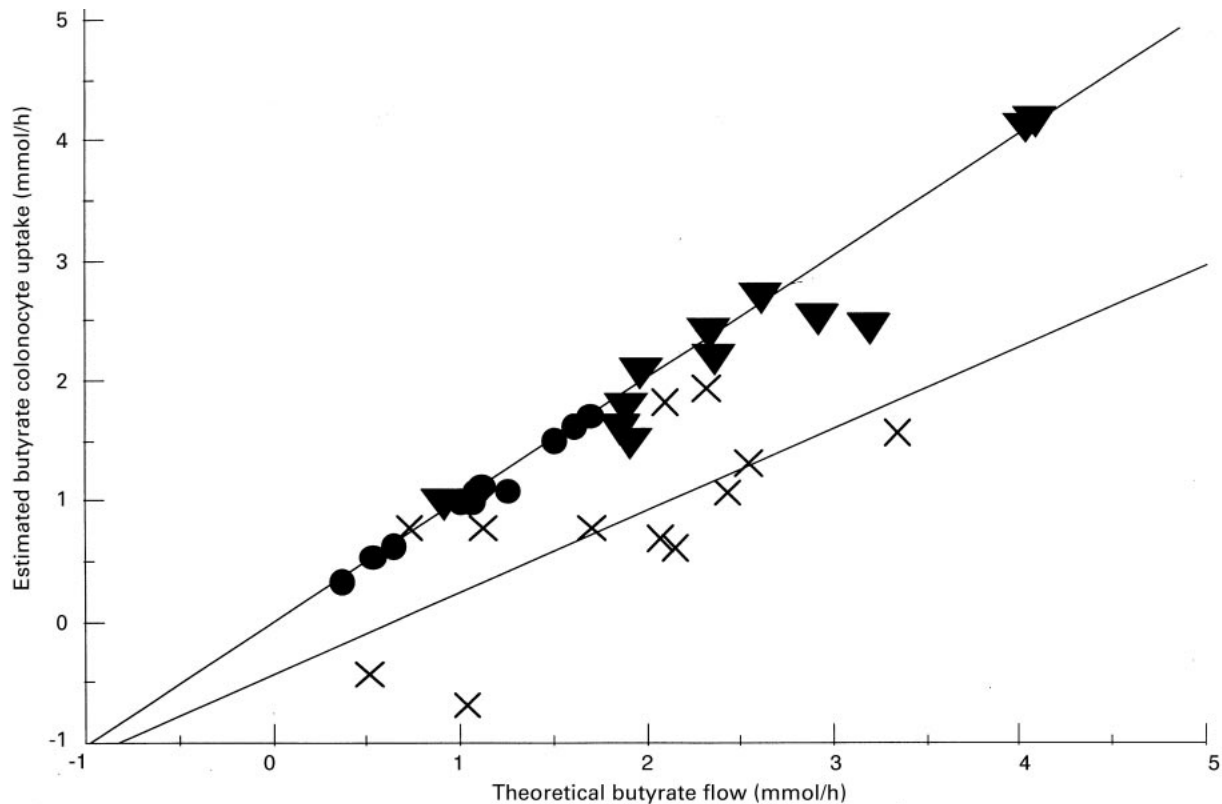


Fig. 3. Relationship between theoretical butyrate flow and estimated uptake of butyrate by the colonic mucosa in pigs following consumption of a morning meal containing raw potato starch (\times), high-amylose maize starch (\bullet) or retrograded high-amylose maize starch (\blacktriangledown). The regression equations are: $y = -0.436 + 0.678x$ (r^2 0.515; $P = 0.0086$) for the raw potato starch; $y = 0.022 + 0.926x$ (r^2 0.979; $P < 0.001$) for the two maize starches. The butyrate uptake by the colonic mucosa differed significantly between starches ($P = 0.0001$) but the slopes of the equations were not significantly different ($P = 0.1106$).

various RS sources, and the proportion metabolised by colonocytes, remain unknown.

The present study was undertaken to investigate the absorption of the three main SCFA produced during caeco-colonic fermentation of three RS sources, with a particular interest in butyrate. The method used to quantify absorption is based on simultaneous determination of the portal blood flow rate and measurement of porto-arterial differences in blood concentrations of SCFA (Noah *et al.* 2000).

In the present study, as well as in previous studies of nutrient absorption (R erat *et al.* 1987, 1993; Ellis *et al.* 1995), there was no significant influence of meal composition on the mean blood flow rate. Like several authors (R erat *et al.* 1987, 1993; Ellis *et al.* 1995), we noted that the blood flow increased just after a meal and during the first 4 h postprandially, then decreased dramatically.

The SCFA concentrations observed in arterial blood in the present study were in good agreement with values obtained in previous studies. Mean arterial concentrations measured in carotid blood were consistent with the values (90–190 $\mu\text{mol/l}$) reported by R erat *et al.* (1987, 1993). In all cases, acetate was the only SCFA detected (Topping *et al.* 1985; R erat *et al.* 1987; Yen *et al.* 1991). Indeed, propionate and butyrate appearing in portal blood are usually totally removed by the liver, whereas part of the acetate is released into peripheral blood (Demign e & R em esy, 1994).

The mean portal concentration of SCFA (all values pooled; 303 $\mu\text{mol/l}$) was similar to values obtained by Giusi-P erier *et al.* (1989) with a diet containing only 6 % of a poorly-fermented carbohydrate. Our diets also contained low amounts of fermentable material (15 g RS per meal) in order to simulate a human diet (Stephen, 1991; Southgate, 1998).

The rate of appearance of SCFA in the portal vein after a meal differed according to time period and type of starch. At the beginning of the blood collection SCFA appearance was between 4.0 and 11.0 mmol/h. Two reasons could account for this observation. First, the duration of the fasting period (16 h) may not have allowed a complete fermentation of the indigestible fraction of the previous meals, as shown by R erat *et al.* (1987). Second, some host products (such as mucin of the mucus layer and other endogenous proteins) are utilised by intestinal microflora (Conway, 1995) and their fermentation leads to SCFA production. In relation to the RHS diet, the amounts of SCFA were consistently higher than those with both the other diets, but no dramatic increase in SCFA was observed from 4 h after the experimental meal. This observation could be explained by the fact that the carry-over effect from the previous meal containing RHS was larger than that of the other diets. This possibility is consistent with our previous data (Martin *et al.* 1998), indicating that RHS contains a highly-resistant starch fraction which is not

fermented after a 24 h *in vitro* fermentation with pig caecal microflora. It can be expected that, *in vivo*, this RS fraction was slowly fermented in the most distal part of the colon. This hypothesis is indeed confirmed by our earlier data (Martin *et al.* 1998); we measured a significantly higher amount of SCFA in the distal part of the colon with RHS starch (5.1 (SEM 2.6) mmol) than with PoS (0.6 (SEM 0.5) mmol) and HS (2.0 (SEM 0.5) mmol) starches. PoS led to the highest absorption of SCFA, suggesting faster fermentation in the hindgut.

As far as butyrate is concerned, this SCFA is known to be the preferential fuel of colonocytes. Theoretically, the butyrate produced in the digestive lumen is totally absorbed and metabolised by colonocytes (Darcy-Vrillon *et al.* 1996). In our study, the highest amount of butyrate measured in the portal vein during the 14 h period following the experimental meal was observed with PoS. We estimated the theoretical uptake of butyrate by the colonic mucosa. It appeared that the calculated theoretical flow of butyrate produced from RS fermentation was similar for PoS and RHS. However, the colonic mucosa uptake was significantly greater for RHS than for PoS. The results of the present study indicate that the butyrate produced by RHS and HS from *in vivo* fermentation is almost entirely metabolised by the colonic mucosa. After PoS ingestion part of the butyrate produced by PoS fermentation appears in the portal vein. In the present study, the quantity of total SCFA carried across the colonic epithelium could be 1.5 $\mu\text{mol}/\text{cm}^2$ per h if the area of the hindgut is estimated according to Argenzio (1982; 200 cm^2/kg body weight). This value is lower than that previously obtained by Argenzio & Southworth (1975; 3 $\mu\text{mol}/\text{cm}^2$ per h). These authors calculated a mucosal uptake of total SCFA of about 1.5 $\mu\text{mol}/\text{cm}^2$ per h, which is consistent with the butyrate uptake of 0.5 $\mu\text{mol}/\text{cm}^2$ per h calculated according to our data.

Many studies have attempted to demonstrate the beneficial role of RS in the prevention of colonic cancers by stimulating digestive fermentation, especially butyrate production (Bingham, 1990). Nevertheless, Young *et al.* (1996) demonstrated that rats fed a diet containing 20 % PoS had larger and more frequent tumours than rats consuming a basic diet or the same diet enriched with wheat bran. Other authors (Perrin, 1996; Sakamoto *et al.* 1996; Young *et al.* 1996) have also obtained contradictory results with different RS sources in relation to the potential beneficial effects of RS (and butyrate production) on aberrant crypt foci in rats exposed to carcinogens. Our results could partially explain those findings. Our data suggest different metabolism of the butyrate produced by different sources of RS; the butyrate produced by the fermentation of PoS may not be used efficiently by the colonocyte. Some authors suggested that different RS may well have different effects in the bowel lumen (Mallett *et al.* 1988; Mathers & Dawson, 1991; Young *et al.* 1996). It has been suggested that the presence of P bonds could partially explain the effect of PoS in the digestive tract (Demigné & Remésy, 1982). These authors suggested that the effect of PoS was associated with an increase in caecal blood flow and a more acidic caecal pH. However, in our previous study (Martin *et al.* 1998) we did not observe a

more acidic pH in the digestive contents of pigs fed the PoS diet.

Conclusion

The present study demonstrates that the consumption of diets containing various types of RS induces different patterns of appearance of SCFA in the portal blood. Among the three RS sources tested, only the PoS starch led to a significant appearance of butyrate in the portal blood. It seems that RS fermented in the most distal part of the colon (RHS in the present study) could be more beneficial for a healthy colon, since uptake of butyrate by the colonocytes is much higher. On the other hand, PoS could produce a large amount of butyrate without any benefit to the colonic epithelium. In order to prevent or to treat diseases of the colon, it would appear to be necessary to select RS sources not only with respect to their potential butyrate production, but also the *in vivo* metabolism of butyrate by the colonic mucosa.

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