Effect of Carbohydrates on Digestion in the Cat\(^1,2\)

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**Expanded Abstract**

Indexing Key Words:  
- cat  
- carbohydrate  
- protein digestibility  
- mineral absorption  
- fecal pH  
- organic acids  
- gas production

It has been shown in many species that the intake of poorly digestible carbohydrates or carbohydrate overload may induce considerable changes in intestinal metabolism, such as increased production of organic acids and a decreased pH of the digesta. Carbohydrates can also interfere with the digestion of protein and the absorption of minerals (Mühlum et al. 1989, Rensing 1984, Schünemann et al. 1989). Because the carnivorous cat has only a limited capacity for carbohydrate digestion (Kienzle 1993a, Kienzle 1993b, Kienzle 1993c, Kienzle 1993d), such effects might be enhanced in the cat or might occur after the intake of comparatively small amounts of carbohydrates or after the intake of carbohydrates that are known to be readily digestible in other species. In the present study the effects of various carbohydrates on the concentration of organic acids, the pH and water content of digesta and feces and on apparent digestibility of protein and apparent absorption of minerals were investigated.

**Materials and Methods.** Fifty-nine adult cats (1.7–6.4 kg body weight, aged 1–5 y, females, intact or neutered males) were divided into nine dietary groups with the following carbohydrate sources (in dry matter): 37\% raw potato starch (STARCH1), 35\% raw maize starch (STARCH2), 29\% cooked maize starch (STARCH3), 36\% sucrose (SUC), two levels of lactose (LAC1 11\% and LAC2 28\%), 40\% glucose (GLUC), 39\% galactose (GAL) and a carbohydrate-free control diet (FAT). The diets are described in detail elsewhere (Kienzle 1994).

The cats were adapted to the diets \(\geq 3\) wk before the start of the experiment. The animals were kept for \(\geq 3\) wk in cages that allow a separate collection of urine and feces. They had free access to food and water. Crude nutrients in food and feces were determined by Weender analysis (Nehring 1963) and major minerals after wet digestion with atomic absorption spectroscopy (Ca, Mg) flame emission spectroscopy (Na, K) or colorimetrically (P). Fecal pH was measured with an electric pH meter.

Short-chain fatty acids were determined in the supernatant via gas chromatography after dilution of fresh samples with water and centrifugation. A mixture of formiate (100 parts) and methylvalerianate (1 part) was added (0.1 ml to 1 ml supernatant) as an internal standard. For lactate, samples were deproteinized with HClO\(_4\) (0.6 mol/l). Supernatants were diluted with glycine/hydrazine buffer (0.4/0.5 mmol/l, pH 9) and centrifugation was repeated. Analysis for l- and d-lactate were carried out enzymatically with l- and d-lactate dehydrogenase, respectively, in glycine/hydracine buffer (Bergmeyer 1970). For the determination of in vitro gas production from feces, 10 g fresh feces were incubated with and without addition of water (1:3 wt/vol) in glass fermenters under anaerobic conditions at 37\°C.

**Results.** Fecal pH as well as concentration of organic acids were altered considerably by feeding carbohydrates [Table 1]. Compared with the FAT diet, fecal pH was lower after the intake of starch, especially raw starch and disaccharides, but not after feeding glucose or galactose. Lactic acid level in feces showed a high variation. High maximal values as well as low concentrations were observed in the groups LAC2, STARCH1 and STARCH2, whereas there were...
always only small amounts in the carbohydrate-free control diet. Concentration of short-chain fatty acids amounted to 300–400 mmol/kg fresh feces in the starch diets, in the control group and in group SUC, whereas it was 50–170 mmol/kg fresh feces in the other groups fed the sugar diets.

Dry matter of feces was high in the control group, FAT, in the diets with raw starch and monosaccharides. It was lower in group STARCH3 and lowest in the groups with disaccharides, where soft feces and diarrhea were observed. Gas production from feces was negligible in the control group and all sugar diets, whereas considerable amounts of gas were obtained by incubation of feces from both diets with raw starch.

Addition of water to the feces before incubation enhanced gas production significantly (Table 2). Protein digestibility was impaired significantly by both raw starch diets [Table 2]. Apparent absorption of magnesium and phosphorus were enhanced in group SUC. Apparent absorption of sodium was lowest in group STARCH1 and highest in group STARCH3. Compared with diet FAT, potassium absorption was impaired in group STARCH2.

Discussion. The acidifying effect of raw starch and disaccharides on feces can be explained by incomplete digestion of carbohydrates in the small intestine (Kienzle 1993a, Kienzle 1993b) and increased microbial fermentation in the large bowel, whereas the monosaccharides were probably absorbed almost completely in the small intestine. Digestibility of carbohydrates, dry matter and pH of feces did not correspond in a simple way. This can be explained by various factors influencing microbial fermentation and production of organic acids. One of these factors is probably the velocity of the carbohydrate breakdown by microorganisms in the large bowel that can be expected to be slow for raw starch because the structure of the granules does not only prevent access of pancreatic but also of microbial amylases (Dreher et al. 1984). On the other hand, microbial fermentation of cooked starch and especially of sugars can be expected to be fast.

Lack of water appears to be another limiting factor for fermentation in the feline large bowel. The digesta in the ileum and the large bowel of the cat are comparatively dry (Kienzle 1993b). When the cats were on a raw starch diet, the water content in chyme was as low as 60% (Kienzle 1993b). As shown by the in vitro experiments, the fermentation of raw starch and also the production of osmotically active microbial metabolites from starch is considerably accelerated in a watery environment or, conversely, is slowed down in a dryer milieu. In contrast to raw starch, the intake of osmotically active disaccharides or cooked starch increases water content in the digesta (>80%) (Kienzle 1993c) and feces.

| Table 1 | pH, dry matter and organic acid in the feces
<table>
<thead>
<tr>
<th>Diet</th>
<th>pH</th>
<th>Dry matter</th>
<th>Short-chain fatty acids</th>
<th>l-Lactate</th>
<th>Maximal d-Lactate</th>
<th>Maximal pH</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>%</td>
<td>mmol/kg wet weight</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>STARCH 1</td>
<td>5.33 ± 0.30</td>
<td>56.2 ± 3.6</td>
<td>321 ± 109*</td>
<td>2.5 ± 6.1</td>
<td>19.0 (13)</td>
<td>4.8 ± 7.9 (13)</td>
</tr>
<tr>
<td>STARCH 2</td>
<td>5.72 ± 0.36*</td>
<td>50.9 ± 4.7*</td>
<td>311 ± 122*</td>
<td>6.1 ± 8.2</td>
<td>23.6 (8)</td>
<td>2.1 ± 6.0 (13)</td>
</tr>
<tr>
<td>STARCH 3</td>
<td>6.25 ± 0.71**</td>
<td>50.3 ± 7.2**</td>
<td>380 ± 175*</td>
<td>2.6 ± 4.0</td>
<td>8.5 (4)</td>
<td>—</td>
</tr>
<tr>
<td>SUC</td>
<td>6.00 ± 0.48**</td>
<td>38.6 ± 8.8</td>
<td>356 ± 119*</td>
<td>2.4 ± 4.0</td>
<td>8.5 (9)</td>
<td>1.6 ± 2.3 (9)</td>
</tr>
<tr>
<td>GLUC</td>
<td>7.15 ± 0.64*</td>
<td>61.4 ± 6.6</td>
<td>95 ± 27*</td>
<td>3.5 ± 6.6</td>
<td>16.8 (6)</td>
<td>3.4 ± 4.8 (6)</td>
</tr>
<tr>
<td>GAL</td>
<td>6.96 ± 0.25**</td>
<td>60.7 ± 10.3*</td>
<td>124 ± 35**</td>
<td>2.7 ± 0.9</td>
<td>4.7 (11)</td>
<td>1.9 ± 0.7 (11)</td>
</tr>
<tr>
<td>LAC 1</td>
<td>6.38 ± 0.44*</td>
<td>46.2 ± 8.2*</td>
<td>172 ± 55*</td>
<td>2.6 ± 1.3</td>
<td>4.1 (10)</td>
<td>2.3 ± 1.5 (10)</td>
</tr>
<tr>
<td>LAC 2</td>
<td>5.36 ± 0.19*</td>
<td>38.1 ± 9.3*</td>
<td>58 ± 8*</td>
<td>9.6 ± 13.3</td>
<td>33.1 (5)</td>
<td>4.7 ± 9.4 (5)</td>
</tr>
<tr>
<td>FAT</td>
<td>7.22 ± 0.37*</td>
<td>52.5 ± 7.1**</td>
<td>307 ± 139**</td>
<td>0.1 ± 0.3</td>
<td>1.1 (13)</td>
<td>0.6 ± 1.1 (13)</td>
</tr>
</tbody>
</table>

1 Values are mean ± SD, with n in parentheses.
2 See text for description of diets.
3* Means not sharing the same superscript letters are significantly different based on Tukey test. In this table Tukey test was used in an explorative way, because in some cases there were several samples from the same cat. Therefore, a significant difference was marked only for P < 0.01.

| Table 2 | Gas production from feces during 4 h of incubation in relation to diet and dilution of feces
<table>
<thead>
<tr>
<th>Diet</th>
<th>Undiluted</th>
<th>1:3 Water</th>
</tr>
</thead>
<tbody>
<tr>
<td>STARCH 1</td>
<td>1.8 ± 1.6 (14)</td>
<td>6.3 ± 3.0** (8)</td>
</tr>
<tr>
<td>STARCH 2</td>
<td>2.1 ± 1.1 (16)</td>
<td>8.5 ± 2.0** (8)</td>
</tr>
<tr>
<td>FAT</td>
<td>Not tested*</td>
<td>0.4 ± 0.5b (11)</td>
</tr>
</tbody>
</table>

1 See text for description of diets.
2 Values are means ± SD, with n in parentheses.
3 Incubation was not possible without dilution in water because the feces were too dry and too hard.
4* Means not sharing the same superscript letters are significantly different based on Tukey test (P < 0.05).
In the present study raw starch led to a decrease of protein digestibility. This agrees with results from other investigations in cats (de Wilde and Jansen 1989, Morris et al. 1977) and has also been observed and extensively discussed in other monogastric species. A combination of factors such as increased passage rate, increased endogenous N-secretion, decreased pH (decreased ammonia production and absorption), increased microbial growth and N-fixation is thought to be responsible for this effect (Ahlborn 1993, Meyer et al. 1989, Sauer and Ozimek 1986). It has been reported first by Ritsert (1914) that lactose can enhance apparent absorption of calcium. This effect was reproduced for calcium, magnesium and sometimes for phosphorus in many species in vivo and in vitro and also in the absence of microbial fermentation (Ahlborn 1993, Andrieux and Sacquet 1985, Favus and Angeid-Backman 1984, Wassermann 1964). The mechanism of action is still not completely understood. Martin and Deluca (1969) postulated a change of transmucosal potential difference (displacement of glucose by lactose leading to a decreased co-transport of glucose and sodium) that was demonstrated by Favus and Angeid-Backman (1984) in the USSING-chamber. In the present investigation the effects of lactose were not significant; however, sucrose had a significant effect on absorption of magnesium and phosphorus. In cats the activity of sucrase in the small intestinal mucosa is within a similar range as lactase in adult individuals of other species (Kienzle 1993d). The impact of sucrose on absorption of magnesium and phosphorus indicates that the lactose effect on these parameters is not specific but can be expected with other low digestible disaccharides.

Whereas diet had little systematic effect on the apparent absorption of sodium and potassium, the fecal excretion of both elements was strictly correlated to the amount of feces [Na, \( r = 0.95 \); K, \( r = 0.98 \); \( P < 0.01 \)] regardless of fecal dry matter content or even of the occurrence of diarrhea.

**LITERATURE CITED**


