Utilization of α-amylase (*EC* 3.2.1.1) resistant maize and pea (*Pisum sativum*) starch in the rat

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1. The extent of utilization of α-amylase (*EC* 3·2·1·1)-resistant retrograded starches in vivo was assessed in male Wistar rats (about 100 g body-weight). All animals were given a fibre-free semi-synthetic basal diet (SS) containing sucrose as the only carbohydrate source, *ad lib.*, for 13 d. On day 14, after an overnight fast, rats were allocated to one of five dietary treatments (*n* 30):1, fibre-free basal SS diet; 2–5, basal SS diet supplemented with 100 g sucrose, Solka floc (cellulose), resistant maize starch (RCS) or resistant pea (*Pisum sativum*) starch (RPS)/kg diet. Animals allocated to each dietary treatment were divided into three groups of ten rats which were given the appropriate diet for 8 or 9, 17 or 18 and 29 or 30 d (8/9, 17/18 or 29/30 d groups respectively). Rats were fed on 12 g diet/d (treatment 1) or 13·2 g diet/d (treatments 2–5) for the first 20 d, and 14 or 15·4 g/d respectively until the end of the experiment. Rats fed on the supplemented basal diets were thus given 10% more food to allow for the addition of the test carbohydrate. Faecal carbohydrate excretion was determined at intervals in the 17/18 d groups. At the end of each experimental period animals were killed after consuming their daily food ration and small intestinal length, weight of caecal and ileal contents and tissue, and pH of caecal contents measured. The amount of carbohydrate in the caecal and ileal contents from the 8/9 and 17/18 d groups was determined.

2. Weights of ileal and caecal contents, caecal tissue and faecal output were significantly greater at all time points for rats fed on the resistant starches compared with those fed on basal and sucrose-supplemented diets. Values were higher for RPS-fed rats than for RCS-fed rats.

3. The quantity of carbohydrate recovered from ileal and caecal contents showed that both RCS and RPS were partially digested and absorbed as carbohydrate, but that RPS was digested to a lesser extent.

4. The concentration of carbohydrate decreased between the ileal and caecal sites when RPS and RCS were given but was essentially unchanged when cellulose was given. This is consistent with rapid fermentation of a fraction of these starches.

5. Faecal carbohydrate elimination in the 17/18 d groups fed on RCS and RPS declined with time, which suggested an adaptive response resulting in increased utilization of the starches. This adaptive response was slower in the RPS-fed rats than the RCS-fed rats.

6. The present study indicates that, in the rat, there are significant differences in the utilization of resistant starches from different sources.

The starch in cooked foods, e.g. bread, breakfast cereals and potato, is known to retrograde on storage. Retrogradation, the formation of crystallites (predominantly small aggregates of highly structured hydrogen-bonded amylose) (Collinson, 1968), results in a fraction of the starch becoming resistant to hydrolysis by α-amylase (*EC* 3.2.1.1) both in vitro (Kerr, 1950) and in vivo (Bjorck *et al.* 1986). Other starch complexes, e.g. starch–lipid, may also be present, but these have been shown to be susceptible to slow digestion by α-amylase (Holm *et al.* 1983). Starch fractions resistant to α-amylase are collectively called resistant starch (RS) (Englyst *et al.* 1982) and manipulation of variables during processing of high-starch foods may be used to alter the levels of RS occurring in the product (Berry, 1986).

In vitro studies suggest that the α-amylase-resistant fraction of starches would be resistant to in vivo digestion and, therefore, unavailable as carbohydrate. However, it is known that the efficiency of in vivo digestion is generally greater than that found in vitro (Dreher *et al.* 1984) and it has been reported that RS from high-amylose maize is susceptible to hydrolysis by human gut microflora (Englyst & Macfarlane, 1986). It might be expected therefore that at least some of the RS present in the diet would be digested in the small intestine and that the remainder would be largely utilized via hydrolysis and

microbial fermentation in the large bowel. Findings relating to RS digestion and fermentation in vivo, however, are limited and there is no knowledge of the possible differences in the utilization of RS from different food sources.

In the present study the fate and effects of α-amylase RS prepared from maize and pea (*Pisum sativum*) starches was investigated in the rat. The RS were incorporated into semi-synthetic diets at 100 g/kg and given to rats for between 8 and 30 d. At the end of each experimental period (8/9, 17/18 or 29/30 d) small intestine length, weights of caecal and ileal contents and tissue, and caecal pH were recorded. The amount of carbohydrate in caecal and ileal contents was measured and faecal carbohydrate excretion determined. The possibility of an adaptational response to longer-term feeding of these starches was also investigated. For comparison, rats fed on a basal semi-synthetic diet and a basal diet supplemented with sucrose (totally available as carbohydrate) or cellulose (unavailable as carbohydrate and substantially resistant to fermentation) were included in the study.

MATERIALS AND METHODS

Extraction of pea starch

Peas (var. Scout; 1 kg) were soaked for 1 h in running tap water, covered with water and left to soak overnight at 4°, washed thoroughly in tap-water and then homogenized (Ultra-turrax, Janke & Kunkle GmbH) for 2–3 min in approximately 5 litres sodium chloride solution (20 g/l). The slurry was washed through a 1 mm sieve with enough water to generate approximately 10 litres filtrate, which was passed through a 125 μm sieve and left to settle for 1 h at room temperature. The resulting supernatant fraction was poured off and the remaining material centrifuged at 2000 rev./min for 10 min at 10°. The supernatant fraction was removed and the residue mixed with 1 litre distilled water and recentrifuged. This procedure was repeated twice more and the residue suspended in absolute alcohol before filtration (Whatman filter paper no. 541) under vacuum. The residue was spread thinly on trays and left in a fume cupboard overnight to allow the solvent to evaporate. The dry residue was stored in air-tight containers. Samples of the material were subjected to acid hydrolysis using a modification of the method of Saeman *et al.* (1954) (12 M-sulphuric acid at 1° for 18 h followed by dilution to 1 M-H_2SO_4 and heating to 100° for 2 h in a boiling water-bath). Glucose, determined by a glucose oxidase (*EC* 1.1.3.4)–peroxidase (*EC* 1.11.1.7) method (Boehringer, cat. no. 124036), showed that the residue contained approximately 970 g glucan/kg on a dry weight basis. Scanning electron microscopy showed that the material was mainly composed of starch granules with only minute traces of cell wall material.

Preparation of RS

Starch (Snowflake maize starch; Corn Products Co. (UK) Ltd, Manchester) or pea starch (400 g) was suspended in 4 litres calcium chloride solution (4 g/l) and heated at 80–90° until the viscosity increased to the point where the starch would not settle out. Gelation of the starch was completed by autoclaving at 121° for 20 min after which the gel was left at 1° for 48 h to retrograde. The retrograded gels were warmed to room temperature. To this was added 375 ml sodium chloride solution (10 g/l) containing 40 g crude porcine α-amylase (Sigma Chemical Co., Poole, Dorset) which had been centrifuged to remove suspended solids. The mixture was homogenized, left to stand for 10 min, remixed, poured into 10-litre Duran glass bottles with loose-fitting tops and incubated at 37° overnight. After mixing, the material was centrifuged at 2000 rev./min for 10 min at 10°, the supernatant fraction discarded, and the residue thoroughly washed with distilled water and recentrifuged five times before freeze drying and weighing. Approximately 40% of the pea starch and 20%

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

Basal diet ‡	
Casein	168
Sucrose	692
Maize oil	80
Minerals*	40
Vitamin mix†	20
Methionine	2
Test diets ‡ (basal diet with the addition (100 g/kg diet) of one of the following)	
Sucrose	
Cellulose§	
Resistant maize starch‖	
Resistant pea (*Pisum sativum*) starch‖	

* Provided (g/kg diet): $CaHPO_4$ 13·00, $CaCO_3$ 8·2, KCl 7·03, Na_2HPO_4 7·4, $MgSO_4$, H_2O 4·00, $MnSO_4.H_2O$ 0·18, $ZnCO_3$ 0·01, $FeSO_4.H_2O$ 0·144, $CuSO_4$ 0·015 KIO_3 0·001.

† Provided (mg/kg diet): nicotinic acid 60, cyanocobalamin in mannitol (Glaxo) 50, calcium D-pantothenate 40, thiamin hydrochloride 10, riboflavin 10, pteroylmonoglutamic acid 5, D-biotin 1, menadione 1, Rovimix E-25 (Roche) 300, Rovimix A-500 (Roche) 25, Rovimix D_3-500 (Roche) 15, choline bitartrate 1800.

‡ For feeding regimen see below.

§ Solka floc (Johnsen, Jurgensen and Wettre Ltd, Wokingham, Berks).

‖ For details of preparation of resistant starches, see p. 292.

of the maize starch remained after this procedure and this material was designated as the RS fraction. Scanning electron microscopy showed that it was an amorphous material and no intact starch granules were observed.

Animals and diets

Male Wistar rats (*n* 150), weighing approximately 100 g, were randomly allocated to one of five dietary treatments, each consisting of three groups of ten animals. Rats were caged singly in polypropylene cages with wire-mesh bottoms and tops in a room at 21°, having a 12 h light–12 h dark cycle. Water was available at all times. All animals were given a fibre-free basal semi-synthetic diet, with sucrose as the only source of carbohydrate, *ad lib.* for 13 d. On day 14, after an overnight fast, rats were given the following diets (Table 1): treatment 1, fibre-free basal semi-synthetic diet; treatments 2–5, basal diet supplemented by the addition of 100 g sucrose, Solka floc (cellulose), resistant maize starch (RCS) or resistant pea starch (RPS)/kg diet. Rats in each dietary treatment were fed on the diet for 8 or 9, 17 or 18 and 29 or 30 d (8/9, 17/18 or 29/30 d groups respectively). Five rats from each dietary treatment were killed in random order on each of the specified days. It was necessary to kill the rats in each of these groups over a 2 d period so that all the animals were examined between 2 and 4 h after consuming their daily portion of food, during which time the animals would be in a steady state with regard to stomach emptying and digestion (G. Livesey, unpublished results). Throughout the study food intake was limited to an amount that the rats would consume in 1 h, between 9·30 and 10·30 hours. This feeding regimen was adopted so that all the animals had a similar feeding pattern throughout the study and hence would be strictly comparable. Animals in the 8/9 and 17/18 d groups of treatment 1 (basal diet only) received 12 g/d, whilst those in the 29/30 d group received 12 g/d for the first 20 d and 14 g/d thereafter. Rats in treatments 2–5 (supplemented basal diet) were given 10% more food each day to allow for the addition of the test material. Rats in all treatments therefore received the same amount of basal diet throughout the study. Body-weights of every animal were recorded at intervals during the study and immediately after killing.

Faecal collections

Faeces from each of the five dietary treatments in the 8/9 and 17/18 d groups were collected and pooled daily by group and dietary treatment for subsequent dry-weight measurements. In addition faeces from the 17/18 d groups were analysed as intervals for carbohydrate content. Faeces from the rats in the 29/30 d groups were collected from individual animals and pooled for each animal for 7-d periods for dry weight measurements and future determination of energy balance. All faeces were kept at −20° between collections and before analysis.

Sampling of tissues and digesta

Rats were deeply anaesthetized by intraperitoneal injection of sodium pentabarbital (160 mg/ml; 2 ml/kg body-weight) and killed by cervical dislocation. The abdomen was opened, the caecum isolated by ligaturing to prevent leakage of the contents, the small intestine removed and the total length of small intestine measured with minimal stretching. The contents of the ileum (distal 50% of small intestine) were collected for the determination of dry matter by gently squeezing out with forceps into a plastic vial. Total caecal weight was then recorded and the pH of the contents measured with a microelectrode. Caecal contents were retained for wet–dry weight and carbohydrate analysis, and caecal tissue was taken for wet–dry weight determination. Caecal and ileal tissues and contents were freeze-dried for dry matter determinations. After drying, the digesta were ground to a uniform powder by vigorously shaking the vial after the addition of two, 12 mm, PTFE-coated magnetic stirrer bars. Freeze-dried faeces were ground in a small coffee mill. All dried ground samples and tissues were stored at room temperature in air-tight plastic vials.

Carbohydrate determination

Dry digesta (50 mg) were weighed into 50-ml screw-top glass centrifuge tubes containing a 12 mm PTFE-coated stirrer bar, and 2 ml cold (4°) 12 M-H_2SO_4 added. The carbohydrate was dispersed by stirring for 18 h at 1° and hydrolysed for 2 h at 100° in a boiling water-bath with continuous stirring after dilution to 1 M-H_2SO_4. Glucose was measured using a glucose oxidase–peroxidase method. Ileal contents were checked for sucrose using high-performance liquid chromatography. Free sugars, extracted from 50 mg dry ileal contents using 3 × 10 ml boiling ethanol (800 ml/l) were reduced to dryness under vacuum at 50°, made up in acetonitrile–water (70:30, v/v) and separated on a Waters carbohydrate column (Millipore–Waters). The mobile phase, acetonitrile–water (70:30, v/v), was pumped at 2·5 ml/min and eluted components detected by refractive index.

Statistics

The GENSTAT package was used for all statistical analysis. Means for body-weight gain and faecal dry matter output for the five diets were compared by one-way analysis of variance (Table 2). Means for small intestinal length, dry weights of ileum and ileal contents, dry weights of caecum and caecal contents, and caecal pH for rats fed on the five diets over the three experimental periods were compared by a two-way analysis of variance (Table 3). Since there was no significant interactive (time × diet) effect, means for each experimental time period were averaged over diets and means for each diet were averaged over time. The carbohydrate contents of the dry ileal and caecal contents for four of the diets were compared by two-way analysis of variance at each of two experimental time periods (8/9 and 17/18 d) after $\log_{10}$ transformation of the values to equalize variances (Table 4). Geometric means are also tabulated in Table 4 to assist interpretation of the results.

Table 2. *Food intake, body-weight gain and faecal dry matter output of rats fed on a basal semi-synthetic diet (SS) or SS diet with added (100 g/kg) sucrose, cellulose, resistant maize starch (RCS) or resistant pea* (Pisum sativum) *starch (RPS) for 29–30 d**
(Values are means for ten rats)

Dietary treatment*...	Basal	Sucrose	Cellulose	RCS	RPS	SED (45 df)	LSD
Food intake (g)	345·0	379·5	379·5	379·5	379·5	—	—
Body-wt gain (g)	88·0	105·0	97·0	120·0	112·0	4·30	8·66
Faecal output (g)	10·7	10·7	42·3	14·1	20·1	0·84	1·69

SED, standard error of difference between any two means (for statistical treatment, see p. 294); LSD, least significant difference ($P < 0.05$).

* For details of dietary treatments, see p. 293.

Standard error of differences (SED) of means and the residual degrees of freedom are given in each table to allow the significance of any differences in comparable values to be found by reference to statistical tables: $(\text{mean}_1 - \text{mean}_2)/\text{SED} = t$ with tabulated residual degrees of freedom.

RESULTS

Rats fed on the unsupplemented basal diet had a lower body-weight gain over the 29/30 d experimental period than all other groups ($P < 0.05$), and those rats fed on the RCS-supplemented diet had the highest mean value for body-weight gain (Table 2).

There were marked and consistent differences in faecal output between the five dietary treatments. Rats fed on the basal and sucrose-supplemented diets produced similar amounts of faeces, expressed as a mean dry weight (g/rat), over the 29/30 d experimental period with values for the RCS, RPS and cellulose treatments being 32, 88 and 295% greater ($P < 0.001$) than the basal and sucrose-supplemented treatments respectively (Table 2).

The effect of cellulose and the RS on small intestinal growth appeared to be minimal, but both the RCS- and RPS-fed rats had significantly increased ($P < 0.001$) dry weight of caecal tissue compared with rats fed on the other three diets, rats given the RPS having the highest mean value (Table 3). Mean dry weight of caecal contents was also significantly higher ($P < 0.05$–$P < 0.01$) in the RPS-fed rats compared with all other groups and this was accompanied by a significant increase ($P < 0.001$) in dry weight of ileal contents, and a reduction ($P < 0.001$) in the pH of caecal contents, compared with the basal and sucrose-supplemented animals. Similar but generally less marked differences were seen in the rats given RCS (Table 3). The caecal tissue weight of the rats fed on cellulose was not significantly increased compared with rats given the basal or sucrose-supplemented diets, although the dry weights of ileal and caecal contents recovered from these animals were significantly higher ($P < 0.001$) than those for the basal and sucrose-supplemented groups. Although it is known that sucrose is rapidly hydrolysed and absorbed in the proximal intestine, it was considered possible that the complex carbohydrate added to the semi-synthetic diet may have influenced the site of sucrose absorption thus resulting in the presence of sucrose in the ileum at the time of death. This would have affected the subsequent carbohydrate analysis of the ileal contents. However, no sucrose was detected in the ileal contents of any of the animals. At the end of both the 8/9 and 17/18 d feeding

Table 3. *Small intestinal (SI) length, dry weight of ileum and ileal contents, dry weight of caecum and caecal contents and caecal pH of rats fed on a basal semi-synthetic diet (SS) or SS diet with added (100 g/kg) sucrose, cellulose, resistant maize starch (RCS) or resistant pea* (Pisum sativum) *starch (RPS)**

(Values are means for each experimental time period (days) averaged over diets, and means for each diet averaged over experimental time periods)

	Ileum			Caecum		
					Contents	
	SI length (mm)	Tissue dry wt (mg)	Contents dry wt (mg)	Tissue dry wt (mg)	dry wt (mg)	pH
Time period (d)						
8–9	1130	163	184	178	270	6·97
17–18	1130	161	208	170	320	7·20
29–30	1140	172	316	215	399	7·14
SED (135 df)	11	3·0	14·3	7·0	16·9	0·04
Diet*						
Basal (SS)	1130	164	183	164	221	7·33
Sucrose	1140	175	175	165	245	7·26
Cellulose	1130	159	350	166	401	7·05
RCS	1140	158	218	205	325	6·92
RPS	1130	171	256	238	457	6·95
SED (135 df)	14	3·9	18·5	9·0	21·8	0·06

SED, standard error of difference between any two means (for statistical treatment, see p. 294).
* For details of dietary treatments, see p. 293 and Table 1.

Table 4. *Carbohydrate (as glucose) expressed as a percentage of dry weight of ileal and caecal contents from rats fed on a basal semi-synthetic diet (SS) or SS diet with added (100 g/kg) cellulose, resistant maize starch (RCS) or resistant pea (*Pisum sativum*) starch (RPS) for both 8/9 and 17/18 d experimental periods**

(Values are $\log_{10}$ means with geometric means for ten rats)

Dietary treatment*	Basal	Cellulose	RSC	RPS	SED (72 df)
8/9 d					
Ileal contents					
$\log_{10}$	−0·426	1·684	1·383	1·646	0·0545
Geometric mean (%)	0·4	48·3	24·2	44·3	—
Caecal contents					
$\log_{10}$	−0·598	1·764	0·839	1·011	—
Geometric mean (%)	0·3	58·1	6·9	10·3	—
17/18 d					
Ileal contents					
$\log_{10}$	−2·000	1·697	1·437	1·697	0·0436
Geometric mean (%)	0·01	49·8	27·4	49·8	—
Caecal contents					
$\log_{10}$	−0·901	1·745	−0·229	1·217	
Geometric mean (%)	0·1	55·6	0·6	16·5	—

SED, standard error of difference between any two means (for statistical treatment, see p. 294).
* For dietary treatment, see p. 293.

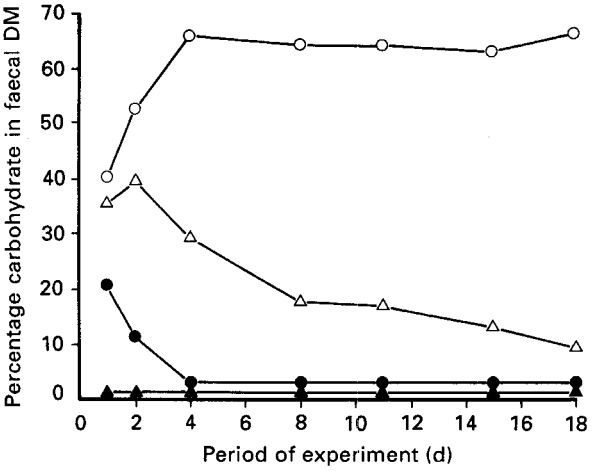

Fig. 1. Changes in faecal carbohydrate (as glucose) excretion expressed as a percentage of faecal dry matter (DM) for rats fed on 12 g basal semi-synthetic (SS) diet/d with sucrose as the only carbohydrate source (▲–▲), or 12 g SS diet plus 1·2 g resistant maize starch (●–●), resistant pea (*Pisum sativum*) starch (△–△) or cellulose (○–○), for 17/18 d. Analyses were performed on faeces collected and pooled daily for ten rats per group.

periods, the caecal contents from the cellulose-fed animals contained the highest ($P < 0{\cdot}001$) proportion of glucan (measured as glucose), values being approximately 57% dry matter, whereas the values for rats fed on the basal diet were < 1% (Table 4). Rats on the RPS treatment had the second highest values. The concentrations of glucan in the ileal and caecal contents from the RPS-fed rats were significantly greater ($P < 0{\cdot}01$) than those for the RCS treatment at both 8/9 and 17/18 d. Differences in total glucan (the product of weight of dry contents and glucan content of dry matter) in the ileum and caecum followed exactly the same trends as those observed for glucan concentration. The glucan content of the dry faeces from the groups maintained on the experimental diets for 17/18 d is shown in Fig. 1. After an initial adjustment period the glucan concentration in faeces from rats in the cellulose treatment stabilized at approximately 65% of the dry matter. The amount of glucan, as a percentage of dry matter, in faeces from the RCS- and RPS-fed rats was initially 20 and 40% respectively and values for both treatments declined with time. By day 18 the glucan values were 2·5 and 10% for RCS and RPS treatments respectively, the RCS-fed rats having reached a minimum value by day 5 whereas the values for the RPS-fed rats continued to fall throughout the 18 d period. Only traces of glucan were found in the faeces from rats fed on the sucrose-supplemented diet (Fig. 1). Faecal carbohydrate excretion followed a similar pattern throughout the 18 d feeding period whether glucan was expressed as a percentage of dry weight or as a percentage of the carbohydrate intake, i.e. apparent digestibility (Figs 1 and 2).

DISCUSSION

It is generally assumed that the cooking of foods before eating makes the starch more available for digestion and absorption. This may occur when the food is eaten shortly after cooking, before significant retrogradation takes place or when the extent or rate of retrogradation is limited by other food components (Foster, 1965). There are, however, many commonly used cooked starchy foods which are often kept for at least a few days,

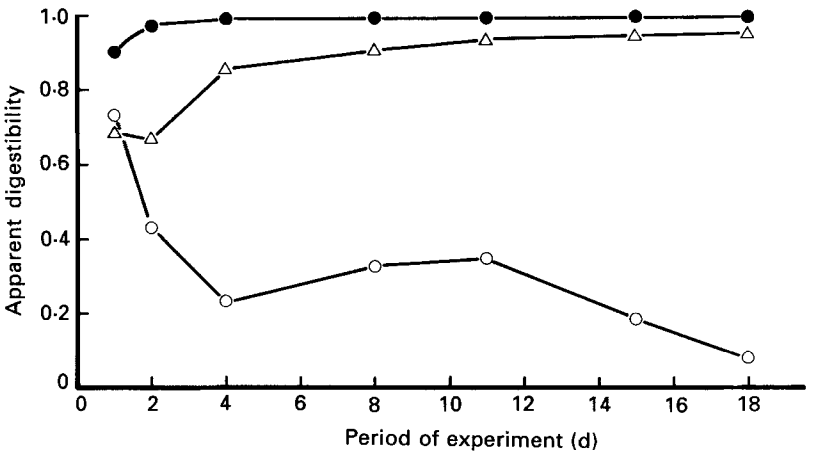

Fig. 2. Apparent digestibility (intake − excreted)/intake) of carbohydrate sources in rats fed on 12 g basal semi-synthetic diet (SS)/d with sucrose as the only source of carbohydrate plus 1·2 g resistant maize starch (●–●), resistant pea (*Pisum sativum*) starch (△–△) or cellulose (○–○)/d for the 17/18 d groups. Analyses were performed on faeces collected and pooled daily for ten rats per group.

and sometimes much longer before being eaten (for example, baked foods such as bread, and canned, frozen and cook–chilled foods) giving sufficient time for retrogradation of starch to occur (Swinkels, 1985). The starch in such foods may behave in a manner similar to the starch gels presently investigated; that is, a variable amount may become resistant to exhaustive α-amylase-catalysed hydrolysis in vitro and to mammalian enzymes in vivo.

Feeding studies have already been conducted using whole foods (Englyst & Cummings, 1985) or starches (Berry, 1986) still containing a large proportion of carbohydrate susceptible to α-amylase. These studies have not discriminated between available starch, starch-resisting mammalian digestive enzymes and starch which escapes digestion for other reasons such as hindrance by the food matrix. In the present study the isolated RS fractions were the only source of starch present in the diets fed to rats.

The increase in dry weight of digesta from the ileum, caecum and that eliminated in the faeces gave the first indication that a proportion of both the RS escaped digestion and fermentation (Tables 2 and 3).

The occurrence of carbohydrate in the faeces of rats fed on cellulose, RPS and RCS (Fig. 1) also illustrated the extent to which these complex carbohydrates escaped digestion and fermentation in vivo. Throughout the whole feeding period RCS was more extensively utilized than RPS, which in turn was utilized more than cellulose. The apparent digestibility of these complex carbohydrates (Fig. 2) during the first few days of the feeding study is consistent with the accumulation of these carbohydrates in the alimentary tract, rather than the rapid elimination in the faeces, together with some adaptation towards increased utilization of the RS. The adaptation appeared to continue slowly for some time with RPS, though was apparently completed by day 5 when RCS was given. Adaptation to the utilization of the RS may, in part, result from recolonization of the large bowel with micro-organisms following the 2-week period when no complex carbohydrates were given.

It has been shown that the two RS used in the present experiment are susceptible to fermentation by rat faecal microflora in vitro (Wyatt & Horn, 1988). Significant decreases ($P < 0·001$) in the pH of caecal digesta occurred in RCS- and RPS-fed rats by comparison

with sucrose-fed animals, which also indicates that these starches undergo some fermentation in vivo. The glucan contents of the dry digesta from the ileum and caecum were similar at 8/9 and 17/18 d in those rats fed on the cellulose supplement. In contrast, the glucan content of the dry caecal digesta was 29 and 23% of the dry ileal contents value at 8/9 d, and 2 and 33% at 17/18 d for RCS and RPS respectively. Thus the RS appear to be much more rapidly fermented than cellulose, with the RCS being more susceptible to fermentation than RPS. Since only traces of carbohydrate were found in the ileal and caecal digesta from the rats given basal or sucrose-supplemented diets, the larger amounts found at these sites in rats given cellulose or RS supplements must have been unabsorbed carbohydrate of dietary origin (Table 4).

At the ileal site, the quantity of carbohydrate recovered from animals fed on the RCS and RPS was approximately 50 and 96% respectively of that from the cellulose-fed rats at both 8/9 d and 17/18 d. A possible explanation for this is that the RCS was to some extent digested and absorbed in the small intestine, the RPS having a similar resistance to digestion as cellulose. The reasons for this are unknown, but may be a result of exposure of the RS to the low pH conditions present in the rat stomach or by removal, in vivo, of factors that confer resistance in RCS to α-amylase hydrolysis in vitro. Alternatively, there may be differences in the rate of transit of the RS along and out of the small intestine. However, the latter suggestion seems unlikely. Since the glucan concentrations of the dry ileal contents were similar in the 8/9 d and 17/18 d groups, there was no evidence of an adaptive increase in the capacity of the small intestine to digest, and thereby salvage carbohydrate, nor was there any increase in small intestinal length in rats fed on the complex carbohydrates such as occur in animals fed on viscous polysaccharides (Johnson *et al.* 1984; Johnson & Gee, 1986).

The apparent digestibility of the RS in the present study (Fig. 2) was generally greater than occurs with most non-starch polysaccharides from whole foods, e.g. carrots (Nyman *et al.* 1986), but similar to some soluble non-starch polysaccharides, e.g. guar gum, gum arabic (Nyman & Asp, 1982; McLean *et al.* 1983). As with non-starch polysaccharides in whole foods and as isolates, the RS increased faecal dry matter. To this extent RS and non-starch polysaccharides are similar. An important difference appears to be the extent to which they are available as carbohydrate.

In summary, in the rat, RCS appears to be partially digested and available as carbohydrate, the remainder being almost totally fermented after an initial adaptive period. In contrast RPS appears both less available and more resistant to fermentation. The present study indicates that substantial differences in utilization in vivo may exist between RS from various foods.

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