Studies on digestion and absorption in the intestines of growing pigs

7. Measurements of the flow of total carbohydrate, total reducing substances and glucose

By I. E. SAMBROOK

National Institute for Research in Dairying, Shinfield, Reading RG2 9AT, Berks.

(*Received* 18 *September* 1978 – *Accepted* 27 *March* 1979)

1. Seventeen pigs were fitted with single re-entrant cannulas in either the duodenum (posterior to the entry of the bile and pancreatic ducts), the mid-jejunum, or the terminal ileum. A further twenty-four pigs were used in a conventional digestibility trial.

2. Three diets were used: these contained barley, fine wheat offal, white fish meal, minerals and vitamins (diet BWF); starch, sucrose, maize oil, cellulose, minerals, vitamins and either groundnut meal (diet SSG) or casein (diet SSC).

3. The quantities of total carbohydrate (TC), total reducing substances (TRS) and glucose (G) passing through the re-entrant cannulas and excreted in the faeces in 24 h were measured. These were used to determine the net absorption of the carbohydrate fractions in the different regions of the intestine.

4. The small intestine was the principal site of absorption of TC, TRS and G, but there were differences between the diets in the quantities of each of these carbohydrate fractions that were absorbed in the different regions of the small intestine studied.

5. The quantities of TRS and G in solution were very low for all diets at all sites, indicating that the rate of absorption of the products of hydrolysis kept pace with their rate of formation.

Carbohydrate is the predominant nutrient of commercial pig diets and provides most of the growing pig's energy supply. An understanding of the processes by which carbohydrate is digested and absorbed, together with a fuller knowledge of requirement, would be a major step towards the possible manipulation of dietary and nutritional factors with consequent improvement in the efficiency of foodstuff utilization.

With this objective, pigs fitted with intestinal re-entrant cannulas are being increasingly used in studies on digestion and absorption. The results of such studies have been discussed by Low (1976). Previous reports from this Institute have covered the flow and pH of digesta and the flow and absorption of mineral and protein fractions of the diet. In this report, the flow and absorption of carbohydrate fractions of digesta are presented.

EXPERIMENTAL

Animals and animal management. Seventeen castrated, male pigs of approximately 30 kg initial live weight from the Institute's Large White herd, were fitted with single Ash-type re-entrant cannulas sited as follows: (a) the duodenum, approximately 0·15 m from the pylorus and posterior to both the bile and pancreatic ducts (six pigs); (b) the mid-jejunum, 2·00–2·50 m from the pylorus (five pigs); or (c) the terminal ileum, approximately 0·30 m from the ileo-caecal junction (six pigs). A further twenty-four pigs of 17–19 kg initial live weight without cannulas were used for a conventional digestibility trial.

Full details of animal housing, metabolism cage design, cannulas, surgery and digesta and faeces collection procedures have been reported by Braude *et al.* (1976).

Diets. Diets BWF, SSG and SSC (for details, see Table 1) contained respectively (g/kg): total carbohydrate (TC) 630·9, 680·2 and 680·0, total reducing substances (TRS) 584·9, 566·7 and 636·7, and glucose (G) 488·1, 478·0 and 592·5. Because initially there were frequent blockages of ileal re-entrant cannulas when diet BWF was fed, this diet was finely

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

Ingredients	Diets BWF and BWF_f*	Ingredients	Diet SSG	Diet SSC
Barley meal	712·5	Maize starch	277·0	612·7
Fine wheat offal	200·0	Sucrose	276·9	100·0
White fish meal	70·0	Maize oil	30·0	30·0
NaCl	2·7	Solka floc‡	20·0	30·0
$CaHPO_4.2H_2O$	5·6	Groundnut meal	350·0	–
$CaCO_3$	6·2	Casein	–	184·0
Vitamin mix no. 1†	2·0	Trace mineral mix§	10·0	10·0
$CuSO_4.5H_2O$	1·0	$CaHPO_4.2H_2O$	17·9	20·6
		$CaCO_3$	4·6	4·6
		Vitamin mix no. 2‖	2·0	2·0
		Choline hydrochloride	1·1	1·1
		NaCl	5·0	5·0
		L-lysine hydrochloride	2·5	–
		DL-methionine hydrochloride	3·0	–

* Diet BWF after milling through a 1 mm mesh; this diet was given to pigs with ileal re-entrant cannulas, and to some pigs in the digestibility trial.

† Supplied (/kg diet): 0·75 mg retinol, 7·50 μg cholecalciferol, 3·25 mg riboflavin, 30·00 μg cyanocobalamin, 15·75 mg nicotinic acid, 13·00 mg pantothenic acid, 3·25 mg pyridoxine, 200·00 mg choline chloride, 2·00 mg DL-α-tocopheryl acetate.

‡ Brown and Co., Berlin, New Hampshire, USA.

§ Supplied (/kg diet): 4·47 g K_2CO_3, 1·73 g $MgCO_3.H_2O$, 0·33 g $FeSO_4.7H_2O$, 60 mg $MnSO_4.H_2O$, 0·10 g $ZnCO_3$, 8·00 mg NaF, 17·50 mg $CuSO_4.5H_2O$, 6·00 mg $CoCl_2$.

‖ Supplied (/kg diet): as vitamin mix no. 1 (omitting choline chloride) and in addition 2·00 mg thiamin, 50·00 μg biotin, 0·50 mg pteroylmonoglutamic acid, 20·00 mg *p*-aminobenzoic acid, 194·00 mg *myo*-inositol, 30·00 mg ascorbic acid, 2·00 mg menaphthone.

milled through a 1 mm mesh before being fed to pigs with ileal re-entrant cannulas in subsequent collections. The finely-milled diet (designated BWF_f) was also fed to six of the pigs in the digestibility trial.

The experimental diet was mixed with water (1:2·5, w:v) immediately before feeding and offered twice daily, at 09.00 and 15.00 hours. The pigs were weighed weekly and fed according to a scale based on their live weight (Barber *et al.* 1972). Pigs of 20 kg live weight received 1·05 kg diet/d and the amount increased linearly so that at 60 kg live weight the pigs received 2·40 kg diet/d.

TC determination. This was by difference according to the equation:

$$TC = \text{dry matter (DM)} - ((\text{nitrogen} \times 6{\cdot}25) + \text{ash} + \text{total lipid})$$

TRS and G determinations. Approximately 4 g homogenized, whole digesta from a pooled sample representative of each 24 h collection, was hydrolysed in 10 ml sulphuric acid (final concentration 0·5 M) for 4 h at 105°. This procedure releases the component monosaccharides, including 95% recovery of xylose in cereal hemicelluloses, with very little (< 3%) release of cellulose-glucose (McAllan & Smith, 1974). Thus the terms TRS and G are exclusive of any contribution from cellulose to these two carbohydrate fractions.

The hydrolysate was filtered and made up to constant volume with distilled water, before 1 ml samples were deproteinized using equimolar solutions of zinc sulphate and barium hydroxide. The precipitate was removed by centrifugation for 15 min at 1500 ***g*** and the supernatant solution was analysed for TRS and G.

TRS content was measured by a modification of the methods of Brown (1961) and Bittner & McCleary (1963), which involved reaction with a cupric-neocuproine chelate in an alkaline medium to produce a highly-coloured cuprous-neocuproine complex. G content was measured by an automated glucose oxidase-peroxidase method (Biochemica Test combination TBAP 15756; Boehringer Corporation (London) Ltd).

The quantity of free TRS (FTRS) and glucose (FG) was measured in the supernatant fraction of the digesta obtained by centrifuging a portion of each 24 h pooled sample for 15 min at 1500 *g*.

Presentation of results. The quantities of TC, TRS and G are expressed as the ratio, weight collected in 24 h: weight ingested in diet and water in 24 h (output: intake; O:I), to indicate the net results of movements across the gut wall in each region of the gut studied.

To aid interpretation of the results, the daily intake and the output at each site for a pig of 40 kg live weight (the mean weight of pigs in these studies) receiving 1·70 kg diet and 4·25 l water/d, have been calculated for each diet.

Statistical treatment of results. An analysis of variance was calculated for the mean 24 h O:I values for each cannulated pig on each diet. The mean values for the four faeces collection periods for each non-cannulated pig on each diet were similarly treated. The standard error of the difference between the means was not the same for each pair of cannulation sites or for each pair of diets, since different numbers of animals completed collections for the various site-diet combinations. The least and greatest values for standard error of the difference are given in the results tables.

The statistical methods used in these studies were described in more detail by Braude *et al.* (1976).

RESULTS

The aim of these studies was that for each cannula site, digesta would be collected from six pigs given each of the three diets in successive 14–21 d periods. Not every animal completed the planned collections for a number of reasons: some were associated with the rapid growth of the animals such as loss of cannulas or leakage around the cannulas, while others were due to palatability and scouring problems associated with diet SSG. Animals were not used for collection unless they were eating normally. The numbers of animals completing collections are shown in the results tables.

Only two pigs completed collections for diet SSG at the duodenum; moreover, the mean TRS and G values for the individual pigs differed greatly. Thus the mean O:I value for diet SSG at the duodenum must be viewed with caution. For diet SSG at the ileum, TRS and G were measured in digesta from only one pig, and the O:I value was excluded from the analysis of variance but is commented upon in the discussion.

TC. The mean 24 h O:I values for TC in digesta and faeces are presented in Table 2.

The 24 h O:I value was similar for all three diets at the duodenum and also at the jejunum, but at the ileum there were significant ($P < 0·05$) differences between the three diets. In the case of faeces, there was no difference between the normal and finely-milled forms of diet BWF in the over-all net absorption of TC, but there were significant ($P < 0·001$) differences between the other diets. Over-all net absorption was greatest for diet SSC (0·98) and least for diet BWF (0·82).

Net absorption of TC anterior to the duodenal cannula for all three diets amounted to 0·10–0·18 of intake. For all diets there was significant net absorption of TC between the duodenum and jejunum ($P < 0·05$) and between the jejunum and the terminal ileum ($P < 0·001$). Further small but significant ($P < 0·05$) apparent absorption of TC occurred in the large intestine for all three diets. The absolute amounts of TC passing each cannula site, as calculated for a 40 kg pig, are shown in Table 7.

The mean concentrations of TC in the digesta and faeces are shown in Table 8. Intake concentration of TC had been reduced to a similar extent for each diet by the time the duodenum was reached, by the absorption of material from the stomach and the addition

Table 2. *Mean 24 h output: intake for total carbohydrate in pigs given different diets (a) for digesta collected from pigs with intestinal re-entrant cannulas at one of three sites, (b) for faeces collected from pigs without cannulas*

(No. of pigs completing collections given in parentheses)

(a) Cannulated pigs

Site of re-entrant cannula*	Diet BWF†	Diet SSG	Diet SSC
Duodenum	0·896 (6)	0·825 (2)	0·874 (6)
Jejunum	0·605 (5)	0·613 (4)	0·684 (4)
Ileum	0·254 (5)	0·147 (2)	0·059 (6)

SE of difference between site means: least value 0·0482, greatest value 0·0836.
SE of difference between diet means: least value 0·0198, greatest value 0·0766.

(b) Pigs without cannulas (six pigs/diet)

	Diet BWF	Diet BWF_t	Diet SSG	Diet SSC
Faeces	0·177	0·173	0·103	0·025

SE of difference between diet means: 0·0039.
SE of difference between means for faeces and ileum: least value 0·0110, greatest value 0·0156.

* For details of sites, see p. 267.

† Diet BWF was finely milled (diet BWF_t) when fed to pigs with ileal cannulas; for details of diets, see p. 267 and Table 1.

Table 3. *Mean 24 h output: intake for total reducing substances in pigs given different diets (a) for digesta collected from pigs with intestinal re-entrant cannulas at one of three sites, (b) for faeces collected from pigs without cannulas*

(No. of pigs completing collections given in parentheses)

(a) Cannulated pigs

Site of re-entrant cannula*	Diet BWF†	Diet SSG	Diet SSC
Duodenum	0·815 (6)	0·544 (2)	0·784 (6)
Jejunum	0·527 (5)	0·360 (5)	0·456 (4)
Ileum	0·148 (5)	0·040 (1)‡	0·030 (5)

SE of difference between site means (except ileum for diet SSG): least value 0·0642, greatest value 0·0887.
SE of difference between diet means (except diet SSG at ileum): least value 0·0065, greatest value 0·1016.

(b) Pigs without cannulas (six pigs/diet)

	Diet BWF	Diet BWF_t	Diet SSG	Diet SSC
Faeces	0·078	0·076	0·021	0·002

SE of difference between diet means: 0·0031.
SE of difference between means for faeces and ileum (except diet SSG): 0·0081.

* For details of sites, see p. 267.

† Diet BWF was finely milled (diet BWF_t) when fed to pigs with ileal cannulas; for details of diets, see p. 267 and Table 1.

‡ Mean value for four collections from single pig. This site–diet combination was excluded from the analysis of variance.

of endogenous secretions to the digesta. Concentrations remained relatively similar in the small intestine but there was an increase during passage through the large intestine for each diet.

TRS. The mean 24 h O:I values for TRS in digesta and faeces are presented in Table 3. The quantity of TRS at the duodenum was considerably less than intake for all three diets. For diets BWF and SSC there was significant ($P < 0·001$) net absorption of TRS between the duodenum and jejunum, and between the jejunum and ileum. Further significant

Table 4. *Mean 24 h output:intake for glucose in pigs given different diets (a) for digesta collected from pigs with intestinal re-entrant cannulas at one of three sites, (b) for faeces collected from pigs without cannulas*

(No. of pigs completing collections given in parentheses)

(a) Cannulated pigs

Site of re-entrant cannula*	Diet BWF†	Diet SSG	Diet SSC
Duodenum	0·799 (6)	0·502 (2)	0·807 (6)
Jejunum	0·488 (5)	0·378 (5)	0·466 (4)
Ileum	0·039 (5)	0·010 (1)‡	0·024 (5)

SE of difference between site means (except ileum for diet SSG): least value 0·0715, greatest value 0·0989.
SE of difference between diet means (except diet SSG at ileum): least value 0·0041, greatest value 0·1299.

(b) Pigs without cannulas (six pigs/diet)

	Diet BWF	Diet BWF_f	Diet SSG	Diet SSC
Faeces	0·006	0·005	0·004	0·001

SE of difference between diet means: 0·0008.
SE of difference between means for faeces and ileum (except diet SSG): 0·0058.

* For details of diets, see p. 267.

† Diet BWF was finely milled (diet BWF_f) when fed to pigs with ileal cannulas; for details of diets, see p. 267 and Table 1.

‡ Mean value for four collections from single pig. This site–diet combination was excluded from the analysis of variance.

($P < 0·01$) apparent absorption of TRS occurred in the large intestine for these two diets. For diet SSG, there was evidence of considerable net absorption of TRS between each of the small intestinal sites, but only a small apparent absorption in the large intestine.

There was significantly more TRS for diet BWF than for diet SSG at the duodenum ($P < 0·05$) and at the jejunum ($P < 0·01$). At both sites, diet SSC was intermediate between, but not significantly different from, the other two diets. At the ileum the O:I value for diet BWF was significantly ($P < 0·001$) higher than for diet SSC, while the value for the single pig representing diet SSG was similar to the mean value for diet SSC. There was no difference between diets BWF and BWF_f in the over-all net absorption of TRS, but all other pairs of diets were significantly ($P < 0·001$) different. Over-all net absorption was greatest for diet SSC (1·00) and least for diet BWF (0·92). The absolute amounts of TRS ingested and passing each cannulation site in 24 h calculated for a 40 kg pig are shown in Table 7.

The mean concentrations of TRS in the digesta and faeces are shown in Table 8. Intake concentration had been considerably reduced by the time the duodenal cannula had been reached, and there was generally a decrease in concentration during passage through the small intestine for all three diets. For diets BWF and SSG the concentration rose markedly during passage through the large intestine.

G. The mean 24 h O:I values for G in digesta and faeces are shown in Table 4.

Considerable net absorption of G occurred anterior to the duodenal cannula for all three diets, although the result for diet SSG must again be regarded with some caution. For diets BWF and SSC there was significant ($P < 0·001$) net absorption of G from each of the other two sections of the small intestine. Considerable net absorption of G from diet SSG was also found. Further significant ($P < 0·01$) apparent absorption of G occurred in the large intestine for diets BWF and SSC, and a small apparent absorption was indicated for diet SSG.

There were no significant differences between the diets in mean O:I value at either the duodenum or jejunum, but the mean value for diet SSG was somewhat lower than that for

Table 5. *Mean 24 h output: intake for total reducing substances in pigs given different diets, for the supernatant fraction of digesta collected from pigs with intestinal re-entrant cannulas at one of three sites*

(No. of pigs completing collections given in parentheses)

Site of re-entrant cannula*	Diet BWF†	Diet SSG	Diet SSC
Duodenum	0·022 (6)	0·012 (2)	0·011 (6)
Jejunum	0·032 (3)	0·030 (3)	0·025 (3)
Ileum	0·004 (4)	0·000 (1)‡	0·002 (4)

SE of difference between site means (except ileum for diet SSG): least value 0·0023, greatest value 0·0032.
SE of difference between diet means (except diet SSG at ileum): least value 0·0004, greatest value 0·0071.

* For details of sites, see p. 267.

† Diet BWF was finely milled (diet BWF_f) when fed to pigs with ileal cannulas; for details of diets, see p. 267 and Table 1.

‡ Mean value for two collections from single pig. This site–diet combination was excluded from the analysis of variance.

Table 6. *Mean 24 h output: intake for glucose in pigs given different diets, for the supernatant fraction of digesta collected from pigs with intestinal re-entrant cannulas at one of three sites*

(No. of pigs completing collections given in parentheses)

Site of re-entrant cannula*	Diet BWF†	Diet SSG	Diet SSC
Duodenum	0·010 (6)	0·005 (2)	0·005 (6)
Jejunum	0·024 (3)	0·018 (3)	0·015 (3)
Ileum	0·004 (4)	0·000 (1)‡	0·002 (4)

SE of difference between site means (except ileum for diet SSG): least value 0·0017, greatest value 0·0024.
SE of difference between diet means (except diet SSG at ileum): least value 0·0006, greatest value 0·0032.

* For details of sites, see p. 267.

† Diet BWF was finely milled (diet BWF_f) when fed to pigs with ileal cannulas; for details of diets, see p. 267 and Table 1.

‡ Mean value for two collections from single pig. This site–diet combination was excluded from the analysis of variance.

the other two diets at both sites. At the ileum, diet BWF had a significantly ($P < 0·05$) higher O:I value than diet SSC, while the mean value for the single pig representing diet SSG was lower than both of the other diets. There was no difference between diets BWF and BWF_f, or diets BWF_f and SSG in over-all net absorption of G, but all other pairs of diets were significantly ($P < 0·05$) different. Over-all net absorption of G was $> 0·99$ for all diets. The amounts of G ingested and passing each intestinal site in 24 h for a 40 kg pig are shown in Table 7.

The mean concentrations of G in digesta and faeces are shown in Table 8. As for the other carbohydrate fractions, the concentration of G in duodenal digesta was considerably lower than the intake concentration. The concentration continued to decrease markedly during passage through the small intestine. In the large intestine there was a further reduction in the concentration of G in digesta from diets BWF and SSC, while for diet SSG the faecal concentration was twice that in the ileum.

FTRS and FG in the supernatant fraction. The mean 24 h O:I values for FTRS and FG in the supernatant fraction of the digesta are shown in Tables 5 and 6 respectively.

For all diets at all sites the proportions of dietary TRS and G present in the supernatant fraction were very low. At the duodenum, the O:I values for diets SSG and SSC were similar and both were significantly ($P < 0·01$) lower than that for diet BWF. At the jejunum

Table 7. *Daily intake, throughput at three sites in the small intestine and faecal output (g) of total carbohydrate (TC), total reducing substances (TRS) and glucose (G), calculated for a pig of 40 kg live weight receiving 1·7 kg meal and 4·25 l water/d*

(Amounts of TRS and G in supernatant fraction are given in parentheses)

	Diet BWF or BWF$_t$	Diet SSG	Diet SSC
TC			
Intake	1072	1156	1156
Duodenum	965	948	1006
Jejunum	643	705	786
Ileum	268*	173	69
Faeces	193 182*	116	23
TRS			
Intake	994	963	1082
Duodenum	810 (22)	524 (12)	848 (12)
Jejunum	524 (32)	347 (29)	493 (27)
Ileum	147* (4)*	39 (0)	32 (2)
Faeces	78 76*	20	2
G			
Intake	830	813	1007
Duodenum	663 (8)	408 (4)	813 (5)
Jejunum	405 (20)	307 (15)	469 (15)
Ileum	32* (3)*	8 (0)	24 (2)
Faeces	5 4*	3	1

* Pigs given diet BWF$_t$.

Table 8. *Mean concentrations of total carbohydrate (TC), total reducing substances (TRS) and glucose (G) in digesta and faeces (mg/g in 24 h in pigs given different diets)*

(Mean values with their standard errors; no. of pigs given in parentheses)

	Diet BWF or BWF$_t$		Diet SSG		Diet SSC	
	Mean	SE	Mean	SE	Mean	SE
TC						
Intake	180·2		194·3		194·3	
Duodenum	54·5	1·91 (6)	67·9	2·90 (2)	77·1	5·03 (6)
Jejunum	44·2	1·57 (5)	52·0	3·07 (4)	87·7	11·45 (4)
Ileum	66·8	2·25*(5)	43·7	3·90 (2)	58·3	2·54 (6)
Faeces	166·0 200·9	3·39 (6) 8·04*(6)	206·3	7·29 (6)	304·4	15·90 (6)
TRS						
Intake	167·1		161·8		181·8	
Duodenum	46·0	2·36 (6)	36·8	7·20 (2)	65·5	6·47 (6)
Jejunum	33·1	1·39 (5)	26·9	2·02 (5)	54·8	5·42 (4)
Ileum	35·3	2·00*(5)	11·3	† (1)	19·5	3·86 (5)
Faeces	67·2 81·0	2·87 (6) 3·74*(6)	33·7	0·86 (6)	22·1	1·93 (6)
G						
Intake	139·5		136·6		169·2	
Duodenum	37·8	2·11 (6)	32·2	6·80 (2)	62·1	6·17 (6)
Jejunum	26·2	0·89 (5)	20·7	2·15 (5)	51·5	4·80 (4)
Ileum	7·8	1·06*(5)	2·4	† (1)	14·1	3·93 (5)
Faeces	4·6 3·9	0·93 (6) 0·55*(6)	5·2	1·02 (6)	9·0	0·72 (6)

* Pigs given diet BWF$_t$.

† Mean value for four collections from single pig.

Table 9. *Mean concentrations of total reducing substances (TRS) and glucose (G) in supernatant fraction of digesta (mg/ml) in 24 h in pigs given different diets*

(Mean values with their standard errors; no. of pigs given in parentheses)

	Diet BWF or BWF_t		Diet SSG		Diet SSC	
	Mean	SE	Mean	SE	Mean	SE
TRS						
Duodenum	1·80	0·095 (6)	0·87	0·046 (2)	1·11	0·065 (6)
Jejunum	2·53	0·086 (3)	2·42	0·275 (3)	3·10	0·172 (3)
Ileum	1·46	0·411* (4)	0·20	† (1)	2·84	0·923 (4)
G						
Duodenum	0·62	0·061 (6)	0·29	0·104 (2)	0·46	0·051 (6)
Jejunum	1·62	0·115 (3)	1·01	0·093 (3)	1·70	0·100 (3)
Ileum	1·09	0·460* (4)	0·04	† (1)	2·51	0·895 (4)

* Pigs given diet BWF_t.
† Mean value for two collections from single pig.

there were no significant differences between the diets, but for each diet the O:I value at this site was significantly ($P < 0·01$) higher than at the duodenum. The O:I value for diet BWF at the ileum was significantly ($P < 0·05$) higher than that for diet SSC, in the case of FTRS but not in that of FG. For diets BWF and SSC the O:I values for FTRS and FG at the ileum were significantly ($P < 0·001$) lower than at the jejunum. In the case of the single pig representing diet SSG at the ileum, both FTRS and FG contents of the supernatant fraction were exceedingly low. The amounts of FTRS and FG calculated for a 40 kg pig are shown in Table 7.

The mean concentrations of FTRS and FG in the supernatant fraction of the digesta are shown in Table 9.

These values were low for all diets at all sites, but at the duodenum those for diet BWF were highest, while at the other two sites those for diet SSC were highest. The FTRS and FG concentrations for diet SSG were the lowest at all three sites. Although the concentrations of both FTRS and FG were higher at the jejunum than at the duodenum for all diets, they were generally lower again by the time the ileum was reached.

DISCUSSION

TC, TRS and G. TC comprised 720, 740 and 760 g/kg DM in diets BWF, SSG and SSC respectively, so it was to be expected that the net absorption of the former should follow closely that of the latter. Thus, the over-all net absorption of TC was 0·82, 0·90 and 0·98 for diets BWF, SSG and SSC respectively compared with corresponding values of 0·78, 0·85 and 0·96 for DM reported by Low *et al.* (1978). Low *et al.* (1978) further reported that 0·91, 0·94 and 0·96 of the over-all DM net absorption from diets BWF, SSG and SSC respectively, occurred in the small intestine; this compares with values of 0·90, 0·94 and 0·96 for TC for the same diets in the present study. For TRS and G the net absorption in the small intestine amounted to 0·92–0·98 and 0·97–0·99 respectively of the over-all net absorption of each.

The carbohydrate from the semi-purified diets SSG and SSC was more highly absorbed than that from diet BWF particularly when measured at the terminal ileum; in the large intestine, however, there was more apparent absorption from diet BWF than from the other two diets. Low *et al.* (1978) reported that finely grinding diet BWF did not affect the over-all net absorption of DM from this diet, and this proved also to be the situation for each of the carbohydrate fractions studied.

There were minor differences between the diets in the quantities of the different carbohydrates absorbed in the different regions of the small intestine, but apart from the TRS and G in diet SSG, most of the net absorption of carbohydrate occurred in the long section of small intestine between the mid-jejunum and terminal ileum. The high level of TRS and G net absorption from diet SSG anterior to the duodenal cannula may be misleading (see p. 269). The anterior small intestine was relatively more important than the mid- and distal portions for carbohydrate absorption since 0·33–0·49 of over-all TC net absorption and > 0·50 of over-all TRS and G net absorption occurred in the 15–20% of small intestine anterior to the mid-jejunum.

The results of this study are in general agreement with those of a number of workers. Kvasnitskii (1951) found that in growing pigs, 0·19 of the starch from a diet containing cooked potatoes and cereals was absorbed from the stomach; for the G from diet BWF in the present study, most of which would have been derived from the cereal starch, the net absorption from the stomach and first 150 mm of the duodenum was 0·20. The values for net absorption of starch and TC from the whole of the small intestine of 0·85 and 0·84 respectively, found by Kvasnitskii (1951) were somewhat different from the values of 0·96 and 0·75 for net absorption of G and TC from diet BWF reported here. These differences may have been due to the differences in diet composition. The values for apparent absorption of starch and TC from the large intestine reported by Kvasnitskii (1951) were 0·09 and 0·11 respectively, compared with 0·03 and 0·08 for G and TC from diet BWF in this study.

Cunningham *et al.* (1963) found that net absorption of TC from a cereal diet anterior to the ileum was 0·73, compared to 0·75 for diet BWF in this study: for a test meal containing maize starch and sucrose in similar proportions to diet SSC, the net absorption of TC was 0·99 compared to 0·94 for the TC from diet SSC itself. The same authors (Cunningham *et al.* 1963) found that G in a small test meal was 0·99 absorbed anterior to the ileum, compared to 0·98 for diet SSC in the present study.

Using digesta collected from slaughtered pigs, Horszczaruk (1971 *b*) found net absorption of TC from a cereal diet was 0·36 for the stomach and first 5·0 m of the small intestine, and 0·71 for the whole of the small intestine. Corresponding values for diet BWF are 0·40 for the stomach and first 2·5 m of the small intestine, and 0·75 for the entire small intestine. Using pigs with simple cannulas in the large intestine Horszczaruk (1971 *a*) found over-all net absorption of TC from a cereal diet to be 0·90, slightly higher than in the present study. These differences may again be accounted for by the differences in diets; those used by Horszczaruk (1971 *a*, *b*) contained potato flakes and wheat starch.

Holmes *et al.* (1973) found net absorption of starch from a maize diet to be 0·94–0·98 at the terminal ileum and 1·00 over-all; these correspond very closely to the 0·98–0·99 net absorption at the terminal ileum and 1·00 over-all for G absorption from the maize starch in diets SSG and SSC.

The net absorption of starch cranial to the ileal cannula reported by Keys & DeBarthe (1974) was 0·79 for a barley diet compared to 0·96 for G from diet BWF in the present study. For a maize diet the value was 0·93, much nearer to the value of 0·98 for net absorption of G from diet SSC which contained maize starch. Over-all values for starch net absorption of 0·94 and 0·99 for the barley and maize diets respectively, compared well with values of 0·99 and 1·00 for over-all net absorption of G from diets BWF and SSC.

FTRS and FG. The carbohydrate content of the digesta supernatant fraction is a dynamic component and gives little indication of absorption from the digesta as a whole; it can, however, indicate whether digestion or absorption has predominated in the preceeding section of the intestine.

In spite of the fact that starch degradation can occur extremely rapidly (Holmes *et al.* 1973; Keys & DeBarthe, 1974) and the large-scale absorption of water from the small

Table 10. *Glucose as a proportion of total reducing substances in diet and water ingested, in digesta at three sites in the small intestine and in faeces, on a 24 h basis*

(Mean values with their standard errors; no. of pigs given in parentheses)

	Diet BWF or BWF_t		Diet SSG		Diet SSC	
	Mean	SE	Mean	SE	Mean	SE
Intake	0·84		0·84		0·93	
Duodenum	0·82	0·018 (6)	0·88	0·022 (2)	0·95	0·012 (6)
Jejunum	0·80	0·016 (5)	0·78	0·043 (5)	0·94	0·018 (4)
Ileum	0·21	0·012*(5)	0·21	† (1)	0·68	0·070 (6)
Faeces	0·07 0·06	0·008 (6) 0·012*(6)	0·16	0·028 (6)	0·43	0·026 (6)

* Pigs given diet BWF_t.
† Mean value for four collections from one pig.

Table 11. *Glucose as a proportion of total reducing substances in the supernatant fraction of digesta at three sites in the small intestine*

(Mean values with their standard errors; no. of pigs given in parentheses)

	Diet BWF or BWF_t		Diet SSG		Diet SSC	
	Mean	SE	Mean	SE	Mean	SE
Duodenum	0·36	0·014 (6)	0·33	0·095 (2)	0·41	0·025 (6)
Jejunum	0·64	0·023 (3)	0·44	0·047 (3)	0·55	0·013 (3)
Ileum	0·75	0·061*(3)	0·10	† (1)	0·90	0·023 (4)

* Pigs given diet BWF_t.
† Mean value for two collections from one pig.

intestine (Low *et al.* 1978), the concentrations of TRS and G in solution did not increase greatly. This indicates that the hydrolytic capacity of the mucosal disaccharidases and the absorptive capacity of the intestinal mucosa of the pig are sufficient to cope with the rapid rate of starch hydrolysis.

It is interesting to note that at the duodenum, diet BWF (from which TC, TRS and G were less well absorbed over all than from diets SSG and SSC) had a higher total content, and a higher concentration of FTRS and FG than the other two diets: this occurred in spite of the higher level of endogenous secretion for diet BWF than for the other diets (Low *et al.* 1978). This situation could arise from a more rapid initial rate of hydrolysis of the carbohydrates in the cereal diet, or less rapid absorption of the products.

G as a proportion of TRS. G comprised 840–930 g/kg of TRS intake; the remaining monosaccharides contributing to the TRS fraction were mannose, ribose, arabinose, galactose, xylose and fructose. The proportion of G in the TRS for whole digesta remained relatively constant in the duodenum and mid-jejunum, but decreased markedly for each diet between the mid-jejunum and terminal ileum (Table 10), indicating that G was absorbed in preference to other reducing substances in this region. This apparent preferential absorption of G continued in the large intestine for all diets. The absorption of G in preference to other reducing substances was most marked for the cereal diet BWF where G comprised the lowest proportion of TRS intake, and least in the case of diet SSC where it comprised the highest.

In contrast to the situation in whole digesta, the proportion of G in the TRS of the supernatant fraction generally increased with passage along the intestine (Table 11); the

Table 12. *Non-glucose content of total reducing substances (g/24 h) in (a) whole digesta (b) supernatant fraction of digesta, from three intestinal sites calculated for a pig of 40 kg live weight receiving 1·7 kg meal and 4·25 l water/d*

	Diet BWF or BWF_t	Diet SSG	Diet SSC
(*a*) Whole digesta			
Duodenum	147	116	35
Jejunum	119	40	24
Ileum	115*	31	8
(*b*) Supernatant fraction			
Duodenum	14	8	7
Jejunum	12	14	12
Ileum	1*	0	0

* Pigs given diet BWF_t.

exception to this was the single pig representing diet SSG at the ileum. This situation is explained by considering the non-G fraction of the TRS in both the whole digesta and the supernatant fraction. This has been calculated in Table 12 by subtracting the value for 24 h flow of G from 24 h flow of TRS (shown in Table 7) for each diet at each site. The non-G TRS in whole digesta was absorbed to a much lesser extent than G itself with passage along the small intestine, hence the decreasing G:TRS value. In the supernatant fraction, however, the non-G TRS decreased almost to zero by the terminal ileum, so G comprised a higher proportion of soluble TRS at this site than at the duodenum.

The rise in the non-G content of the TRS in the supernatant fraction for diets SSG and SSC at the jejunum (Table 12) may be due to some of the fructose released from dietary sucrose not being absorbed immediately, but diffusing back into the lumen (Gray & Ingelfinger, 1966; Gray & Santiago, 1966). By the ileum, however, this material had been completely absorbed.

The author wishes to thank Dr R. Braude for his helpful advice and critical appraisal of the script, Dr H. L. Buttle for surgical preparation of the animals, Dr A. G. Low, Dr I. G. Partridge and Mr R. J. Pittman for assistance with digesta collections and Mrs Rosemary Fulford for advice on statistical evaluation of the results.

REFERENCES

Barber, R. S., Braude, R., Mitchell, K. G. & Pittman, R. J. (1972). *Anim. Prod.* **14**, 199.
Bittner, D. & McCleary, M. (1963). *Am. J. clin. Path.* **40**, 423.
Braude, R., Fulford, R. J. & Low, A. G. (1976). *Br. J. Nutr.* **36**, 497.
Brown, M. E. (1961). *Diabetes* **10**, 60.
Cunningham, H. M., Friend, D. W. & Nicholson, J. W. G. (1963). *Can. J. Anim. Sci.* **43**, 215.
Gray, G. M. & Ingelfinger, F. J. (1966). *J. clin. Invest.* **45**, 388.
Gray, G. M. & Santiago, N. A. (1966). *Gastroenterology* **51**, 489.
Holmes, J. H. G., Bayley, H. S. & Horney, F. D. (1973). *Br. J. Nutr.* **30**, 401.
Horszczaruk, F. (1971*a*). *Biul. Inst. Genet. Hodow. Zwierz. pol. Akad. Nauk* no. 21 p. 101.
Horszczaruk, F. (1971*b*). *Biul. Inst. Genet. Hodow. Zwierz. pol. Akad. Nauk* no. 21 p. 117.
Keys, J. E. & DeBarthe, J. V. (1974). *J. Anim. Sci.* **39**, 57.
Kvasnitskii, A. V. (1951). *Voprosy Fiziologii Pischevarenija u Svinei*, Moscow: Sel'Khozgiz (translated by D. E. Kidder).
Low, A. G. (1976). *Proc. Nutr. Soc.* **35**, 57.
Low, A. G., Partridge, I. G. & Sambrook, I. E. (1978). *Br. J. Nutr.* **39**, 515.
McAllan, A. B. & Smith, R. H. (1974). *Br. J. Nutr.* **31**, 77.

Printed in Great Britain