# Studies on digestion and absorption in the intestines of growing pigs

## 3. Net movements of mineral nutrients in the digestive tract

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1. Pigs growing from 20 to 60 kg live weight were given diets based on barley, weatings and fish meal, or starch, sucrose and groundnut meal or starch, sucrose and casein. Seventeen pigs were fitted with single re-entrant cannulas in the duodenum (posterior to entry of bile and pancreatic ducts), jejunum or terminal ileum and twenty-four non-cannulated pigs were used in a conventional digestibility trial.

2. The amounts of calcium, phosphorus, magnesium, sodium and potassium passing through the re-entrant cannulas and amounts excreted in the faeces were measured. These values were used to calculate the direction and extent of net movements of the five elements through the walls of the four parts of the digestive tract anterior to the collection sites.

3. The small intestine was the principal site of Ca and P absorption but there were differences between the diets in the relative importance of the regions anterior and posterior to the mid-jejunum.

4. Secretion of small amounts of Mg occurred in the anterior small intestine; the ileum and large intestine were the principal sites of net absorption.

5. There was a large net secretion of Na anterior to the duodenal cannulas and further secretion into the anterior small intestine with each diet. There were marked differences between diets in the amounts secreted but the ileal Na concentration was the same in each instance. Absorption occurred in the ileum and large intestine.

6. Secretion of small amounts of K was evident anterior to the duodenal cannulas and net absorption occurred in both parts of the small intestine with each diet.

Little is known of the direction and extent of movement of mineral nutrients across the wall of intermediate sections of the digestive tract of the pig. Moore & Tyler (1955*a*, *b*) studied the absorption and secretion of calcium and phosphorus by analysis of digesta removed from the digestive tract of slaughtered pigs. The absorption of electrolytes has been studied in isolated segments of pig intestine in vivo and in vitro (Nelson, 1968; Butler, Gall, Kelly & Hamilton, 1974; Henriques de Jesus & Smith, 1974*a*, *b*). These techniques do not necessarily indicate the situation prevailing in the live animal under normal dietary conditions. Although there have been a number of studies on pigs with intestinal cannulas (for review, see Low, 1976) with one exception, Savic & Zebrowska (1972), mineral nutrients have been neglected. An understanding of the intestinal absorption and secretion of minerals is an essential prerequisite to understanding their metabolism, particularly in the instance of elements such as Ca for which there is evidence of homoeostatic mechanisms operating at the level of intestinal absorption (for review, see Cramer, 1974). Furthermore, there is a considerable body of evidence indicating the interdependence of mineral elements and other nutrients in the processes of their digestion and absorption. Studies of the intestinal passage and absorption of minerals are therefore an important aspect of investigations into digestive processes. This paper describes a study of the amounts of Ca, P, magnesium, sodium and potassium which passed through the duodenum, mid-jejunum and terminal ileum and which were excreted in the faeces of growing pigs receiving three diverse diets.

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 HCl | 1·1 | 1·1 |
| | | NaCl | 5·0 | 5·0 |
| | | L-lysine HCl | 2·5 | — |
| | | DL-methionine HCl | 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, 7·5 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.

‡ Solka Floc; Brown 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, 195·00 mg *myo*-inositol, 30·00 mg ascorbic acid, 2·00 mg menaphthone.

## EXPERIMENTAL

*Pigs and their management.* Seventeen Large White castrated male pigs were fitted with single re-entrant cannulas at approximately 30 kg live weight; six in the duodenum 0·15 m from the pyloric sphincter (posterior to the points of entry of the bile and pancreatic ducts); five in the mid-jejunum, 2·0–2·5 m from the pylorus; six in the terminal ileum, 0·3 m anterior to the ileo-caecal junction. Twenty-four similar but non-cannulated animals were used in a conventional digestibility trial. Full details were given by Braude, Fulford & Low (1976) in a report on the general aspects of digesta flow in the same pigs.

*Diets.* Details of the composition of diets BWF, SSG, and SSC are given in Table 1. These contained (g/kg) respectively: Ca 8·53, 7·45, 7·50; P 7·22, 4·84, 5·62; Mg 1·51, 1·58, 0·42; Na 2·07, 2·50, 2·40; K 6·71, 7·45, 2·48. Because of frequent blockages of ileal cannulas after feeding the normally-ground diet BWF in preliminary tests, this diet was milled to pass through a 1 mm mesh to give a finely-milled diet (diet $BWF_f$). The latter was fed to all animals with ileal cannulas and was included as a fourth dietary treatment in the digestibility trial.

The dry diet was mixed with water (1:2·5, w/v) and offered twice daily at 09.00 and 15.00 hours. The local water supply contained (mg/l) Ca 40, P 0·2, Mg 24, Na 116, K 14. This source was accounted for in calculating the intake of each element. The animals were weighed weekly and fed according to a scale based on their live weight (Barber, Braude, Mitchell & Pittman, 1972).

*Collection procedures.* Full details of digesta and faeces collections and the techniques used have been given by Braude *et al.* (1976). For each cannulated pig on each diet the trial involved two 24 h collections with hourly sampling from the duodenum or jejunum and four 24 h collections with sampling every 6 h from the ileum. In the digestibility trial with non-cannulated pigs, six replicates of four litter-mates randomly assigned to the four diets were used. Each pig received the same diet throughout the trial and faeces were collected during four 5 d periods evenly spaced through the period of growth from 20 to 60 kg live weight.

*Analyses.* Representative samples of diets, digesta and faeces were analysed for Ca, P, Mg, Na and K. Samples were ashed at 460° and mineral solutions in 0·48 M-hydrochloric acid were prepared according to a standard procedure. Ca and Mg were determined by atomic absorption spectrophotometry and Na and K by flame emission photometry. P was determined colorimetrically by the vanadomolybdate procedure.

*Presentation of results.* The amount of each element in digesta or faeces is expressed as the ratio, weight collected in 24 h: weight in feed and water consumed in 24 h (output: intake) to indicate the direction and extent of net movements of the elements through the gut wall in each region.

For each element the average values for output: intake from the 24 h digesta collections from each pig on a particular diet were subjected to analysis of variance. Average values for the four faeces collections from each of the animals without cannulas were similarly treated. The standard error of the difference between the means is not the same for each pair of cannula sites or for each pair of diets because different numbers of animals completed collections for the various site–diet combinations. The least and greatest values are given in Tables 2–6. The statistical methods used in these studies were described in more detail in a previous paper (Braude *et al.* 1976).

To aid interpretation, the weight of each element ingested and the output at each site have been calculated for a 40 kg pig (approximately the mid-point of the live weight range studied) which, according to the feeding scale used, would have received 1·70 kg diet and 4·25 l water daily.

## RESULTS

The initial aim in these studies was that for each cannula site, digesta collections would be made from six pigs fed each of the diets in successive 14–21 d periods. However, it was not possible to complete all the planned collections for several reasons: the most common reasons for discarding an animal prematurely were loss of cannulas and leakage of digesta from around the cannulas. These difficulties appeared to be associated with the rapid growth of the animals. In addition, a palatability problem was experienced with diet SSG in several animals: collections were only conducted when animals were eating normally. The numbers of animals completing collections for each site–diet combination are indicated in Tables 2–6.

*Ca.* The mean Ca output: intake for each intestinal site and for each diet are presented in Table 2. It was evident that there was little or no net Ca exchange anterior to the duodenal cannulas. Comparison of the duodenal and ileal output: intake values showed significant differences for each diet ($P < 0.05$), but there was an effect of diet on the distribution of absorption between the segments of small intestine proximal and distal to the jejunal cannulation site. With all three diets the mean values for jejunal output: intake were lower than those at the duodenum but only in the instance of diet BWF was the difference significant ($P < 0.05$). With diet BWF no further absorption was evident between the jejunum and the terminal ileum, but differences between these sites were significant for diets SSG ($P < 0.05$) and SSC ($P < 0.01$), indicating major Ca absorption in this region. Comparison of the values for 24 h output: intake from the digestibility study with those at the terminal ileum (Table 2) indicated that there was significant ($P < 0.001$) absorption of Ca from the large intestine with diet SSC but not with diets $BWF_f$ or SSG. Table 7 indicates that there were differences between diets in the absolute amounts of Ca absorbed in the various regions of the gut.

Table 2. *Mean 24 h output:intake for calcium 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*

(*a*) Cannulated pigs (No. of pigs completing collections in parentheses)

| Site of re-entrant cannula* | Diet BWF† | Diet SSG | Diet SSC |
|---|---|---|---|
| Duodenum | 0·98 (6) | 0·96 (2) | 0·96 (6) |
| Jejunum | 0·76 (5) | 0·81 (5) | 0·84 (4) |
| Ileum | 0·75 (5) | 0·52 (2) | 0·50 (6) |

SE of difference between site means: least value 0·077, greatest value 0·133
SE of difference between diet means: least value 0·073, greatest value 0·126

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

| | Diet BWF | Diet $BWF_t$ | Diet SSG | Diet SSC |
|---|---|---|---|---|
| Faeces | 0·67 | 0·67 | 0·57 | 0·25 |

SE of difference between diet means: 0·028
SE of difference between means for faeces and ileum: least value 0·049, greatest value 0·069

* For details of sites, see p. 528.
† Diet BWF was finely milled (diet $BWF_t$) when fed to pigs with ileal cannulas; for details of diets, see p. 528 and Table 1.

Table 3. *Mean 24 h output:intake for phosphorus 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*

(*a*) Cannulated pigs (No. of pigs completing collections in parentheses)

| Site of re-entrant cannula* | Diet BWF† | Diet SSG | Diet SSC |
|---|---|---|---|
| Duodenum | 0·97 (6) | 0·94 (2) | 0·93 (6) |
| Jejunum | 0·67 (5) | 0·81 (5) | 0·72 (4) |
| Ileum | 0·55 (5) | 0·39 (2) | 0·35 (6) |

SE of difference between site means: least value 0·072, greatest value 0·125
SE of difference between diet means: least value 0·063, greatest value 0·110

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

| | Diet BWF | Diet $BWF_t$ | Diet SSG | Diet SSC |
|---|---|---|---|---|
| Faeces | 0·54 | 0·55 | 0·59 | 0·26 |

SE of difference between diet means: 0·026
SE of difference between means for faeces and ileum: least value 0·045, greatest value 0·064

* For details of sites, see p. 528.
† Diet BWF was finely milled (diet $BWF_t$) when fed to pigs with ileal cannulas; for details of diets, see p. 528 and Table 1.

*P.* From the results presented in Table 3 there was evidence of a slight net absorption of P anterior to the duodenal cannulas with diet SSC but not with diet BWF. The situation for diet SSG is difficult to judge since only two animals were represented. There was much net absorption of P in the small intestine with all three diets, as indicated by the highly significant ($P < 0·001$) differences between values for duodenal and ileal output:intake. As with Ca, the distribution of P absorption between the segments anterior and posterior

Table 4. *Mean 24 h output:intake for magnesium 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*

(*a*) Cannulated pigs (No. of pigs completing collections in parentheses)

| Site of re-entrant cannula* | Diet BWF† | Diet SSG | Diet SSC |
|---|---|---|---|
| Duodenum | 0·97 (6) | 0·99 (2) | 1·12 (6) |
| Jejunum | 1·14 (5) | 1·03 (5) | 1·37 (4) |
| Ileum | 1·02 (5) | 0·68 (2) | 0·99 (6) |

SE of difference between site means: least value 0·080, greatest value 0·138
SE of difference between diet means: least value 0·073, greatest value 0·127

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

| | Diet BWF | Diet $BWF_f$ | Diet SSG | Diet SSC |
|---|---|---|---|---|
| Faeces | 0·80 | 0·76 | 0·72 | 0·42 |

SE of difference between diet means: 0·050
SE of difference between means for faeces and ileum: least value 0·070, greatest value 0·099

* For details of sites, see p. 528.
† Diet BWF was finely milled (diet $BWF_f$) when fed to pigs with ileal cannulas: for details of diets, see p. 528 and Table 1.

to the mid-jejunum was diet-dependent. The net amounts of P absorbed anterior to the terminal ileum by the 40 kg pig used as an example were 5·5, 5·0 and 6·2 g/d for diets BWF, SSG and SSC respectively (Table 7). With diet BWF most (4·0 g) was absorbed anterior to the mid-jejunum whereas with diets SSG and SSC the major part (3·5 g) was absorbed posterior to that point. A comparison of the output:intake values for ileal digesta and faeces (Table 3) indicated a significant ($P < 0·01$) net secretion of P in the large intestine in the instance of diet SSG. On the other hand, there was a tendency for net absorption in this region with diet SSC and there was no net change with diet $BWF_f$. A comparison of the absolute amounts of P at each collection site for the different diets is given in Table 7.

*Mg*. The duodenal output:intake ratios presented in Table 4 indicate that there was no net absorption or secretion of Mg anterior to the point of cannulation with diets BWF or SSG but a slight net secretion occurred with diet SSC. Collections from pigs with jejunal cannulas showed in the instance of diet SSG that again the output of Mg was very similar to intake. There were significant ($P < 0·05$) additions of endogenous Mg between the duodenum and mid-jejunum with diet BWF and to a greater extent with diet SSC. The value for Mg output:intake at the terminal ileum for diets SSG and SSC was significantly lower ($P < 0·01$) in each instance than the corresponding jejunal value. There was no significant difference between these sites with diet BWF but the trend was towards absorption with this diet also. The ileal outputs for both diets BWF and SSC were very similar to intake but with diet SSG net absorption of approximately 32 % of the dietary Mg was evident anterior to this point. Comparison of the results of the digestibility study with the corresponding ileal results indicated that there was no further net absorption of Mg in the large intestine with diet SSG. In contrast, there were highly significant differences between the ileum and faeces means for diets BWF ($P < 0·01$) and SSC ($P < 0·001$), indicating that the large intestine was the principal site of net Mg absorption. The intake of Mg was much lower with diet SSC than with diets BWF or SSG. It is important, therefore, to consider the actual amounts passing each site in 24 h. These are given in Table 7.

*Na*. The relationships between the 24 h output of Na at each site and the total Na intake

Table 5. *Mean 24 h output:intake for sodium 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*

(*a*) Cannulated pigs (no. of pigs completing collections in parentheses)

| Site of re-entrant cannula* | Diet BWF† | Diet SSG | Diet SSC |
|---|---|---|---|
| Duodenum | 6·38 (6) | 3·64 (2) | 3·93 (6) |
| Jejunum | 9·71 (5) | 5·47 (5) | 4·16 (4) |
| Ileum | 2·74 (5) | 2·03 (2) | 0·69 (6) |

SE of difference between site means: least value 0·382, greatest value 0·661
SE of difference between diet means: least value 0·181, greatest value 0·313

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

| | Diet BWF | Diet $BWF_f$ | Diet SSG | Diet SSC |
|---|---|---|---|---|
| Faeces | 0·30 | 0·19 | 0·06 | 0·02 |

SE of difference between diet means: 0·019
SE of difference between means of faeces and ileum: least value 0·097, greatest value 0·138

* For details of sites, see p. 528.
† Diet BWF was finely milled (diet $BWF_f$) when fed to pigs with ileal cannulas; for details of diets, see p. 528 and Table 1.

Table 6. *Mean 24 h output:intake for potassium 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*

(*a*) Cannulated pigs (no. of pigs completing collections in parentheses)

| Site of re-entrant cannula* | Diet BWF† | Diet SSG | Diet SSC |
|---|---|---|---|
| Duodenum | 1·27 (6) | 1·12 (2) | 1·61 (6) |
| Jejunum | 0·86 (5) | 0·76 (5) | 0·99 (4) |
| Ileum | 0·30 (5) | 0·26 (2) | 0·15 (6) |

SE of difference between site means: least value 0·116, greatest value 0·200
SE of difference between diet means: least value 0·075, greatest value 0·129

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

| | Diet BWF | Diet $BWF_f$ | Diet SSG | Diet SSC |
|---|---|---|---|---|
| Faeces | 0·34 | 0·32 | 0·15 | 0·05 |

SE of difference between diet means: 0·015
SE of difference between means for faeces and ileum: least value 0·038, greatest value 0·054

* For details of sites, see p. 528.
† Diet BWF was finely milled (diet $BWF_f$) when fed to pigs with ileal cannulas; for details of diets, see p. 528 and Table 1.

from two feeds are given in Table 5. With all three diets there were large net additions of Na anterior to the duodenal cannulas. With diet BWF the duodenal output was more than six times the intake, this being significantly greater ($P < 0·001$) than the corresponding values for diets SSG and SSC. The values for jejunal output:intake indicate that there was also significant net Na secretion into the proximal 2·5 m of the small intestine with diets BWF ($P < 0·001$) and SSG ($P < 0·01$) but not with diet SSC. With diet BWF the throughput of Na at the mid-jejunum approached ten times the intake. From the calculated example given in Table 7 it is clear that there were differences between diets in the absolute amounts of Na

Table 7. *Daily intake, throughput at three sites in the small intestine and faecal output (g) of minerals, calculated for a pig of* 40 *kg live weight receiving* 1·70 *kg diet BWF* ($BWF_t$), *SSG or SSC and* 4·25 *l water/d*

| | Diet BWF or $BWF_t$* | Diet SSG | Diet SSC |
|---|---|---|---|
| Calcium | | | |
| Intake | 14·67 | 12·84 | 12·92 |
| Duodenum | 14·37 | 12·32 | 12·40 |
| Jejunum | 11·15 | 10·40 | 10·85 |
| Ileum | 11·00* | 6·67 | 6·46 |
| Faeces | 9·83 | 7·32 | 3·23 |
| | 9·83* | | |
| Phosphorus | | | |
| Intake | 12·27 | 8·23 | 9·55 |
| Duodenum | 11·91 | 7·74 | 8·88 |
| Jejunum | 8·23 | 6·66 | 6·88 |
| Ileum | 6·75* | 3·21 | 3·34 |
| Faeces | 6·62 | 4·85 | 2·48 |
| | 6·75* | | |
| Magnesium | | | |
| Intake | 2·67 | 2·79 | 0·82 |
| Duodenum | 2·59 | 2·76 | 0·92 |
| Jejunum | 3·04 | 2·87 | 1·12 |
| Ileum | 2·72* | 1·90 | 0·81 |
| Faeces | 2·13 | 2·01 | 0·34 |
| | 2·03* | | |
| Sodium | | | |
| Intake | 4·01 | 4·74 | 4·57 |
| Duodenum | 25·59 | 17·26 | 17·97 |
| Jejunum | 38·96 | 25·94 | 19·02 |
| Ileum | 10·99* | 9·63 | 3·15 |
| Faeces | 1·21 | 0·29 | 0·09 |
| | 0·76* | | |
| Potassium | | | |
| Intake | 11·47 | 12·72 | 4·28 |
| Duodenum | 14·56 | 14·25 | 6·88 |
| Jejunum | 9·86 | 9·67 | 4·23 |
| Ileum | 3·44* | 3·31 | 0·65 |
| Faeces | 3·90 | 1·91 | 0·21 |
| | 3·67* | | |

* Diet BWF was 'normally' ground when fed to pigs with duodenal and jejunal cannulas but was finely ground (diet $BWF_t$) when fed to pigs with ileal cannulas. Both versions of this diet were compared in the digestibility trial; for details of diets, see p. 528 and Table 1.

secreted into the proximal regions of the gut. Between the mid-jejunum and the terminal ileum Na was absorbed with considerable efficiency, as indicated by highly significant ($P < 0·001$) differences between these sites for all diets. However, with diets BWF and SSG absorption in this region was not sufficient to offset the large secretions anterior to the mid-jejunum: Na throughput at the terminal ileum was 2·7 times the intake for diet BWF and 2·0 times intake for diet SSG. In contrast, for diet SSC ileal observations indicated net absorption of approximately 30 % of the Na ingested. For each diet, comparison of the values for faecal output:intake with those for ileal digesta showed that absorption from the large intestine was highly significant ($P < 0·001$). However, although this region was the principal site of net absorption of dietary Na, unidirectional Na absorption was considerably greater in the small intestine than in the large intestine, by virtue of the greater load presented in the form of endogenous secretions.

*K*. The quantity of K passing the duodenum was greater than intake for all three diets Table 6). In each instance there was significant ($P < 0·05$) net absorption of K between the

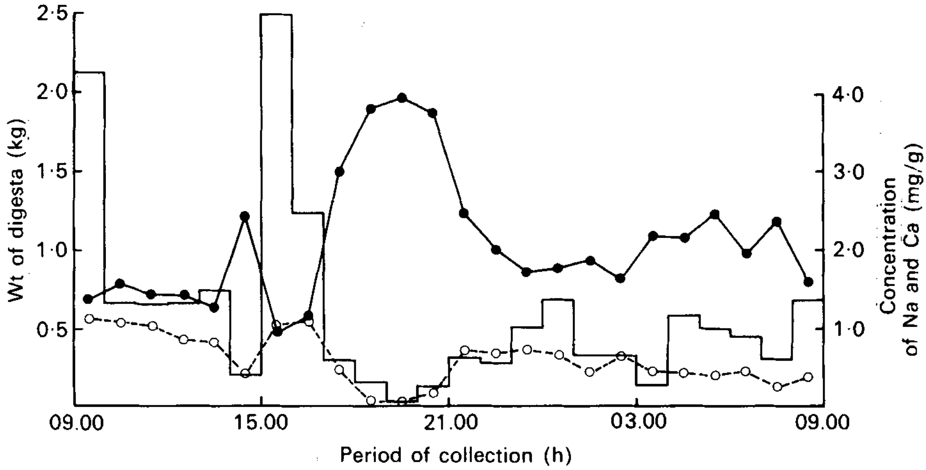


Fig. 1. The relationship of digesta flow (□) and the concentrations of Na (●) and Ca (○) in digesta. Results from a typical 24 h collection from a pig with a duodenal re-entrant cannula, fed diet BWF. (For details, see p. 528 and Table 1.) Animals were fed at 09.00 and 15.00 hours.

duodenum and mid-jejunum. However, the major portion of the small intestine between the mid-jejunum and terminal ileum was the principal region of net K absorption: for each diet the difference between the mean values for output:intake for these two cannulation sites was highly significant ($P < 0·01$). With diet $BWF_f$ there was no absorption or secretion of K in the large intestine but with diets SSG and SSC a further 10–12 % of the dietary intake was absorbed in this region. Since the three diets resulted in different K intakes, again they should not be compared purely on the basis of apparent absorption measurements. The actual amounts secreted or absorbed in each region of the gut are indicated in the example given in Table 7.

Since digesta sampling was carried out hourly in the duodenal and jejunal studies and every 6 h in the ileal studies it was possible to determine the mean diurnal flow patterns for each element at each cannulation site. These patterns were broadly similar for each element and for each diet. At the duodenum and jejunum there was a marked increase in flow-rate for 1–2 h immediately after feeding. Flow continued at all times of the day and night with a general decrease in flow-rate with increasing period after feeding. At the terminal ileum, flow-rate was similar for each of the four 6 h periods but with some tendency for reduced flow between 03.00 and 09.00 hours. Na differed slightly from the other elements in that, duodenal and jejunal flow-rates were more uniform throughout the 24 h period, showing less marked peaks immediately after feeding. There was a distinct difference in the relationship of duodenal digesta flow with digesta Na concentration on the one hand and Ca, P, Mg and K concentration on the other. This is illustrated in Fig. 1 in which results from a typical collection have been plotted, rather than mean values which tend to 'blur' the relationship due to variation between collections in the hour-to-hour flow of digesta. Fig. 1 shows an inverse relationship between hourly digesta output and Na concentration, contrasted with a direct relationship between Ca concentration and digesta flow.

## DISCUSSION

### *Sites of absorption*

*Ca*. With the cereal-based diet (diet BWF) the principal site of Ca absorption was the proximal 2·5 m of the small intestine. This confirms the results of a study by Moore & Tyler

(1955*b*) in which pigs fed on a cereal-based diet were slaughtered after receiving a single meal containing $^{45}$Ca. They observed that absorption of Ca was most active in the proximal fourth of the small intestine.

There are apparently no other reports in the literature on the site of Ca absorption in pigs. However, it is principally from the proximal regions of the small intestine that Ca-binding proteins, believed to represent the carrier mechanism in active Ca absorption, have been isolated in the pig (Fulmer & Wasserman, 1975; Harrison, Hitchman & Brown, 1975). With the two purified diets, SSG and SSC, the region anterior to the mid-jejunum was of comparatively little importance in relation to the total absorption of Ca. It is possible that true absorption in this region was partially masked by Ca secretion which, for some unknown reason, could have been greater with these diets than with diet BWF. In the work of Moore & Tyler (1955*b*), although the absorption of ingested $^{45}$Ca was greatest in the proximal small intestine, in pigs injected with $^{45}$Ca, secretion of the isotope was noted in the same region.

*P*. Moore & Tyler (1955*b*) also studied the absorption of P at intermediate sites in the digestive tract of the pig. They reported that the proximal half of the small intestine was the major site of absorption. This is supported by the results presented here for a comparable diet (diet BWF): with diets SSG and SSC the major site of absorption was posterior to the mid-jejunum but may nevertheless have been the proximal half of the small intestine. Moore & Tyler (1955*b*) reported secretion of endogenous P into the upper intestinal lumen, much of which was subsequently absorbed in the ileum. This suggests that in the duodenal and jejunal observations of the present study, absorption was probably masked to some extent by secretion. It is also possible that the extent of P secretion was not the same for each diet. The lack of any significant net absorption or secretion in the large intestine with diets $BWF_f$ and SSC is in agreement with the observations of Moore & Tyler (1955*b*). With diet SSG net secretion was observed in this region. This finding should be regarded with caution in view of the fact that the value for ileal output:intake was based on results from only two animals. However, the total daily net absorption calculated in the example of a 40 kg pig receiving 1·7 kg diet SSG was only 3·4 g, compared with 5·6 g for diet BWF and 7·1 g for diet SSC. Most of the P in diets SSG and SSC was similarly supplied in a potentially highly available form, suggesting that some factor associated with diet SSG inhibited its net absorption. This could have involved endogenous loss into the lumen of the large intestine, although the reason for this is not readily apparent.

*Mg*. There appears to be no previous direct evidence in the literature concerning the site of Mg absorption in the pig. On the basis of studies involving the perfusion of isolated loops of small and large intestine in the rat, Behar (1974) concluded that the transport of Mg was closely associated with the transport of water and on this basis he suggested that solvent drag was the principal mode of Mg absorption. Observations on the movements of water in the present studies were reported in a previous paper (Low, Partridge & Sambrook, 1978). The present observation that there was a tendency for Mg secretion in the proximal regions of the gut, where water was secreted, while absorption occurred in the ileum and the large intestine, where water was absorbed, is in keeping with the findings of Behar (1974). A report by Annoni & Longoni (1976), concerning plasma Mg levels in pigs and dogs having their small intestines by-passed surgically, seems to implicate the large intestine for Mg absorption in the pig. In the present study the large intestine was the principal site of net absorption of Mg in pigs fed on diets BWF or SSC, but with diet SSG absorption occurred between the mid-jejunum and terminal ileum.

*Na*. With regard to Na the present results support the evidence of a large number of investigations, involving in vitro and in vivo perfusion of segments of intestine, reviewed by Jackson & Smyth (1971). These have shown that while Na moves in both directions across the intestinal mucosa in most regions of the tract, secretion predominates in the anterior small intestine and net absorption occurs in the ileum and colon. The present application of intestinal cannulation has shown that in the pig, under normal feeding conditions, a considerable extent of recycling of the element takes place, on the evidence of jejunal output: intake values ranging from approximately 4 to 10.

*K*. In vitro experiments and in situ perfusion studies have shown that K can be both absorbed and secreted in all regions of the digestive tract but have given no clear indication of the sites of net absorption of dietary K (Jackson & Smyth, 1971). The present results have shown that, in the pig, net secretion of K occurs anterior to a point 0·15 m from the pylorus and net absorption takes place in the small intestine, both anterior and posterior to the mid-jejunum. In the large intestine further small amounts were absorbed when purified diets were fed but there was no net exchange with a cereal-based diet.

## *The influence of diet*

Several factors may have been responsible for the differences between diets in the extent of apparent absorption of the elements studied. There were differences in the amounts of certain elements supplied by the diets: the diets were originally formulated for protein digestion studies and no attempt was made to balance their mineral contents. A major factor of importance is the difference in the form in which a given element was supplied. In diets SSC and SSG most of the mineral supply was in the form of simple mineral-salt supplements, although the groundnut meal in diet SSG made a major contribution to the supply of some elements. With diet BWF the major ingredients, barley, weatings and fish meal, were the principal source of most elements. Furthermore, mineral requirements and hence the efficiency of absorption were probably influenced by differences in growth rate; in the digestibility study average daily gains (g) were 602, 626, 572 and 794 for diets BWF, $BWF_f$, SSG and SSC respectively. The differences between diets in the amount and nature of the supply of individual minerals could also account for the differing importance of the various intestinal regions for the absorption of a particular element. These factors might be expected to alter trans-mucosal concentration and electro chemical gradients, thus altering the propensity for secretion or absorption in different regions. This view is speculative however, since only the total content of each element in digesta was determined, rather than the soluble fraction.

There were marked differences between diets in the magnitude of the two-way flux of Na in the digestive tract. It was previously reported that there were also differences between diets in the flux of water (Low *et al.* 1978) and the net result was that the concentration of Na in digesta at each site studied was similar for all three diets. Mean ($\pm$ SD) Na concentrations (mg/g) for diets BWF, SSG and SSC respectively were: duodenum, $1·4 \pm 0·06$, $1·3 \pm 0·09$, $1·3 \pm 0·10$; jejunum, $2·4 \pm 0·15$, $1·9 \pm 0·12$, $2·0 \pm 0·14$; ileum, $2·7 \pm 0·26$, $2·5 \pm 0·45$, $2·7 \pm 0·23$. These observations represent the homoeostatic mechanisms for achieving specific ionic concentration and osmotic pressure gradients across the intestinal mucosa to permit the absorption of water, minerals and other nutrients. It is pertinent to consider whether the differences between diets in Na secretion and absorption were a consequence or the cause of differences in water secretion and absorption. The ingested diet–water mixture must have had a higher osmotic pressure and ionic concentration with diets SSG and SSC than with BWF due to the high levels of sucrose and free minerals in the former. It might appear that the greater secretion of Na anterior to the duodenum with diet BWF occurred simply in order to balance this situation. However, the greater secretion of Na was accompanied by greater water secretion (Low *et al.* 1978) which would appear to rule out this simple explanation. It seems more likely that other factors governed, or at least modified the flux of water and that Na flux was adjusted accordingly. The probable involvement of dietary fibre in determining the volume of water added to, and retained by, digesta was discussed in the previous paper (Low *et al.* 1978).

*Diurnal flow patterns*

The patterns of flow of the individual mineral elements during the 24 h digesta collections were broadly similar to those reported for whole digesta (Braude *et al.* 1976). Low *et al.* (1978) reported that the duodenal and jejunal flow of water in these same experiments was rather more uniform than the flow of dry matter (DM). In the same way the present observations suggest that the flow of Na was more uniform than that of Ca, P, Mg or K. This reflects the fact that duodenal and jejunal flow of Ca, P, Mg, K and DM are dependent upon the pattern of stomach emptying, whereas, for Na and water this pattern is modified by additions in the form of endogenous secretions into the proximal small intestine. This is illustrated further by considering the relationship between the flow of digesta and its Na content (Fig. 1). This suggests that the concentration of Na in the stomach contents was lower than that in the secretions added in the proximal duodenum: when the rate of stomach emptying was high this diluted the Na in the material collected from the duodenal cannula; when stomach emptying was slow a greater proportion of the material collected consisted of endogenous secretions of high Na concentration. In the instance of Ca (and each of the other elements) the converse situation applied.

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