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Studies on digestion and absorption in the intestines of growing pigs

4. Effects of dietary cellulose and sodium levels on mineral absorption

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1. Seven pigs of 30 kg initial live weight were fitted with re-entrant cannulas in the terminal ileum. Each was fed, in succession, four purified diets having cellulose and sodium levels (g/kg) of 30 and 2·7, 30 and 0·9, 90 and 2·7 or 90 and 0·9, respectively. Collections of digesta (24 h) and 3 or 4 d collections of faeces were made.

2. There was a greater throughput of ileal digesta with the high-cellulose diets than with the low-cellulose diets, mainly due to increased water content, and there was a concomitant reduction in the net absorption of Na from the small intestine. The immediate response to reduced Na intake was increased secretion of Na into the gut lumen anterior to the terminal ileum; this was more pronounced with the high-cellulose diet. Na concentrations in ileal digesta were very similar for all four diets.

3. The apparent absorptions of calcium, phosphorus, magnesium, potassium and zinc were reduced by the high-cellulose diets. In each instance this was due to reduced absorption posterior to the terminal ileum.

In previous studies on pigs with re-entrant cannulas in the duodenum, jejunum and terminal ileum it was found that different diets influenced the gastrointestinal movement of water (Low, Partridge & Sambrook, 1978). It appeared that, as a consequence, the secretion and absorption of sodium were adjusted such that the concentration of the element remained relatively constant at a given intestinal site (Partridge, 1978). Differences in the dietary fibre content were suspected to be the principal cause of these effects. The main objective of the present experiment was to test this hypothesis by measuring the response to the level of cellulose in purified diets, in terms of the output of water and Na in ileal digesta and faeces. It was also of interest to determine whether regulation of intestinal absorption and secretion of other elements were involved in maintaining tonicity. Furthermore, there have been recent suggestions that dietary fibre, particularly the cellulose component, may bind certain elements in the gut contents, thereby reducing their absorption (McConnell, Eastwood & Mitchell, 1974; Reinhold, Ismail-Beigi & Faradji, 1975). The effects of reduced Na intake were studied in conjunction with different cellulose levels to gain further insight into the regulation of intestinal Na flux.

EXPERIMENTAL

Pigs and their management. Eight Large White castrated male pigs of approximately 30 kg live weight were fitted with re-entrant cannulas in the terminal ileum, 0·3 m from the ileo-caecal junction. Seven of these pigs survived to participate in the experiment; the eighth pig died of enteritis shortly after surgery. Methods used in the surgical preparation and housing of cannulated pigs have been described previously by Braude, Fulford & Low (1976).

Diets. Four dietary treatments were compared, conforming to a factorial design with two levels of cellulose and two levels of Na. The composition of the diets is given in Table 1 and their mineral content in Table 2. They were designed to contain (g/kg diet) 30 or 90 cellulose and 2·4 or 0·6 Na. The actual Na intakes were approximately 2·7 and 0·9 g/kg diet due to a contribution from the tap-water (Table 2) mixed with the rations at the rate of 2·5 l/kg immediately before

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

	Diet			
	LC-HS	LC-LS	HC-HS	HC-LS
Maize starch	606·3	610·8	568·5	573·0
Sucrose	100·0	100·0	93·8	93·8
Wood cellulose†	30·0	30·0	90·1	90·1
Maize oil	30·0	30·0	28·1	28·1
Casein	184·0	184·0	172·6	172·6
$CaHPO_4.2H_2O$	20·6	20·6	19·3	19·3
$CaCO_3$	4·6	4·6	4·3	4·3
NaCl	5·0	0·5	5·0	0·5
Trace mineral mix‡	10·0	10·0	9·4	9·4
Vitamin mix§	2·0	2·0	1·9	1·9
Choline HCl	1·1	1·1	1·0	1·0

† 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): 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, 2·00 mg DL-α-tocopheryl acetate, 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.

Table 2. *Mineral content of experimental diets (g/kg)† and tap-water (mg/l)*

	Diet				
	LC-HS	LC-LS	HC-HS	HC-LS	Water
Ash	31·2	27·2	28·6	26·4	362
Calcium	7·07	6·97	6·51	6·97	40
Phosphorus	5·28	5·37	5·10	5·22	0·2
Sodium	2·43	0·60	2·50	0·65	116
Potassium	2·39	2·17	1·79	1·99	14
Magnesium	0·52	0·48	0·51	0·51	24
Zinc	0·065	0·061	0·064	0·065	< 0·05

† Air dry basis: diets contained approximately 900 g dry matter/kg.

feeding. The low-cellulose diets were fed according to the restricted scale of Barber, Braude Mitchell & Pittman (1972), based on live weight at the weekly weighing. The high-cellulose diets were fed according to a parallel scale allowing 6·6 % more diet, in order to maintain similar intakes of nutrients other than cellulose and Na. Animals were fed twice daily at 09.00 and 15.00 hours.

Collection procedures. Each pig was given each of the diets in succession. The three animals forming the first group were subjected to the high-cellulose treatments first, followed by the low-cellulose treatments. For the second group of four pigs the order was reversed. For each cellulose level each animal was allowed a minimum of 6 d to become adapted to the higher Na treatment and then a 24 h collection of ileal digesta was made. Either 3 or 4 d later, pigs were abruptly changed to the low Na variant of that particular cellulose level at the 09.00 hour feed and a 24 h diesta collection commenced at that time. The original intention was to conduct a further 24 h collection after allowing the animal several days to become adapted to the low Na intake; this was abandoned when it was found that all pigs of the first group began to refuse feed 2 d after introduction of diet HC-LS and continued to do so until changed to diet LC-HS.

The system used for the collection, sampling and return of digesta has been described previously (Braude *et al.* 1976). A modification in the present trial was the use of a simplified digesta-return system consisting of a polyethylene funnel connected by a polyvinyl chloride tube to the distal cannula. Although the return vessel used previously was extremely satisfactory for work with duodenal and jejunal cannulas, there were difficulties in its use for ileal collections due to the greater viscosity, low rate of passage and small volume of ileal digesta. For all collections sampling was at 6 h intervals.

An intensive programme of digesta collections was considered desirable in view of the relatively short expected useful life of cannulated pigs (see Braude *et al.* 1976). This restricted the possibility for simultaneous faeces collections which were limited to two, 3 or 4 d collections from each pig, representing the high Na variants of both cellulose treatments (diets LC-HS and HC-HS). The commencement of faeces collections coincided with the start of the 24 h digesta collections on these diets. Minor adjustments were made to the recorded weights of faeces to account for the removal of ileal digesta samples.

Analyses. Representative samples of diets, ileal digesta and faeces were analysed for dry matter (DM), ash, calcium, phosphorus, magnesium, Na, potassium and zinc according to the methods described previously (Low *et al.* 1978; Partridge, 1978).

Presentation of results. The amounts of digesta and faeces are expressed as the ratio, weight collected in 24 h:weight of feed plus water consumed in 24 h (ouput:intake). The amounts of DM, water and minerals are similarly expressed as a proportion of their intake. Values for output:intake were subjected to analysis of variance according to the 2×2 factorial design.

RESULTS

As indicated previously the first group of pigs refused feed persistently from 2 d after the introduction of diet HC-LS until they were changed to diet LC-HS. Consequently the intention to collect digesta after a period of adaptation to the low-Na diets was abandoned. It is not clear whether the observed feed refusal was strictly a response to the low Na intake since at the end of the trial, pigs of the second group were successfully maintained on diet HC-LS for several days. By this time, however, considerable leakage of digesta from around the cannulas was evident, which prevented further meaningful collections.

The average growth rate of the pigs during the collection period (approximately 35–50 kg live weight) was 649 g/d. There were two missing values: one 24 h ileal digesta collection on diet HC-LS and one faeces collection on diet HC-HS were abandoned, both due to leakage around the cannulas towards the end of the experiment.

Ileal observations

The relationships between the ileal output and dietary intake of each of the components studied are presented in Table 3. The higher level of dietary cellulose resulted in a greater volume of whole digesta. For a hypothetical 48 kg pig, fed according to the scales used, the 24 h throughputs of digesta at the terminal ileum for the high- and low-cellulose diets would have been approximately 2 kg and 1 kg respectively, for a difference in cellulose intake of only 130 g. The increase in cellulose level significantly increased the ileal organic matter (OM) output:intake. This was probably due purely to the increase in the amount of cellulose in the ileal digesta since the difference in OM output was only 100 g for the 48 kg pig. Most of the increase in the weight of digesta with the high-cellulose diets was due to an increase in water content. In absolute terms the difference in 24 h ileal water throughput amounted to 844 g for the 48 kg pig.

The increased water flow was accompanied by a marked increase in the Na output: intake. These adjustments were such that the concentration of Na in ileal digesta remained constant: average values were 2·73 and 2·76 mg/g for the low-cellulose and high-cellulose

Table 3. *Effect of dietary cellulose and sodium content on output:intake of total material, organic matter, water and minerals for digesta collections from the terminal ileum of pigs*

	Diet						
	LC-HS	LC-LS	HC-HS	HC-LS	Mean effects†		
Cellulose (g/kg) ...	30	30	90	90			
Na (g/kg) ...	2·7	0·9	2·7	0·9			SE‡
No. of collections	7	7	7	6	Cellulose	Na	
Digesta: diet + water	0·16	0·14	0·24	0·30	0·12**	0·02	0·037
Organic matter	0·06	0·05	0·10	0·11	0·05***	0·00	0·012
Water	0·19	0·17	0·28	0·36	0·15**	0·03	0·046
Ash	0·43	0·45	0·48	0·52	0·06	0·03	0·050
Na	0·54	1·56	0·85	2·65	0·70**	1·41***	0·195
Potassium	0·10	0·10	0·12	0·19	0·06	0·04	0·041
Calcium	0·57	0·50	0·56	0·40	0·06	0·11*	0·051
Phosphorus	0·36	0·33	0·31	0·27	0·06	0·04	0·031
Magnesium	1·01	0·98	0·97	0·79	0·12	0·10	0·086
Zinc	0·90	0·95	0·76	0·65	0·22**	0·03	0·064

Levels of significance: * $P < 0·05$, ** $P < 0·01$, *** $P < 0·001$.
† There were no significant cellulose level × Na level interactions.
‡ Standard error of the mean effects (17 df).

diets respectively. Values for ileal output:intake for K, Ca, P and Mg were not significantly influenced by dietary cellulose but the apparent absorption of Zn anterior to the terminal ileum was significantly greater with the high-cellulose diets than with the low-cellulose diets.

Reducing the Na level in both the low- and high-cellulose diets was without effect on the volume of ileal digesta or on digesta OM, water and total ash content. However, the values for Na output:intake given in Table 3 indicate considerable net secretion of Na at the terminal ileum with the low-Na diets, while net absorption occurred with the higher dietary Na level. The combination of high-cellulose and low-Na contents (diet HC-LS) clearly had an additive effect in increasing Na output:intake. Again, these marked effects on the rate of Na recycling resulted in similar digesta Na concentrations: average values were 2·77 and 2·73 mg/g for the high and low Na intakes respectively. The only other element significantly affected by Na intake was Ca for which the apparent absorption anterior to the terminal ileum was enhanced by the low Na level.

Neither cellulose level nor Na level in the diet influenced the pH of ileal digesta. The mean pH was 7·8.

Faecal observations

The effects of dietary cellulose level on the values for faecal output:intake for the major components of faeces and for individual mineral nutrients are indicated in Table 4. The total weight of faeces was increased approximately threefold by the increase in cellulose intake. This was due in part to an increase in the OM output which in the main was probably undigested cellulose. However, there was also a substantial increase in the faecal water output:intake. As at the terminal ileum, the increased output of water was associated with an increased Na output:intake. However, the absorption of Na by the large intestine was extremely efficient with both diets and the difference in faecal loss of Na was only approximately 1 % of dietary intake. In faeces, unlike ileal digesta, Na concentration was affected by diet: mean concentrations were 0·72 and 0·50 mg/g for the low- and high-cellulose diets respectively.

The over-all apparent absorption of each of the other elements studied was significantly

Table 4. *Effect of dietary cellulose content on output: intake of total material, organic matter, water and minerals for faeces collections from pigs*

	Diet		
	LC-HS	HC-HS	
Cellulose (g/kg) ...	30	90	
Na (g/kg) ...	2·7	2·7	SE†
No. of collections	7	6	
Faeces: diet + water	0·010	0·031	0·0032***
Organic matter	0·015	0·054	0·0065***
Water	0·006	0·020	0·0030**
Ash	0·169	0·265	0·0236**
Na	0·009	0·018	0·0024**
Potassium	0·035	0·140	0·0333*
Calcium	0·256	0·366	0·0378*
Phosphorus	0·192	0·262	0·0235*
Magnesium	0·274	0·385	0·0361*
Zinc	0·396	0·631	0·0503**

Levels of significance: * $P < 0{\cdot}05$, ** $P < 0{\cdot}01$, *** $P < 0{\cdot}001$.
† Standard error of difference between diet means (6 df).

lower with the high-cellulose diet than with the low-cellulose diet. Comparing values for the ileal (Table 3) and faecal (Table 4) output: intake it is clear that in each instance the difference was due to reduced absorption of the element from the large intestine. It is notable that in the instance of Zn the over-all absorption (faeces measurement) was much lower with the high-cellulose diet than with the low-cellulose diet, whereas absorption anterior to the terminal ileum was greater with the former diet. Thus, with the low-cellulose diet the large intestine was the principal site of Zn absorption with little occurring anterior to the terminal ileum; with the high-cellulose diet the relative importance of the two intestinal regions was reversed.

DISCUSSION

The results of the present trial support the evidence from studies on fibre in human nutrition, reviewed by Cummings (1973) and Eastwood (1974), that increased dietary fibre increases the weight of faeces due to its water-binding capacity. Similar effects were noted in pigs by Cooper & Tyler (1959*a*). Furthermore, the present results show that this effect causes a much increased volume of ileal digesta, confirming observations in pigs by Cooper & Tyler (1959*a*) and Farrell & Johnson (1970).

In a previous experiment (Partridge, 1978) it was shown that differences in the water space within the gut lumen, induced by different diets, alter the secretion and absorption of Na such that luminal Na concentration remains constant. It was suspected that dietary fibre content was responsible for these effects. In the present trial confirmation of this was obtained in respect of dietary cellulose level. By comparing the present results for a purified diet containing 90 g cellulose/kg with those for a cereal-based diet containing 72 g acid-detergent fibre/kg (Partridge, 1978), it appears that pure cellulose is considerably less efficient than cereal fibre in promoting water retention and hence Na retention by ileal digesta. This is in line with the observations of Cooper & Tyler (1959*a*, *b*, *c*) who noted that faeces weight was increased to a much greater extent by bran than by powdered cellulose. While it is clear from the present work that pure cellulose has an important water-binding effect in the digestive tract, other factors possibly related to the physical and chemical nature of the fibre must also be important.

The increased Na output:intake at the terminal ileum occurring in response to both increased cellulose and reduced Na intake was not accompanied by any increase in secretion or reduction in absorption of any other element studied. This suggests that only Na regulation was concerned in the maintenance of luminal cation concentration although Field, Dailey, Boyd & Swell (1954) showed in fistulated dogs, that prolonged feeding of diets extremely low in Na (involving forced feeding) caused a gradual reduction in ileal Na concentration and a concomitant increase in K concentration such that the combined concentration remained constant.

There is no obvious explanation for the apparent enhancement of Ca absorption anterior to the terminal ileum in association with reduced Na intake.

Increasing the level of cellulose from 30 to 90 g/kg diet significantly reduced the apparent absorption of each element studied. With the exception of Na there was no reduction in the apparent absorption of minerals anterior to the terminal ileum. Only that proportion of the total absorption of each element which occurred in the large intestine was reduced by the high-cellulose diet. Zn absorption anterior to the terminal ileum was enhanced with the high-cellulose diet although not sufficiently to offset the reduced absorption from the large intestine. This suggests a compensatory adaptation to reduced Zn absorption from the large intestine.

It has long been known that high fibre intake, particularly in the form of wholemeal bread, reduces the absorption of minerals (e.g. McCance & Widdowson, 1942). Until recently this has been attributed to the formation of insoluble phytate salts in the gut since phytate is an important component of whole cereal grains. Recent evidence supports the present findings that dietary cellulose may influence mineral absorption, independent of any effect of phytate. In vitro work has shown that fibre extracted from many vegetables (McConnell *et al.* 1974) and dephytinized wholemeal bread, bran and pure cellulose (Reinhold *et al.* 1975) acts in the manner of a cation-exchange resin in binding mineral elements. Preliminary observations by Reinhold *et al.* (1975) on the effects of pure cellulose consumption by men showed that faecal excretion of Zn, iron and Mg, but not Ca, was increased. Reduced Zn absorption in rats fed high levels of cellulose was reported by Becker & Hoekstra (1971).

Properties of cellulose other than its cation-binding capacity may also be involved in its ability to reduce mineral absorption. Cation binding does not explain the reduced absorption of P noted here, and also by Reinhold *et al.* (1975). It is possible that the increased water content of digesta associated with the high-cellulose diet may have affected mineral absorption by reducing the trans-mucosal concentration and electrochemical gradients in the large intestine. It is also possible that the higher water content may have accelerated the passage of digesta through the large intestine, thus reducing the opportunity for mineral absorption. Increased rate of passage has been a feature of some experiments with high-fibre diets in man (Cummings, 1973; Eastwood, 1974).

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