The flow of endogenous nitrogen in the digestive tract of young pigs

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1. Twenty pigs were given one of five diets containing 0·9–39·2 g nitrogen/kg dry matter (DM) during the period 13–27 d of age.

2. The pigs were fed hourly, from 22–27 d of age, with a diet sprayed with an indigestible marker, ^{103}Ru-labelled Tris (1,10-phenanthroline)-ruthenium (II) chloride. All pigs were slaughtered at 27 d of age.

3. Flows of endogenous N estimated by feeding the diet containing 0·9 g N/kg and by regression analysis using results from all diets, were similar.

4. Flows of endogenous N were: stomach 1·8, duodenum 4·5, jejunum 4·2, ileum 3·5, caecum 2·7, large intestine 2·6 and faeces 1·7 g/kg DM intake.

5. Values are given for the flow of endogenous amino acids to the ileum.

6. Of the DM, 70% was digested anterior to the duodenum and for N the value was 10%. The percentage of N digested anterior to the jejunum was 70.

During the passage of food through the alimentary tract, considerable quantities of endogenous protein are added in the form of digestive secretions and desquamated mucosal cells. Estimates have been made of the size of this addition of endogenous protein. Nasset (1965) suggested that it was several times greater than the protein content of the diet, although much lower estimates were made by recent workers (Buraczewska *et al.* 1975; Zebrowska *et al.* 1975).

There are a number of individual components which can be added to make the total endogenous nitrogen flow. Corring (1975) found that pancreatic secretions amounted to 3–4 g N/d for the 45 kg pig or 11% of the dietary N intake. Horszczaruk *et al.* (1974) estimated from studies with isolated loops of jejunum that the total endogenous N secretions in the intestines could be 10–22 g/d.

Zebrowska *et al.* (1975) fitted 50 kg pigs with re-entrant cannulas in the duodenum and ileum and estimated endogenous N secretion to be 5–7 g/d at the duodenum and 3 g/d at the ileum. However, subsequently Low & Zebrowska (1977) found that these values were influenced by the technique of digesta collection.

The flow of N to the duodenum, jejunum, ileum and faeces in two pigs given a protein-free diet was measured by Wilson & Leibholz (1981 *b*), but more information is required on the flow of endogenous N in all parts of the digestive tract, and this was measured in the present experiment, both by regression analysis and by giving an N-free diet to young pigs.

MATERIALS AND METHODS

Diets

Five diets with increasing N content were prepared as shown in Tables 1 and 2. All diets were pelleted before feeding (5 mm screen).

Animals

Twenty Large White × Landrace male pigs were taken from sows at 10 d of age (mean weight 3·7 kg). The pigs were housed in two groups for a preliminary period of 3 d. At 13 d of age pigs were allocated, by restricted randomization on the basis of initial live weight, to

Table 1. *Ingredients of the diets*

Diet... Variable ingredients (g/kg)*	1	2	3	4	5
Dried skim milk	—	60	230	400	570
Dried whole milk	—	150	150	150	150
Lactose	870	710	550	390	230
Dicalcium phosphate	40	30	20	10	—
Soya-bean oil	40	—	—	—	—

* All diets contained (g/kg): 20 calcium stearate, 20 Solka Floc (Brown Co., Berlin, New Hampshire, USA); 10 vitamin and mineral supplement supplying (mg/kg diet): 1·5 retinol, 0·025 cholecalciferol, 20 α-tocopherol, 2 menadione, 200 ascorbic acid, 20 μg cyanocobalamin, 1·5 thiamin, 6 riboflavin, 20 nicotinic acid, 10 pantothenic acid, 3 pyridoxine, 1 g choline chloride, 0·3 folic acid, 0·1 biotin; minerals (mg/kg): 1000 sodium, 2600 potassium, 400 magnesium, 100 iron, 10 copper, 40 manganese, 70 zinc, 2 cobalt, 0·1 selenium, 0·1 iodine. Other additives (mg/kg): 100 ethoxyquin, 50 oxytetracycline, 50 neomycin sulphate.

four replicates per diet and one pig per cage. Diets were offered *ad lib.* to 22 d of age and water was available from nipple drinkers. Cages were in a draught-free room maintained at 30°.

Faeces and urine were collected from 22–27 d of age. Food intake was measured daily and pigs were weighed weekly.

Indigestible marker was sprayed on the diets given between 22 and 27 d of age and feed was restricted to 150 g/d, fed hourly. The marker during this period was ^{103}Ru-labelled Tris-(1,10-phenanthroline)-ruthenium (II) chloride (^{103}Ru-P) and details of the procedures have been described by Wilson & Leibholz (1981*a*). The daily intake of the isotope was approximately 2 μCi ^{103}Ru-P.

At 27 d of age, exactly 15 min after an hourly feeding, the pigs were anaesthetized by intravenous administration of Surital (sodium thiamylal; Parke Davis & Co., Sydney). The intestinal tract was removed under these conditions to prevent, as much as possible, the shedding of epithelium into the intestinal lumen. The length of the small intestine was measured and then divided into three equal parts (designated as duodenum, jejunum and ileum). All digesta was rapidly removed from the intestines, stomach, caecum and colon, weighed, the pH determined and stored at −20°.

Analytical methods

Digesta samples were homogenized and samples were counted in an Auto Gamma Spectrophotometer (Model 5320; Packard Instrument Co. Inc., Ill.). Dry matter (DM) was determined in a forced-air oven at 95°. Amino acids in feed and digesta samples were determined using ion-exchange chromatography (TSM Amino Acid AutoAnalyzer; Technicon Equipment Ltd, Sydney). Samples were hydrolyzed in 6 M-hydrochloric acid for 24 h at 136°.

RESULTS

Performance of pigs

The weight gains and N retention (Table 2) increased linearly as the dietary N content of the diets increased.

The flow of digesta (Table 3) through the stomach increased with increasing protein content of the diet, although 150 g air-dry food/d was offered to each pig. However, the total flow of digesta in the duodenum was similar for all diets. The flow of digesta through the jejunum and ileum decreased as the N content of the diets increased. The N content

Table 2. *Weight gains and feed intakes of young pigs (13–22 d of age) before feed restriction*

Nitrogen in diets (g/kg dry matter)...	0·9	9·7	20·5	30·2	39·2	SEM	Significance of linear effects
Gain (g/d)	−60	−14	15	101	186	16·1	*
Feed intake (g/d)	126	127	130	252	246	47·8	*

* $P < 0·05$.

Table 3. *Flow of digesta (g/d) in young pigs*

Nitrogen in diets (g/kg)...	0·9	9·7	20·5	30·2	39·2	SEM	Significance of linear effect
Stomach	500	539	804	927	1112	150·1	*
Intestinal section							
Duodenum	1424	1179	1239	1012	1133	60·3	NS
Jejunum	589	490	597	468	311	85·4	NS
Ileum	423	345	282	221	206	73·9	NS
Caecum	59·5	40·5	83·2	67·8	73·0	31·5	NS
Large intestine	29·5	40·2	51·2	50·2	46·0	22·3	NS

NS, not significant, * $P < 0·05$.

Table 4. *Retention time of digesta (min) in young pigs*

Nitrogen in diets (g/kg)...	0·9	9·7	20·5	30·2	39·2	SEM	Significance of linear effect
Stomach	147·7	105·1	71·2	77·0	65·9	34·1	*
Intestinal section							
Duodenum	29·5	25·0	29·0	18·0	20·8	7·6	NS
Jejunum	54·0	73·2	59·8	48·5	75·2	17·4	NS
Ileum	106·0	95·5	148·7	123·8	68·5	35·1	NS
Caecum	455	400	373	321	425	100·2	NS
Large intestine	1012	974	1140	1008	1056	101·1	NS
Total	1804	1573	1822	1597	1711	161·3	NS

NS, not significant, * $P < 0·05$.

of the diets did not have a significant ($P < 0·05$) effect on the flow of digesta through the caecum or large intestine.

Retention time (Table 4) of digesta in the stomach was reduced with increasing protein content in the diets given to the pigs, but retention time of digesta in the rest of the tract was similar for all diets.

Flow of DM (Table 5) through the stomach was similar to the DM intake of the pigs given all diets. The digestion and absorption of DM in the duodenum was between 63 and 72% of that apparently digested in the whole tract. There were no differences between the diets.

Flow of N (Table 6) through the stomach of the pigs was greater than the N intake for

Table 5. *Flow of dry matter* (DM) (*g/d*) *in young pigs*

Nitrogen in diets (g/kg)...	0·9	9·7	20·5	30·2	39·2	SEM	Significance of linear effect
DM intake	122·8	118·9	107·4	137·1	140·6	7·02	NS
Stomach	111·9	115·3	105·4	140·6	141·9	9·16	NS
Intestinal section							
Duodenum	40·4	47·6	36·0	53·6	43·8	4·38	NS
Jejunum	23·8	23·3	23·6	21·9	19·9	3·30	NS
Ileum	17·5	14·8	17·5	14·1	12·4	2·57	NS
Caecum	6·55	5·42	9·75	8·70	6·77	1·36	NS
Large intestine	6·15	6·95	9·50	9·47	6·96	1·25	NS
Faeces	5·40	5·60	7·00	7·01	6·17	1·19	NS

NS, not significant.

Table 6. *Flow of nitrogen* (*g/d*) *in young pigs*

N in diets (g/kg)...	0·9	9·7	20·5	30·2	39·2	SEM	Significance of linear effect
N intake	0·11	1·22	2·32	4·35	5·80	0·098	*
Stomach	0·35	1·40	2·88	5·15	6·22	0·245	*
Intestinal section							
Duodenum	0·60	1·42	2·49	4·24	5·21	0·355	*
Jejunum	0·69	0·67	1·03	1·82	1·90	0·214	*
Ileum	0·38	0·58	0·78	0·80	0·82	0·101	*
Caecum	0·26	0·40	0·53	0·51	0·40	0·076	NS
Large intestine	0·24	0·38	0·49	0·48	0·32	0·057	NS
Faeces	0·19	0·25	0·25	0·26	0·26	0·049	NS
Retention	−0·33	0·10	1·08	3·10	4·60	0·121	*

NS, not significant, * $P < 0{\cdot}05$.

the pigs given all diets. This was also the situation for the flow of N to the duodenum in the pigs given the diets containing only 0·9 and 9·7 g N/kg. Although the greatest absorption of DM occurred in the duodenum, the major sites of N absorption were the jejunum and ileum.

Flow of N through the stomach, duodenum, jejunum and ileum was postively correlated with the N intake (Table 7), but there was no correlation between N intake and N flow in the caecum, large intestine or faeces. This suggests that the N in these parts of the digestive tract was mainly from endogenous secretions or of microbial origin rather than undigested dietary N.

Endogenous N flow has been calculated by regression analyses (Table 7) and found to be 1·75, 4·48, 4·16, 3·44, 2·71, 2·61 and 1·69 g N/kg DM intake for the stomach, duodenum, jejunum, ileum, caecum, large intestine and faeces respectively.

Flow of amino acids to the ileum

The amino acid composition of the ileal contents (Table 8) was similar for the pigs given all five diets with the exception of a higher glycine and lower lysine content in the ileal digesta of the pigs given the almost N-free diet. The amino acid content of the dietary protein was

Table 7. *Regression of N flow (g/d) v. dietary N intake (g/d) in young pigs given 125 g dry matter (DM)/d*

	Intercept	$SE_{intercept}$	Slope	SE_{slope}	r	Endogenous N (g/kg DM intake)
Stomach	0·220	0·076	1·073	0·053	0·979*	1·75
Intestinal section						
Duodenum	0·561	0·192	0·723	0·133	0·788*	4·48
Jejunum	0·522	0·147	0·247	0·101	0·748*	4·16
Ileum	0·443	0·032	0·085	0·022	0·671*	3·44
Caecum	0·339	0·035	0·0081	0·024	0·114	2·71
Large intestine	0·326	0·026	0·0060	0·019	0·078	2·61
Faeces	0·211	0·016	0·0119	0·016	0·110	1·69

* $P < 0·05$.

Table 8. *Percentage of individual amino acids of the sum of sixteen amino acids in the diet and ileal digesta in young pigs*

Nitrogen in diet (g/kg)...		0·9	9·7	20·5	30·2	39·2	
Amino acid	Diet			Ileum			SEM
Essential							
Arginine	3·9	5·3	7·8	7·5	7·4	6·3	0·86
Histidine	3·2	3·8	4·1	3·9	3·5	2·8	0·58
Isoleucine	6·5	3·0	4·9	4·3	4·1	4·5	0·49
Leucine	10·0	6·4	6·0	5·7	5·8	5·7	0·78
Lysine	9·1	6·5	7·6	9·8	9·3	10·6	1·01
Methionine	3·0	1·0	1·3	1·5	1·0	1·0	0·24
Cystine	1·2	1·1	1·5	1·5	1·3	1·5	0·28
Phenylalanine	5·5	3·2	3·1	2·8	2·8	3·8	0·33
Threonine	4·4	5·8	5·9	5·3	6·4	6·2	0·54
Valine	8·3	8·7	6·6	6·5	8·4	8·5	0·65
Non-essential							
Alanine	3·8	6·7	7·0	5·8	7·1	6·8	0·68
Aspartic acid	10·0	9·8	8·9	9·1	8·9	8·2	0·70
Glutamic acid	19·4	9·3	11·9	14·3	12·7	10·9	0·80
Glycine	2·4	19·1	12·4	9·4	11·9	12·6	1·31
Tyrosine	4·6	2·7	2·5	2·3	2·4	3·0	0·26
Serine	4·5	7·4	8·1	7·6	7·0	6·8	0·56

Table 9. *The flow of amino acids to the ileum (g/d) in young pigs*

Nitrogen in diet (g/kg)... Amino acid	0·9	9·7	20·5	30·2	39·2	SEM	Significance of linear effect
Essential							
Arginine	0·11	0·19	0·33	0·29	0·31	0·030	NS
Histidine	0·08	0·12	0·14	0·14	0·12	0·019	*
Isoleucine	0·07	0·13	0·20	0·20	0·20	0·029	*
Leucine	0·13	0·18	0·22	0·26	0·23	0·031	*
Lysine	0·13	0·21	0·37	0·39	0·45	0·028	*
Methionine	0·03	0·04	0·05	0·04	0·04	0·004	NS
Cystine	0·03	0·05	0·05	0·05	0·05	0·005	NS
Phenylalanine	0·07	0·09	0·12	0·12	0·17	0·021	*
Threonine	0·12	0·18	0·20	0·28	0·26	0·023	*
Valine	0·18	0·20	0·27	0·33	0·40	0·032	*
Non-essential							
Alanine	0·14	0·20	0·21	0·30	0·33	0·028	*
Aspartic acid	0·19	0·22	0·35	0·32	0·35	0·030	NS
Glutamic acid	0·21	0·34	0·59	0·52	0·44	0·033	NS
Glycine	0·40	0·38	0·41	0·56	0·60	0·039	NS
Tyrosine	0·05	0·08	0·09	0·10	0·12	0·022	*
Serine	0·18	0·24	0·31	0·29	0·32	0·038	NS

NS, not significant, * $P < 0·05$.

different from that of the ileal digesta, with higher concentrations of isoleucine, leucine, methionine, phenylalanine and glutamic acid. This would suggest that the amino acids in ileal digesta were largely of endogenous origin. However, some dietary N was present in ileal digesta as there was a positive correlation between dietary N intake and the flow of

Table 10. *Regression of amino acid flow (g/d) to ileum to dietary nitrogen intake (g/d) in young pigs*

Amino acid	Intercept	$SE_{intercept}$	Slope	SE_{slope}	r	Endogenous amino acid flow (g/kg dry matter intake)
Essential						
Arginine	0·180	0·0167	0·0123	0·0096	0·243	1·44
Histidine	0·041	0·0111	0·0329	0·0078	0·419*	0·33
Isoleucine	0·100	0·0086	0·0119	0·0059	0·427*	0·80
Leucine	0·143	0·0093	0·0141	0·0064	0·458*	1·14
Lysine	0·131	0·0140	0·0410	0·0098	0·602*	1·05
Methionine	0·038	0·0003	0·0002	0·0011	0·027	0·30
Cystine	0·038	0·0013	0·0018	0·0023	0·172	0·30
Phenylalanine	0·067	0·0043	0·0078	0·0030	0·520*	0·54
Threonine	0·132	0·0090	0·0173	0·0063	0·573*	1·06
Valine	0·176	0·0120	0·0184	0·0084	0·458*	1·41
Non-essential						
Alanine	0·152	0·0108	0·0161	0·0074	0·452*	1·22
Aspartic acid	0·226	0·0119	0·0141	0·0083	0·364	1·81
Glutamic acid	0·280	0·0261	0·0296	0·0181	0·359	2·24
Glycine	0·345	0·0180	0·0094	0·0125	0·174	2·76
Tyrosine	0·058	0·0035	0·0061	0·0025	0·507*	0·46
Serine	0·200	0·0091	0·0087	0·0096	0·212	1·60

* $P < 0.05$.

total N, histidine, isoleucine, leucine, lysine, phenylalanine, threonine, valine, alanine and tyrosine to the ileum (Tables 7 and 10). The increasing flow of amino acids to the ileum for the pigs given increasing dietary N intakes is shown in Table 9.

DISCUSSION

The flow of endogenous N in the digestive tract was similar when measured by regression analysis or by giving an almost N-free (0·9 g N/kg) diet. Zebrowska & Buraczewska (1972) found that endogenous N secretion in the stomach and duodenum was unaffected by the protein level in the diet. However, in more recent reports by Krawielitzki *et al.* (1979) and Buraczewska *et al.* (1979), the flow of endogenous N and methionine to the duodenum was greater in pigs given a diet containing wheat gluten than when the diet given was N-free. Carlson & Bayley (1970) found that estimates of endogenous N flow by regression analysis in pigs given casein and those determined directly in pigs given an N-free diet were similar, but regression analysis with soya-bean meal as the source of dietary protein underestimated endogenous N. From the present experiment, it may be concluded that endogenous N flow can be estimated by giving an almost N-free diet or by regression analysis from pigs given diets containing casein.

The endogenous N in the stomach was found to be 1·75 g/kg DM intake. There appears to be no other estimate of the total endogenous N in the stomach of the pig although gastric digestion due to the activity of pepsin is known to occur in growing pigs (Lawrence, 1972). Other sources of endogenous N would be the sloughing of epithelial cells and saliva. Arkhipovets (1956) measured parotid saliva flow and protein content. Extrapolation of his values to younger pigs would indicate a flow of saliva N of 0·4–0·8 g/d. The volume of gastric secretion has been measured in isolated stomach pouches of the pig (Kvasnitskii, 1951), and the protein content has been measured in other species. Again, by extrapolation the daily N contribution from these secretions may be 1 g/d. If there was no absorption of N in the stomach, this would mean that the sloughing of epithelial cells would not be a major contribution to the endogenous N in the stomach.

Several estimates of endogenous N flow to the duodenum have been made. The pancreas secretes 3–5 g N/d (Corring *et al.* 1972; Corring, 1975) and the gall bladder secretes 2 g N/d (Sambrook, 1981) in 35–45 kg pigs. This would be approximately 2·7 g N/d per kg DM intake. In addition to the secretions from the pancreas and the gall bladder, the duodenal mucosa is glandular (Brunner's glands) and from this tissue there is a viscous, alkaline secretion which contributes to the endogenous N in the duodenum. The sloughing of epithelial cells would be the other source of endogenous N. The total endogenous N flow in the duodenum has been estimated to be approximately 3·0–3·9 g/d per kg DM intake with 40 kg pigs given N-free diets (Buraczewska *et al.* 1975; Zebrowska *et al.* 1975; Krawielitzki *et al.* 1979). Slightly higher values of 5 g N/d per kg DM intake were obtained by Köhler *et al.* (1978) and by Buraczewska *et al.* (1979). Köhler *et al.* (1978) estimated endogenous N secretion by dilution of N^{15}-labelled feed. These values are similar to the value of 4·5 g N/d per kg DM intake measured in the present experiment.

The flow of endogenous N to the jejunum was 4·2 g N/d per kg DM intake which is higher than a measurement of 2·5 g N/d per kg DM intake made by Zebrowska *et al.* (1975) with two pigs fitted with re-entrant cannulas. Horszczaruk *et al.* (1974) measured a secretion of 1–2 g N/d into the jejunum.

The amount of endogenous N passing the terminal ileum has been estimated at 1·4–1·8 g/d per kg DM intake by numerous workers (Buraczewska *et al.* 1975; Zebrowska *et al.* 1975; Krawielitzki *et al.* 1979; Wünsche *et al.* 1979) in pigs given N-free diets. In the present experiment and in that of Wilson & Leibholz (1981*b*), the flow of endogenous N was estimated as 3·0–3·5 g N/d per kg DM intake in the whole lower third of the intestine. It is also possible that the epithelial cells make a larger contribution to the flow of endogenous N in smaller pigs (5 kg *v.* 30–50 kg).

The values of 2·7 and 2·6 g N/d per kg DM intake for the flow of endogenous N through the caecum and large intestine cannot be compared with the results of other workers, as there are no reported values for this area of the digestive tract.

The endogenous N in faeces was estimated as 1·0–1·3 g/d per kg DM intake by Carlson & Bayley (1970), Buraczewska *et al.* (1979) and Wilson & Leibholz (1981*b*), 1·7 g N/d per kg DM intake in the present experiment and 1·9 g N/d per kg DM intake in the work of Holmes *et al.* (1974). Feeding conditions and age of the pigs may explain these differences.

The amino acid composition of ileal contents showed some similarity to that of the diet in that the regression equation for amino acid intake and flow to the ileum was significant for histidine, isoleucine, leucine, lysine, phenylalanine, threonine, valine, alanine and tyrosine with r^2 values of 0·17–0·36. These results are similar to those of Zebrowska & Buraczewska (1972) and Holmes *et al.* (1974) obtained with cannulated pigs.

Buraczewska *et al.* (1979) and Wünsche *et al.* (1979) described the flow of endogenous amino acids through cannulas in the terminal ileum of pigs even an N-free diet, and their values are approximately half those in the present experiment for the whole lower third of the small intestines; similarly the flow of total endogenous N was approximately half the level of the present study, as mentioned earlier. All the results discussed previously have referred to the flow of endogenous N in the digestive tract. It must be remembered that these values are the balance between the secretion of endogenous N and its reabsorption along the tract. However, the rate of absorption of endogenous N may be less than that of dietary N (Zebrowska & Buraczewska, 1972; Zebrowska *et al.* 1976).

In the experiments of Wilson & Leibholz (1981*b*) no absorption of N occurred in the duodenum while the apparent absorption of N in the present experiment was up to 18%, and its absorption was largely completed by the jejunum. This difference can be explained by the sectioning of the small intestines. In the work of Wilson & Leibholz (1981*b*), the duodenum was 1·5 m in length, jejunum 2·0 m and ileum approximately 5·5 m. In the present experiments the sections were each one-third of the total lengths of the intestines or approximately 3 m.

Addition of protein to the diets increased the net secretion of water to the stomach. This observation is difficult to explain, especially as there is little hydrolysis of protein in the stomach of young pigs (Wilson & Leibholz, 1981*b*). The flow of digesta to the duodenum was similar for all diets.

The N content of the diets ranged from 0·9 to 39·2 g/kg DM. By regression, it was calculated that the N content of the diet required for maintenance of live weight was 12·8 g/kg and that for zero N balance was 7·2 g/kg. The values of 39·2 g N/kg DM should have approached the requirement of maximum weight gains for pigs given casein diets (Wilson & Leibholz, 1979) (Table 2).

The absorption of 70% DM and 18% N took place in the duodenum. Of the absorption of N, 70% occurred between the duodenum and jejunum. This big difference in sites of absorption of N and DM was not observed by Zebrowska *et al.* (1975) nor Wilson & Leibholz (1981*b*). The results from the present experiments agree with those of Leibholz (1981) where the sampling procedure was similar to that of the present experiment. The casein in the present diets should have been substantially hydrolysed in the duodenum (Liebholz, 1981), so this could not explain the difference in the absorption of N and DM. However, the present diets contained lactose which may be more readily absorbed than the starch in the diets given to pigs by Zebrowska *et al.* (1975) and Wilson & Leibholz (1981*b*).

It may be concluded that the flow of endogenous N can be estimated from the regression technique in pigs given increasing amounts of casein or for pigs given a nearly N-free diet.

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