

Studies on absorption and secretion of ^{15}N endogenous nitrogen along the digestive tract of pigs

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ABSTRACT

The experiment was carried out on 3 pigs of 30 kg body weight each fitted with re-entrant cannulas into duodenum and ileum. One pig was given for 5 days ^{15}N labelled and the others two unlabelled ammonium sulphate with diet. Total-N and ^{15}N -labelled nitrogen balance and course of excretion with faeces and urine were estimated. Rates of absorption, secretion and reabsorption were determined using the method of digesta exchange between previously ^{15}N -labelled and unlabelled pigs during the next 6 experimental days. Secretion in the upper part of digestive tract was 5.3 g/day (15% of intake) and absorption about 1% of intake; in the small intestine corresponding values were 8.9 and 38.7 g N/day (25 and 110% of intake and in the large intestine 1.9 and 8.4 g N/day (5.6 and 24% of intake), respectively. Total absorption was to 134% of N intake, and the overall reabsorption of endogenous N compounds secreted into the gut lumen – 90%. The amount of endogenous N decreased from duodenum to ileum and to faeces (5.3, 3.8, 1.6 g N/day) while the relative proportion in comparison to the total N increased from 13 to 35 and 39% in digesta of duodenum and ileum and faeces, respectively.

KEY WORDS: pigs, endogenous nitrogen, absorption, secretion

INTRODUCTION

The absorption of nitrogenous compounds in the digestive tract is accompanied by the secretion of endogenous nitrogen into the intestinal lumen. These processes occur simultaneously and the conventional digestion trial allows to measure only the apparent absorption of nitrogen or amino acids. It is difficult to measure the amount of endogenous nitrogen in different segments of the digestive tract as one can not distinguish accurately between the endogenous and exogenous components of the digesta. From the methods reviewed by Souffrant (1991) the ^{15}N -isotope dilution technique seems to be useful for measuring the

amount of endogenous nitrogen in digesta passing along the digestive tract in pigs given protein containing diets (de Lange et al., 1990). By measuring the ^{15}N excess in endogenous nitrogen, labelled by means of continuous infusion of ^{15}N -compound, and in digesta, the proportion of endogenous to total protein can be calculated.

The ^{15}N -isotope dilution method in combination with other experimental techniques can be applied to study recycling of endogenous nitrogen (Souffrant et al., 1986; Krawielitzki et al., 1990). The isotope dilution method seems to provide discrimination between the endogenous and exogenous nitrogen in the intestinal digesta and allows better approximation of the amount of endogenous nitrogen entering the lumen of the digestive tract.

The main objective of the present study was to measure the amount of endogenous N secreted and absorbed in different segments of the digestive tract by exchange of intestinal digesta between pigs treated with ^{15}N or untreated one.

MATERIAL AND METHODS

Animals. Three male pigs of about 30 kg body weight were fitted with re-entrant cannulas at the duodenum distal to the opening of the pancreatic duct and in the ileum about 20 cm before the ileo-caecal junction. The animals were given a diet containing 18% crude protein (Table 1) in two equal portions of 600 g each at 7.00 and 19.00 h; the feed was mixed with water (1:2 w/v) immediately before feeding. The animals were kept in individual metabolic cages permitting quantitative collection of faeces and urine.

TABLE 1

Composition of the diet (g/kg)

Maize starch	508.6
Soya-bean meal	428.0
Cellulose	23.0
Mineral and vitamin mix.	30.0
DL-methionine	0.4
Dry matter	888
In DM:	
total protein	183.8
crude fibre	43.9
ether extract	8.5
ash	45.0

Experimental design. During the first (labelling) 5 days pig No 1 received 15 g/d $^{15}\text{NH}_4$ -sulphate with 91.5 at. % ^{15}N excess in two equal portions with the feed, and animal No 2 and No 3 were given the same amounts of unlabelled

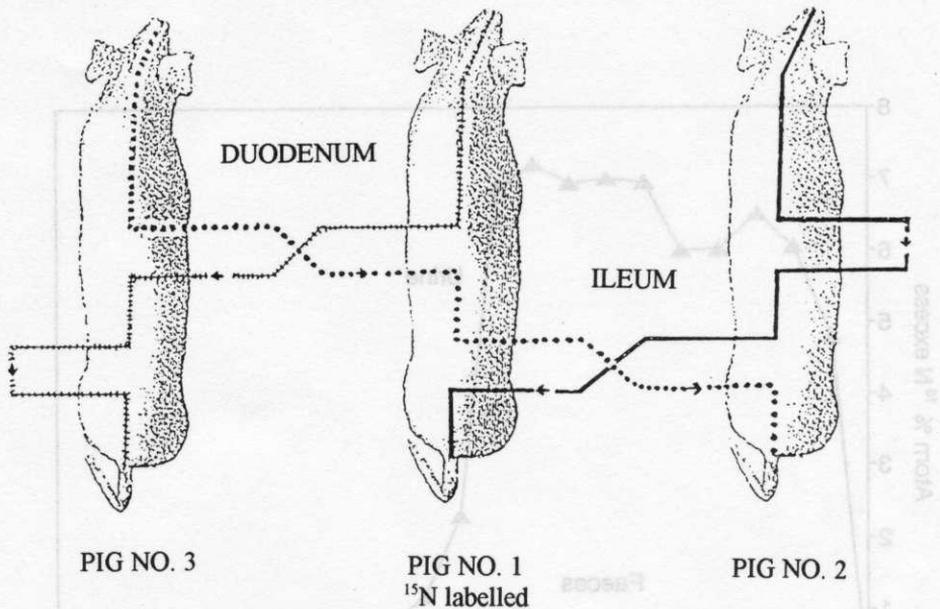


Fig. 1. Scheme of digesta exchange between animals

ammonium sulphate. On day 6 the animals were not given ammonium sulphate to make sure that all $^{15}\text{NH}_4$ -sulphate was absorbed from the digestive tract. During the following 5 days (main period) the digesta from the duodenum and ileum of pigs No 1, 2 and 3 were collected quantitatively and exchanged according to scheme given in Figure 1. Urine and faeces were collected from all the pigs during the whole experiment. At the end of the experiment the animals were killed and samples of the digesta and tissue of different segments of the digestive tract, and also organs and the whole carcass, were taken for analysis.

Samples collection and preparation. Urine was collected into the bottles containing 100 ml of 5% sulphuric acid and sampled every 12 h. Faeces were preserved with few drops of chloroform and sampled also every 12 h. The duodenal and ileal digesta were collected quantitatively, measured every hour and 5% aliquots were pooled for 6 h during the first and for 12 h during the subsequent days of the main period. All samples were kept at 0°C during collection and then stored at -25°C until analyzed.

Total nitrogen was determined by the Kjeldahl method. ^{15}N was measured using ^{15}N -analyzer Isonitromat 5201. In samples of the digesta and tissues total N and ^{15}N enrichment were measured in both TCA precipitable and soluble fractions.

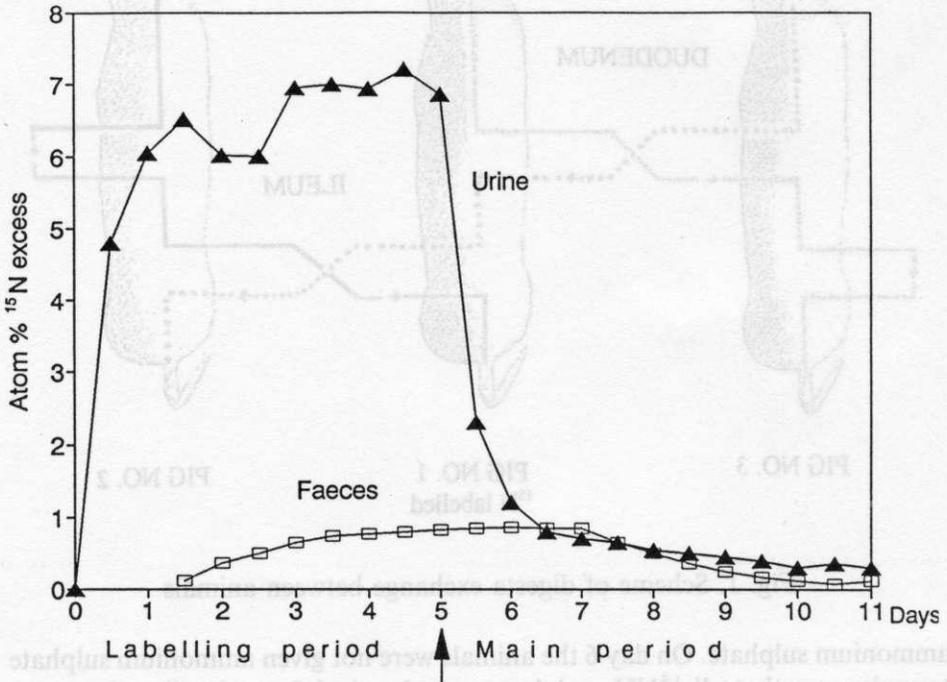


Fig. 2. Atom % ¹⁵N excess in urine and faeces of pig No. 1

RESULTS

Total N and ¹⁵N balance during the first (labelling) period. The mean apparent digestibility of nitrogen during the labelling period was 90.4 and nitrogen retention accounted for 26% of N intake as calculated from the ¹⁵N content in the carcass. ¹⁵N excretion in urine (Figure 2) has started soon after intake of the meal with the first portion of ammonium sulphate and has been increasing for two days reaching a plateau on third day of labelling period. The excretion of ¹⁵N in urine declined immediately when intake of ¹⁵N-ammonium sulphate was stopped.

Faecal excretion of ¹⁵N started about 36 h after ¹⁵N-ammonium sulphate intake, increased steadily and reached plateau after 3.5 days. The amount of ¹⁵N excretion in faeces began to decrease after 2 days without ¹⁵N intake. Cumulative excretion of ¹⁵N in urine and faeces is shown in Figure 3.

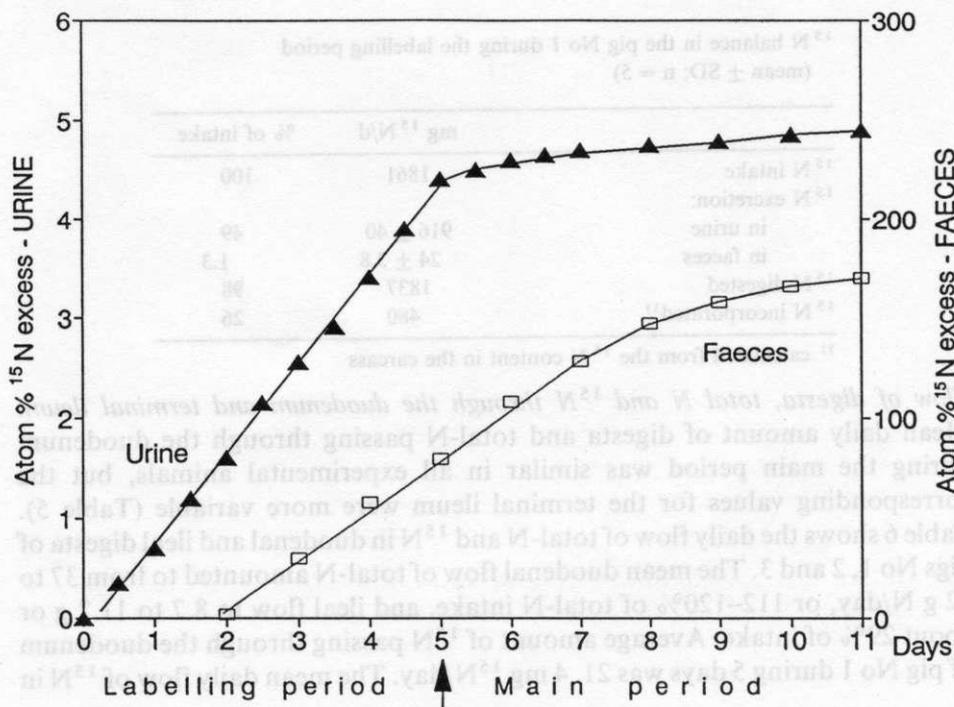


Fig. 3. ¹⁵N excretion with urine and faeces in pig No. 1 (cumulative)

The total balance of ¹⁵N in pig No 1 calculated from the amount of ¹⁵N excreted in urine and faeces during the labelling period and found in the carcass (Table 2) was 76.3% of ¹⁵N given.

Average daily excretion of total-N in urine of pigs No 1, 2 and 3 during the main period was similar to that in the labelling period and amounted to from 11.1 to 13.8 g (Table 3). Excretion of ¹⁵N in urine of the pig No 1 declined markedly from 0.79 on the first day to 0.31 at. % ¹⁵N excess on day 5. In the urine of pigs No 2 and 3 ¹⁵N excess was low, only 0.05 at. %.

Mean amount of total N and ¹⁵N excreted in faeces during the main period is shown in Table 4. Some of the ¹⁵N excreted in faeces of pig No 1 during the first and second day could come from the ¹⁵N given, however, that excreted on days 3, 4 and 5 originated only from ¹⁵N secreted into the large intestine and averaged 8.12 mg ¹⁵N/day. ¹⁵N in the faeces of pigs No 2 and 3 represented undigested endogenous ¹⁵N derived from endogenous ¹⁵N of

pig No 1 (Figure 1) and accounted for 2.13 and 1.33 mg ¹⁵N/day in animals 2 and 3, respectively.

TABLE 2

¹⁵N balance in the pig No 1 during the labelling period
(mean ± SD; n = 5)

	mg ¹⁵ N/d	% of intake
¹⁵ N intake	1861	100
¹⁵ N excretion:		
in urine	916 ± 40	49
in faeces	24 ± 3.8	1.3
¹⁵ N digested	1837	98
¹⁵ N incorporated ¹⁾	480	26

¹⁾ calculated from the ¹⁵N content in the carcass

Flow of digesta, total N and ¹⁵N through the duodenum and terminal ileum. Mean daily amount of digesta and total-N passing through the duodenum during the main period was similar in all experimental animals, but the corresponding values for the terminal ileum were more variable (Table 5). Table 6 shows the daily flow of total-N and ¹⁵N in duodenal and ileal digesta of pigs No 1, 2 and 3. The mean duodenal flow of total-N amounted to from 37 to 42 g N/day, or 112–120% of total-N intake, and ileal flow to 8.7 to 11.2 g or about 29% of intake. Average amount of ¹⁵N passing through the duodenum of pig No 1 during 5 days was 21.4 mg ¹⁵N/day. The mean daily flow of ¹⁵N in

TABLE 3

Total N and ¹⁵N excretion in urine during consecutive days of the main period in the pig No 1, 2 and 3

	D a y				
	1	2	3	4	5
<u>Pig No 1</u>					
Total N, g	10.24	6.65	13.09	13.70	11.92
¹⁵ N-excess, at. %	0.79	0.52	0.46	0.35	0.31
¹⁵ N, mg	81.27	34.69	60.50	47.95	36.95
<u>Pig No 2</u>					
Total N, g	10.95	11.84	15.92	14.45	16.26
¹⁵ N-excess, at. %	0.023	0.047	0.04	0.053	0.5
¹⁵ N, mg	2.57	5.57	6.37	7.69	8.13
<u>Pig No 3*</u>					
Total N, g	14.24	13.48	12.54	—	—
¹⁵ N-excess, at. %	0.045	0.053	0.072	—	—
¹⁵ N, mg	6.41	7.41	9.41	—	—

* Pig No 3 was used in the experiment for 3 days only because of technical reasons

TABLE 4

Total N and ¹⁵N excretion in faeces during consecutive days of the main period in pigs No 1, 2 and 3

	D a y				
	1	2	3	4	5
Pig No 1					
Total N, g	2.30	3.29	3.07	4.97	5.96
¹⁵ N-excess, at. %	0.87	0.60	0.34	0.16	0.10
¹⁵ N, mg	20.03	19.77	10.44	7.95	5.98
Pig No 2					
Total N, g	2.06	4.03	1.75	1.67	5.03
¹⁵ N-excess, at. %	0.00	0.08	0.10	0.09	0.04
¹⁵ N, mg	0.00	3.22	1.80	1.50	2.01
Pig No 3*					
Total N, g	2.07	3.45	4.09	-	-
¹⁵ N-excess, at. %	0.00	0.03	0.04	-	-
¹⁵ N, mg	0.00	1.03	1.64	-	-

* Pig No 3 was used in the experiment for 3 days only because of technical reasons

TABLE 5

Daily amount of the digesta (kg) and total nitrogen (g) passing through the duodenum and terminal ileum during the main period (mean ± SD, n = 5)

Pig No	D u o d e n u m		I l e u m	
	Amount of digesta kg	N-total g	Amount of digesta kg	N-total g
1	13.02 ± 0.72	42.4 ± 3.1	2.74 ± 0.26	8.7 ± 1.7
2	13.18 ± 1.81	38.3 ± 2.6	3.41 ± 0.48	9.6 ± 1.7
3*	12.42 ± 1.20	36.8 ± 5.1	3.60 ± 0.37	11.2 ± 2.3

* mean of 3 days

duodenal digesta of pigs No 2 and 3 were only 4.4 and 5.1mg ¹⁵N/day, respectively.

Due to secretion of ¹⁵N labelled nitrogenous substances into the lumen of the small intestine of pig No 1 the ileal digesta were enriched in ¹⁵N. The total flow of ¹⁵N in ileal digesta during the 5 days amounted to 46.1 mg in pig No 1; 6.1 mg in pig No 2 and 18.4 mg No 3. Time course of ¹⁵N excess in urine, faeces and duodenal and ileal digesta of pig No 1 are shown in Figure 4. It illustrates that although the values of ¹⁵N excess in urine, duodenal and ileal digesta differed, the slope of decline with time was similar.

The calculated half-life of ¹⁵N were: 3.75; 3.70 and 4.50 days for urine,

TABLE 6

Total N and ¹⁵N flow through the duodenum and ileum of pigs No 1, 2 and 3 during 5 consecutive days of the main period

	Pig No 1		Pig No 2		Pig No 3*	
	Total-N g	¹⁵ N mg	Total-N g	¹⁵ N mg	Total-N g	¹⁵ N mg
	D u o d e n u m					
1	47.21	31.2	41.34	0.0	42.55	1.9
2	41.20	24.7	36.14	7.3	32.92	8.2
3	38.86	17.2	39.75	4.0	35.00	5.3
4	42.03	18.9	39.14	1.9	-	-
5	42.60	14.9	35.15	0.0	-	-
	I l e u m					
1	8.53	15.0	9.68	0.9	10.31	6.6
2	6.68	9.0	9.70	0.0	14.07	7.1
3	7.99	8.3	7.15	0.0	9.37	4.7
4	9.00	7.5	11.84	2.4	-	-
5	11.30	6.2	9.42	2.8	-	-

* Pig No 3 was used in the experiment for 3 days only because of technical reasons

TABLE 7

Summary of the mean daily total-N and ¹⁵N passage along the digestive tract (arrows indicate the digesta exchange pattern, see Fig. 1)

	Pig No 1		Pig No 2		Pig No 3	
	N, g	¹⁵ N, mg	N, g	¹⁵ N, mg	N, g	¹⁵ N, mg
Intake	32.87	-	35.28	-	34.10	-
Duodenum:						
outflow	36.82	-	42.35	21.16	38.30	-
inflow	40.23*	20.05	34.98*	-	36.39	-
Ileum:						
outflow	11.25	6.19	8.71	8.09	9.56	-
inflow	10.69*	5.88*	9.08*	-	8.27*	7.09*
Faeces	4.23	1.93	3.92	8.07	2.91	1.93

* 5% was taken for analysis

duodenal and ileal digesta, respectively, and an average life of N in the pig's body calculated according to the formula $T = \frac{t_{1/2}}{0.693}$ was about 5.75 days. The slope of ¹⁵N in faeces was much steeper ($t_{1/2} = 1.05$ days) and there was no relationship to the average life of N in the body. Apparently, this could be caused by the twofold exchange of digesta. The average passage rate of total N and ¹⁵N is

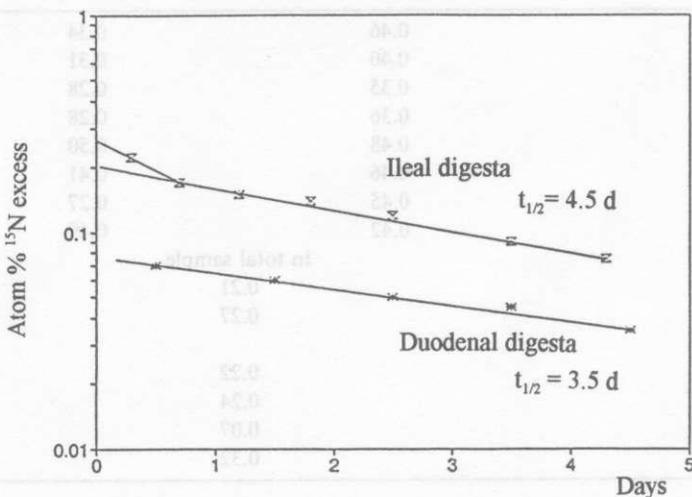
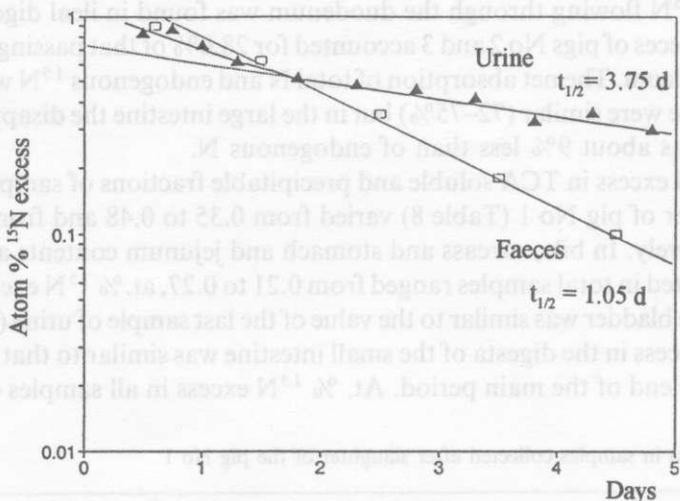


Fig. 4. Time course of at % ¹⁵N excess in urine, faeces and duodenal and ileal digesta of pig No. 1

summarized in the Table 7 taking into consideration the exchange of digesta between the animals and subtraction of the N amount in the 5% samples. The mean flow of total N through the duodeum and ileum accounted for 114.8 and 30.3% of N intake, and the content of N in ileal digesta accounted for 26.4% of that passing through the duodeum. The mean amount of faecal N accounted for 11.9% of N intake and 39.3% of that passing through the ileum. In pig No

3 30.2% of ^{15}N flowing through the duodenum was found in ileal digesta. ^{15}N excreted in faeces of pigs No 2 and 3 accounted for 28.0% of that passing through the terminal ileum. The net absorption of total N and endogenous ^{15}N within the small intestine were similar (72–75%) but in the large intestine the disappearance of total N was about 9% less than of endogenous N.

At. % ^{15}N excess in TCA soluble and precipitable fractions of samples taken after slaughter of pig No 1 (Table 8) varied from 0.35 to 0.48 and from 0.27 to 0.50, respectively. In bile, carcass and stomach and jejunum contents at. % ^{15}N excess estimated in total samples ranged from 0.21 to 0.27, at. % ^{15}N excess in the content of the bladder was similar to the value of the last sample of urine (Table 3). At. % ^{15}N excess in the digesta of the small intestine was similar to that found in digesta at the end of the main period. At. % ^{15}N excess in all samples collected

TABLE 8

^{15}N at. % excess in samples collected after slaughter of the pig No 1

Sample	TCA soluble fraction	TCA precipitable fraction
Duodenum	0.46	0.34
Ileum	0.40	0.31
Jejunum	0.35	0.28
Colon	0.36	0.28
Liver	0.48	0.50
Pancreas	0.46	0.41
Muscle	0.45	0.27
Serum	0.42	0.49
	In total sample	
Bile		0.21
Carcass		0.27
Content of:		
stomach		0.22
jejunum		0.24
colon		0.07
bladder		0.32

after slaughter of pigs No 2 and 3 was negligible.

DISCUSSION

Studies by Pahle et al. (1985), Krawielitzki et al. (1979) have shown that at. % ^{15}N excess in the TCA-precipitable fraction of the pancreas and TCA-soluble fraction of serum may indicate labelling of endogenous nitrogen secreted into the lumen of the digestive tract. Basing on that assumption at. % ^{15}N excess in endogenous nitrogen secreted in pig No 1 was calculated to be 0.41 at. % ^{15}N excess which agreed well with the value 0.47 at. % ^{15}N excess found in our earlier

experiment (unpublished data). That value corresponds with the ^{15}N -excess in tissue protein of fast turnover rate e.g. TCA-precipitable fraction of the small intestine tissue 0.34 at.% and liver 0.50 at.% ^{15}N excess. The respective values from the unpublished experiment were 0.47 and 0.62 at.% ^{15}N excess. The labelling of N in the duodenal content collected 12 h after feeding and in the urine were also similar to the calculated value 0.41 at.% ^{15}N excess. Taking the 0.41 mean at.% ^{15}N excess for the nitrogen secreted, the proportion of endogenous N in the duodenal and ileal digesta and in faeces were calculated according to the values given in Table 7 and the following equation:

$$\text{Endogenous N, mg/d} = 100 \times \frac{^{15}\text{N amount in digesta or faeces (mg/d)}}{^{15}\text{N-excess at.\% of endogenous nitrogen}}$$

Absorption of total N in the three different sections of the digestive tract was calculated from the difference of the N-input which represented the amount of N passing through, and N-secreted into the particular section, and the amount of N flowing out. Because the amount of endogenous N secreted into the lumen of this particular section and being absorbed there is difficult to evaluate, the quantities of N truly absorbed are underestimated and they represent only minimum values which may be especially low in the small intestine where processes of secretion and reabsorption are very intensive.

Assuming, however, that the rate of absorption of the unlabelled endogenous N was similar to the ^{15}N labelled endogenous N, we calculated the amount of secreted and immediately re-absorbed N in particular section of the intestine. The results of these calculation indicated:

1. The secretion of nitrogen into the stomach and proximal duodenum (including the bile and pancreatic juice) was 5.3 g/day and accounted for 14.6% of N-intake. This was within the range of values found with other methods (Juste, 1982; Low, 1982; Buraczewski, 1986; Souffrant et al., 1986).

2. The amount of N absorbed in the stomach and short proximal part of the duodenum was only 0.12 g/day and was smaller than that found by Żebrowska et al. (1982); the difference could be attributed to the different experimental design and methods used.

3. Based on the ^{15}N balance in the small intestine of pig No 3, the calculated minimum secretion was 1.97 and absorption 31.73 g N/day, while maximum secretion was 8.93 and absorption 38.69 g N/day. Within the large intestine the total amount of N secreted was 1.97 and that absorbed 8.45 g/day. Total amount of N secreted in entire digestive tract ranged from 9.21 to 16.17 g/day, equivalent to 25 and 46% of N-intake. The average amount of N absorbed was 47.3 g/day about 134% of intake. The endogenous N secreted into the lumen of the digestive tract was reabsorbed in 89.9% (minimum 82.1%). The absolute amount of endogenous N in the digesta decreased along the gut from 5.3 in the duodenum,

to 3.8 in the ileum and to 1.7 g/day in faeces; in contrast to the relative proportion of endogenous N in total N which increased from 13 to 35 and 39%, respectively.

The mucosa of the small intestine is an important secretory tissue since more nitrogen enters the intestinal lumen with the intestinal juice than with the pancreatic secretion and the bile (Juste, 1982). One may calculate using the data of Simon et al. (1979 and 1982) and McNurlan et al. (1979) that about 9 g N could be secreted by the mucosa of the small intestine and 3 g by the large intestine of pigs. These values are in good agreement with our estimates of 8.93 g and 1.97 g N/day secreted into the lumen of the small and large intestines, respectively, and those found by Buraczewska (1979) and Souffrant et al. (1986). Most of the endogenous nitrogen entering the small intestine was reabsorbed during the passage of the digesta along the gut. In the present experiment it was estimated that 82 to 90% of endogenous N was reabsorbed before the end of ileum which agrees with the value of 85% obtained by Souffrant et al. (1986) and 78% calculated by Low (1982).

The average amount of nitrogen excreted in urine during the main period accounted for 12.8 g N/d (37.5% of N intake) that was about 5% less than in the labelling period; this difference was caused by removing 5% aliquots of the duodenal and ileal digesta. The ^{15}N excreted in urine of pig No 1 during the main period originated from the breakdown of body protein. In contrast to that, the ^{15}N in the urine of pigs No 2 and 3 came from the absorbed, endogenous ^{15}N -labelled nitrogen, introduced into their intestines by the digesta exchange. ^{15}N entering the large intestine (pig No2) was absorbed there in about 75% and most of it was excreted in urine, indicating that it was absorbed as ammonia from deaminated ^{15}N labelled amino acids. Within the whole gut 90% of endogenous ^{15}N was absorbed; about 1/3 thereof was excreted in urine and 2/3 were retained in the body.

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STRESZCZENIE

Badania nad wchłanianiem i sekrecją endogennych ^{15}N związków azotowych w przewodzie pokarmowym świni

Doświadczenie przeprowadzono na 3 knurkach o średniej masie ciała 30 kg, z przetokami mostkowymi dwunastnicy i jelita biodrowego. Zwierzęta żywiono paszą o zawartości 8% białka ogólnego w SM podając po 600 g paszy co 12 godz. W czasie pierwszych 5 dni doświadczenia (okres wstępny) świnią No 1 otrzymywała z paszą znakowany ^{15}N siarczan amonu, a zwierzęta No 2 i 3 siarczan amonu zwykły. W okresie wstępnym zbierano kał i mocę i oznaczano bilans N i ^{15}N oraz tempo wydalania ^{15}N w kale i moczu. W następnych 5 dniach doświadczenia (okres właściwy) zaprzestano podawania znakowanego azotu i zbierano ilościowo treść dwunastnicy i jelita biodrowego wymieniając treść wg. schematu: treść dwunastnicy od naznaczonego ^{15}N zwierzęcia No 1 podawano do dwunastnicy świni No 3 zaś treść dwunastnicy tej świni podawano świni No 1. Treść jelita biodrowego świni No 1 wymieniano z treścią jelita biodrowego No 2. Pozwoliło to na oszacowanie metodą rozcieńczeń izotopu wielkości sekrecji i wchłaniania azotu z kolejnych odcinków przewodu pokarmowego: 1 – żołądek i początek dwunastnicy; 2 – jelito cienkie; 3 – jelito grube. Do pierwszego odcinka wydzielano się 5,3 g N/dobę co stanowiło 15% w odniesieniu do azotu pobranego. Dobowa sekrecja N do odcinka drugiego wynosiła 8,9 g (25% N pobranego), a do odcinka trzeciego 1,9 g N/dobę. W odcinku pierwszym ulegało wchłonięciu 0,2 g N/dobę, w drugim – 38,7 g N/dobę (110% w stosunku do N pobranego), w trzecim – 8,4 g N/dobę (24% N pobranego). Ilość N endogennego w treści dwunastnicy, jelita biodrowego i w kale wynosiła 5,3; 3,8 i 1,6 g N/dobę, odpowiednio, co stanowiło 15; 35 i 39% azotu ogólnego. Azot endogenny wydzielony do światła przewodu pokarmowego ulegał wchłonięciu w około 90%. N i ^{15}N wchłonięty w jelicie grubym został prawie w całości wydalony w moczu.