Nitrogen secretion and absorption in different segments of the digestive tract estimated by digesta exchange between ^{15}N-labelled and unlabelled sheep[*]

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ABSTRACT

Three male sheep of about 25 kg body weight fitted with a cannula into the rumen and reentrant cannula in the proximal duodenum and in the distal ileum were used for this study. Sheep No. 1 was infused intraruminally with ^{15}N urea (1g /d, 95 atom% ^{15}N) for labelling with ^{15}N, Nos. 2 and 3 with unlabelled urea. All animals were fed 800 g DM /d of a hay and concentrate diet (40 : 60) containing 15.4 % crude protein and 15.3 % crude fibre, divided into 6 feeding portions per day. After reaching a quasi-steady state in the ^{15}N level of animal No. 1, passage of total N and ^{15}N throughout the duodenum and the ileum, N excretion in faeces and urine were estimated. On day 7 and 8 of the experiment the duodenal and ileal digesta were exchanged between the labelled animal (No. 1) and the unlabelled ones (No. 2, 3) according to the respective scheme. Digesta flow was measured directly during 48 h and 3% aliquots were sampled for analysis of N and ^{15}N content. The contents of N and

[15]N were also estimated in faeces, urine and blood. The obtained data were used for calculation of the passage and absorption of exogenous N and the secretion, absorption and reabsorption of endogenous N in three digestive sections from mouth to proximal duodenum, from duodenum to ileum, and from ileum to rectum.

The flow of total N, exogenous N and endogenous N decreased from duodenum to ileum and faeces, but the relative content of endogenous N increased from 36 to 54 %. N-secretion was highest in the first section of the digestive tract (9.9 g N/d = 60% of the secretion in total digestive tract) and absorption was highest in the second section (14.1 g N/d = 46 % of total absorption). Endogenous origin N was about 54 % of faecal N. Faecal loss, 2.0 g endogenous N/d, was only about 12% of the total endogenous N (16.5 g N) secreted into the lumen during the intestinal passage of digesta. Total reabsorption of endogenous N amounted to 88%. The results demonstrate the high dynamics of N metabolism during digestion in ruminants.

KEY WORDS: sheep, passage rate, ^{15}N, endogenous N, exogenous N, absorption, secretion, reabsorption

INTRODUCTION

Absorption of nitrogen compounds along the digestive tract of animals is accompanied by secretion of endogenous nitrogen into the intestinal lumen and both of these processes occur simultaneously. It is difficult to quantify them because of the lack of accurate methods for differentiation between endogenous and exogenous compounds of the digesta (Krawielitzki et al., 1990, 1996). In ruminants the situation is even more complicated because of their ability to utilise NPN compounds for protein synthesis and to recycle N into the rumen (Kowalczyk et al., 1975; Ivan et al., 1981; Żebrowska and Kowalczyk, 1991; Van Bruchem et al., 1997). Nitrogen digestibility in the gastro-intestinal tract and N recycling are influenced by different factors. Better understanding of the processes of N absorption, secretion and recycling in different sections of the digestive tract is required to increase N utilization and to reduce N excretion by ruminants.

Therefore, the main objectives of the present study with growing sheep were to determine:
− the proportion of endogenous N:exogenous N in different sections of the ruminant digestive tract,
− to estimate the amount of endogenous N secreted and absorbed in different sections of the digestive tract,
− to evaluate the reabsorption of endogenous N along the intestine.

These processes were investigated by means of digesta exchange between ^{15}N-labelled and unlabelled animals.

MATERIAL AND METHODS

Animals

Three 5-month-old Polish Merino male sheep of about 25 kg body weight were fitted with a cannula in the rumen and re-entrant cannulas at the duodenum distal to the pancreatic duct opening and at the ileum about 25 cm before the ileo-caecal junction. Animal No. 1 was also equipped with a catheter into the jugular vein for blood sampling.

Feeding

The animals were given 800 g dry matter of a cut meadow hay and concentrate diet (40:60) daily. The pelleted concentrate was composed of ground barley 82.2%, soyabean meal 15.8% and vitamin-mineral mixture 2.0%. The diet contained in 1 kg of dry matter: 154 g crude protein, 153 g crude fibre, 63.5 g ash, 16.7 g ether extract and 11.0 MJ ME. Rations were fed in 6 equal portions in 4 h intervals. Water was available *ad libitum*. Feed refusals were collected and weighed daily.

Housing

During the recovery period the animals were housed individually in pens on sawdust bedding. During the experiment they were kept in metabolic cages permitting quantitative collection of faeces and urine and sampling of ruminal, duodenal and ileal digesta.

Experimental design and sampling

The experiment was divided into 3 periods: labelling (day 1-6); digesta exchange (day 7-8) and clearance (day 9-10). Four weeks after surgery during the labelling and exchange periods animal No. 1 was continuously infused intraruminally with 1g/d uniformly labelled ^{15}N urea (95% ^{15}N atom excess). Animals No. 2 and 3 were simultaneously infused intraruminally with the same amount of unlabelled urea.

During the two days of the exchange period the duodenal and ileal digesta were collected continuously, measured and 3% aliquots from 4 h intervals were pooled for 24 h samples and then frozen at $-20°C$ until analysis for nitrogen and ^{15}N content. Digesta was kept during collection at $0°C$ and after sampling warmed to $38°C$ and exchanged between animals according to the scheme given in Figure 1.

Faeces and urine were collected during all 3 experimental periods. Collected faeces was preserved with a few drops of chloroform, measured and sampled
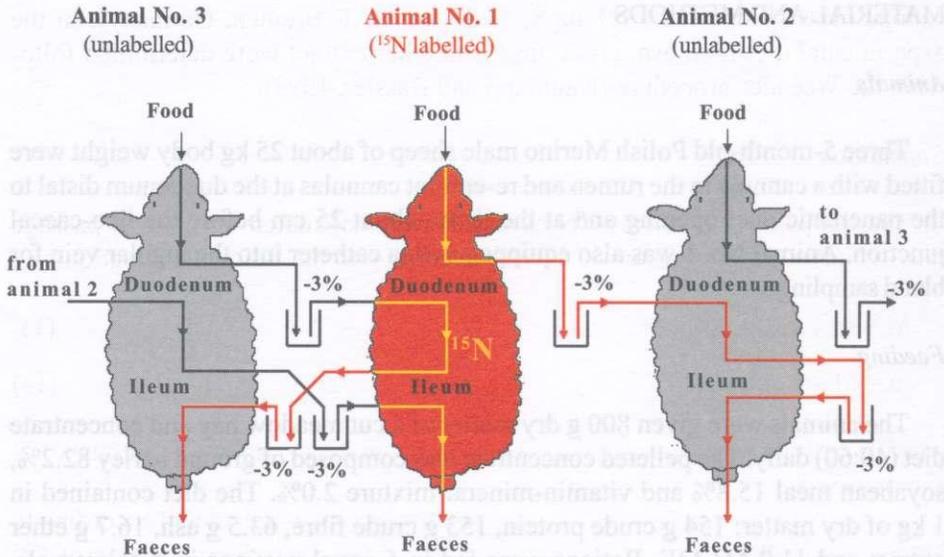
Figure 1. Scheme of digesta exchange between labelled and unlabelled sheep

every 24 h. Urine was collected using the device described by Kowalczyk et al. (1996) into vessels with 100 ml 6N sulphuric acid in intervals of 24 h except on day 1 (start of labelling period) and day 9 (first day of clearance period) where intervals of 4 h were chosen.

The obtained data were used to calculate passage and absorption of exogenous N and secretion, absorption and reabsorption of endogenous N for three sections of the digestive tract: mouth-duodenum, duodenum-ileum, and ileum-rectum.

Samples of about 50 ml rumen fluid and 5 ml blood from the jugular vein were taken before the morning feeding at 8.00 during all three experimental periods. Bacterial mass from the rumen samples was separated by fractional centrifugation according to Beever et al. (1974). After filtration feed particles were separated by centrifugation at 2800 x g for 10 min at 5°C and then bacteria from the supernatant by centrifugation at 20.000 x g for 30 min at 2°C. The bacterial mass was freeze-dried and analyzed for N and ^{15}N content. ^{15}N% atom excess was determined in blood plasma obtained by spinning blood samples for 20 min at 5000 rpm .

During the clearance period the decay of ^{15}N in blood and urine was observed for animal No. 1 after ending the infusion of ^{15}N-urea. From these data the half-life of the metabolic pool and the average dwelling time for N in the body of the animals were estimated.

All samples were stored at -20°C until analysis for N by the Kjeldahl method and for ^{15}N after chemical preparation according to Voigt et al.(1980) by means of

isotope mass spectrometry (Delta S, Finnigan MAT, Bremen, Germany). In the experimental diet DM, ash, crude fibre and ether extract were determined following the Weender procedure (Naumann and Bassler, 1993).

Calculation

The ^{15}N passage rates (mg ^{15}N excess/d) were calculated from the N passage rate (g N/d) and the ^{15}N [atom% excess] according to the following equations:

$$M = m \times a/100 \ \times 15/14 \tag{1}$$

$$m = M \times 100/a \times 14/15 \tag{1a}$$

where M = mg ^{15}N excess; m = mg N (here mg endogenous N); a = atom% ^{15}N excess (see Schubert, 1995).

The amount of endogenous N in digesta and faeces was calculated according to Voigt et al. (1996) and to Van Bruchem et al. (1997) from the proportion of ^{15}N [atom% excess] of this fraction and ^{15}N excess of the blood plasma NPN fraction and the N content of the fraction using the equation:

$$\text{endogenous N [g/d]} = N\ [g/d] \ \times \ \frac{^{15}N \text{ excess in digesta resp. faeces}}{^{15}N \text{ excess in plasma NPN}} \tag{2}$$

The exogenous N in digesta N and faecal N were calculated as the difference of total and endogenous N:

$$\text{exogenous N [g/d]} = \text{total N [g/d]} - \text{endogenous N [g/d]} \tag{3}$$

The data of total N, endogenous N and exogenous N of duodenal digesta, ileal digesta, and faeces and the appearance, and disappearance rates of N and ^{15}N during passage through the different intestinal sections were the basis for further computing N secretion and N absorption in the 3 digestive segments: mouth-duodenum, duodenum-ileum, and ileum-anus.

RESULTS

All sheep were in good condition during the whole experiment. Feed intake was diminished from 19.1 g N/d during the labelling period to 17.6 g N/d during the exchange period (both including 0.45 g N/d from urea infusion).

N balance

The nitrogen balance of the three experimental animals estimated during the 6-day labelling period is shown in Table 1, which demonstrates an average balance of 6.9 g N/d corresponding to protein accretion of 43 g/d that is the normal value for sheep under such conditions. On average 41.4 % of N intake was excreted in urine and 22.2 % in faeces. The corresponding data for ^{15}N were 50.2 % of the ^{15}N infusion dose in urine and 6% by faeces.

TABLE 1

Nitrogen balance during the 6 day labelling period

Animal	No. 1	No. 2	No. 3	x̄	± SD
N intake (total), g/d	19.44	17.32	20.47	19.08	1.61
Food N, g/d	18.99	16.85	20.00	18.61	1.61
N infusion, g/d	0.45	0.47	0.47	0.47	0.01
N excretion					
urine N, g/d	8.31	5.97	9.41	7.90	1.76
faeces N, g/d	4.27	4.46	4.00	4.24	0.24
N accretion, g/d	6.86	6.89	7.06	6.94	0.11
% of intake	35.3	39.8	34.5	36.5	2.86
Apparent digestibility, %	78.0	74.2	80.5	77.6	3.13

Course of ^{15}N level

One of the main conditions for the estimation of endogenous N in different sections of the intestine was the steady-state of labelling animal No. 1 and reaching a steady-state in ^{15}N level before starting the exchange period, which was the main period of the experiment.

Figure 2 demonstrates the course of ^{15}N level in microbial protein isolated from the rumen and Figure 3 the course of ^{15}N level in the TCA-soluble fraction of blood plasma of animal No 1. Both figures show an exponential increase of ^{15}N reaching a plateau within the labelling period of 6 days. Figure 3 demonstrates additionally:
– a small decrease of the ^{15}N plateau during the exchange period (day 7-8) caused by the exchange of labelled digesta in the duodenum of animal No. 1 against unlabelled digesta of animal No. 3 during this period,
– exponential decay of ^{15}N content during the clearance period (day 9-10),
– that the exponential decrease during the clearance period was nearly the same as the exponential increase during the labelling period.
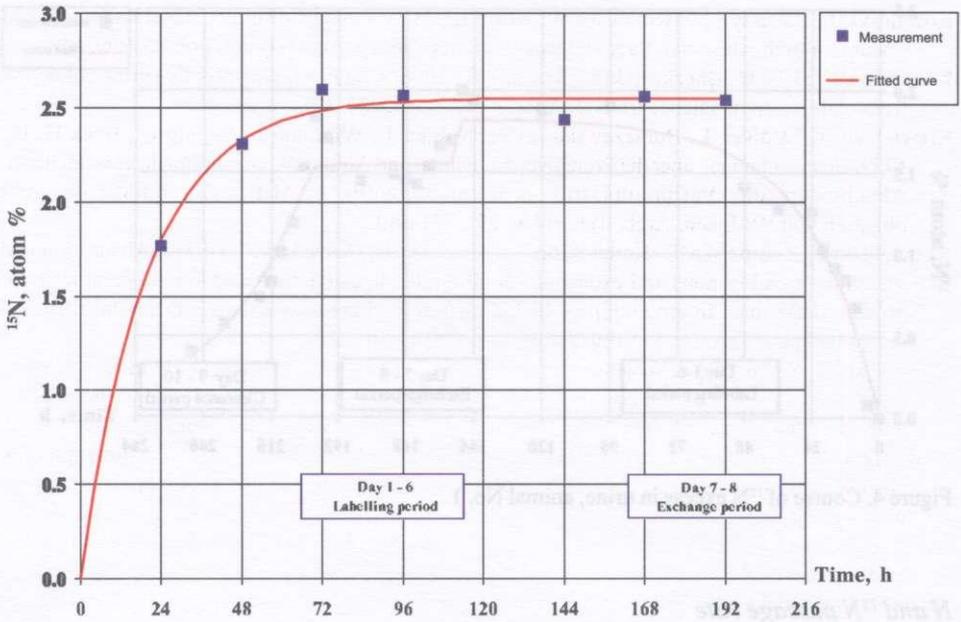An analogous course was shown for ^{15}N excess in urine (Figure 4).

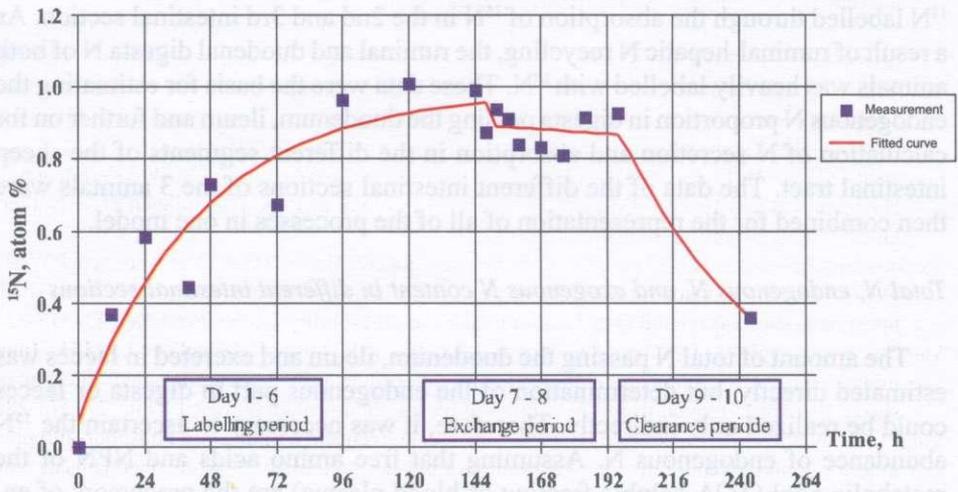Figure 2. Course of ^{15}N excess in microbial protein in the rumen, animal No. 1

Figure 3. Course of ^{15}N excess (atom%) in blood plasma (TCA soluble fraction), animal No. 1
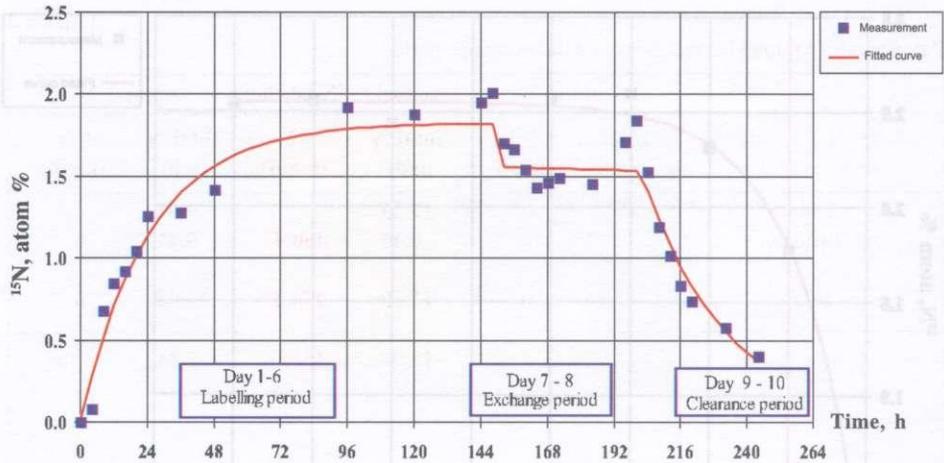
Figure 4. Course of ^{15}N excess in urine, animal No. 1

N and ^{15}N passage rate

The values for N and ^{15}N passage were estimated during the 48 h exchange period for all three animals; the values beginning with feed intake, duodenal passage, ileal passage, and excreted faeces are given in Table 2. For animal No. 2 the N intake during the exchange period was considerably smaller than in the labelling period, which was taken into account in the calculations.

During the exchange period the unlabelled animals No. 2 and No. 3 also became ^{15}N labelled through the absorption of ^{15}N in the 2nd and 3rd intestinal section. As a result of ruminal-hepatic N recycling, the ruminal and duodenal digesta N of both animals was heavily labelled with ^{15}N. These data were the basis for estimating the endogenous N proportion in digesta passing the duodenum, ileum and further on for calculation of N secretion and absorption in the different segments of the sheep intestinal tract. The data of the different intestinal sections of the 3 animals were then combined for the representation of all of the processes in one model.

Total N, endogenous N, and exogenous N content in different intestinal sections

The amount of total N passing the duodenum, ileum and excreted in faeces was estimated directly, but determination of the endogenous part in digesta or faeces could be realized only indirectly. Therefore, it was necessary to ascertain the ^{15}N abundance of endogenous N. Assuming that free amino acids and NPN of the metabolic pool (TCA-soluble fraction of blood plasma) are the precursors of endogenous N compounds secreted into the digestive tract, the ^{15}N level of this frac-

TABLE 2

Passage rates for total N and ^{15}N excess the exchange period

	Animal 3		Animal 1 ^{15}N-labelled		Animal 2	
	Total N (g/d)	^{15}N (mg/d)	Total N (g/d)	^{15}N (mg/d)	Total N (g/d)	^{15}N (mg/d)
Feed + Infusion	17.6 0.47	0	17.23 0.45	460.4	9.57 0.47	0
= Intake	17.63	0	17.68	460.4	10.04	0
Duodenum -3%	14.97	1.13	15.54	251.7	5.84	5.65
			Digesta exchange			
	from animal 3 to animal 1		from animal 1 to animal 2		from animal 2 to animal 3	
Reentrance	5.67	5.48	14.52	1.1	15.08	244.1
Ileum -3%	3.06	0.95	5.18	7.99	5.43	66.65
			Digesta exchange			
	from animal 3 to animal 1		from animal 1 to animal 3		from animal 2 to animal 2	
Reentrance	5.02	7.75	2.97	0.92	5.27	64.65
Faeces	3.24	3.92	2.97	10.59	3.66	38.01
Urine	6.78	3.73	9.39	164.6	10.93	58.27

metabolic pool (TCA-soluble fraction of blood plasma) are the precursors of endogenous N compounds secreted into the digestive tract, the ^{15}N level of this fraction can be considered to be a suitable indicator for ^{15}N labelling of endogenous N (Krawielitzki et al., 1979; Hernandez et al., 1981; Pahle et al, 1981; Bergner and Bergner, 1982). The ^{15}N level of TCA soluble plasma N was estimated for animal No. 1 as 0.873 atom% excess and for animal No. 2 as 0.253 atom % excess. Assuming this as indicator for endogenous N and using equation 1 follows:

for animal No. 1 : 1 mg ^{15}N in digesta = 107 mg endogenous N

for animal No. 2 : 1 mg ^{15}N in digesta = 369 mg endogenous N.

Using these proportions the amount of endogenous N can be calculated in digesta and faeces by means of the isotope dilution method (equations 1-3). Calculated passage rates for total N, exogenous N, and endogenous N from feed ingested over the duodenum, and ileum to faeces are demonstrated in Table 3.

TABLE 3

Nitrogen passage rate through the duodenum, ileum and in faeces g N/d (average of two animals only)

	Intake	Rumen	Duodenum	Ileum	Faeces
Total N	17.7	12.9	15.2	5.5	3.7
Exogenous N	17.7	9.8	9.8	3.8	1.7
Endogenous N	0	3.1	5.4	1.7	2.0
Proportion of endogenous N in total N, %		24	36	31	54

It is seen that the amount of total N, exogenous N, and endogenous N decreased during passage from the duodenum to ileum and to faeces, but the relative parts of endogenous N increased from 36% in the duodenum to 54% in the faeces. The endogenous N part of the ileal digesta (31 %) did not differ significantly from that of the duodenal digesta but seems somewhat underestimated. During an additional experiment the flow of bile and pancreatic juice was estimated as 2.3 g N /d under these conditions, enabling the calculation of the N flow rate out of the rumen.

Secretion and absorption of endogenous and exogenous N in different digestive tract sections

Beside the exogenous and endogenous N fractions in duodenal digesta, ileal digesta and faeces, the rates of secretion and absorption for the 3 digestive segments were also estimated using the N and ^{15}N passage rates measured during the exchange period of the experiment. Absorption of exogenous N was estimated as the difference of total N and endogenous N for all 3 segments. The secretion and absorption rates for the different segments of the intestinal tract are summarized in the diagram (Figure 5).

The values given in Figure 5 show that:

– secretion was highest in section 1 (9.9 g N/d up to the duodenum including the bile and pancreatic juice),

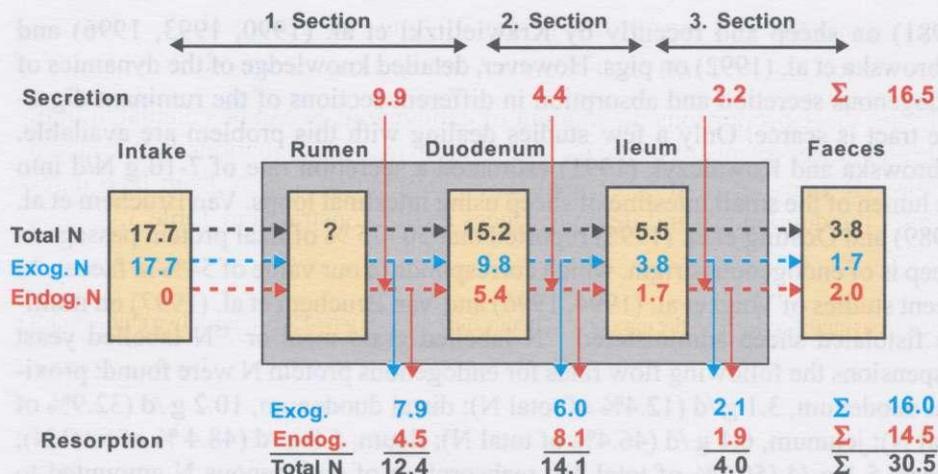– secretion into the small intestine behind the pancreatic duct was 4.4 g N/d,

Figure 5. Secretion and absorption rates in the 3 segments of the intestinal tract, g N/d

– total N secretion was 16.5 g N /d , nearly the amount of N ingested,
– absorption was highest in section 2 (duodenum – ileum) reaching a value 14.1 g
  N/d, which is about half of the N absorbed in the whole digestive tract,
– relatively high absorption occurred in section 3 (large intestine),
– total absorption of N amounted to 30.5 g/d, which was about 175% of N ingested,
– the apparent ileal N digestibility was 68.9 % and faecal 78.5 %, whereas the true
  ileal N digestibility was 78.5% and faecal 90.4% ,
– reabsorption of endogenous N was high and amounted to 88 %. Only 2.0 g /d = 12%
  of the endogenous N secreted into the gut was lost in faeces.

DISCUSSION

It is difficult to measure the amount of endogenous nitrogen in different seg-
ments of the digestive tract because one can not distinguish accurately between
nitrogen of endogenous and exogenous origin in the digesta (Low and Żebrowska,
1989). From the different methods reviewed by Souffrant (1991) the ^{15}N isotope
dilution technique seems to be most suitable for this purpose. The application of this
method developed for estimation of endogenous secretion in monogastric ani-
mals (Bergner et al., 1984; de Lange et al., 1990; Krawielitzki et al., 1990;
Żebrowska et al., 1992; Huisman et al., 1992, 1993) is more complicated for rumi-
nants because of rumen digestion and the ruminal-hepatic recycling (Kowalczyk
et al., 1975).

The method of digesta exchange between fistulated ^{15}N labelled and unlabelled
animals for investigation of endogenous secretion had been used by Ivan et al.

(1981) on sheep and recently by Krawielitzki et al. (1990, 1993, 1996) and Żebrowska et al. (1992) on pigs. However, detailed knowledge of the dynamics of endogenous secretion and absorption in different sections of the ruminant digestive tract is scarce. Only a few studies dealing with this problem are available. Żebrowska and Kowalczyk (1991) estimated a secretion rate of 7-10 g N/d into the lumen of the small intestine of sheep using intestinal loops. Van Bruchem et al. (1989) and Oosting et al. (1995) reported that 50 -75 % of ileal protein passage in sheep is of endogenous origin, which corresponds to our value of 54% in faeces. In recent studies of Voigt et al. (1994, 1996) and Van Bruchem et al. (1997) on multiple fistulated sheep administered ^{15}N labelled grass meal or ^{15}N labelled yeast suspensions the following flow rates for endogenous protein N were found: proximal duodenum, 3.1 g /d (12.4% of total N); distal duodenum, 10.2 g /d (32.9% of total N); jejunum, 6.1 g /d (46.4% of total N); ileum, 5.0 g /d (48.4 % of total N); faeces, 5.1 g /d (50.7% of total N); reabsorption of endogenous N amounted to 71%. These findings correspond with those of the presented study. Only for secretion of endogenous N in the second intestinal section (small intestine) our value (4.4 g N/d) is lower and probably underestimated in relation to the findings of Van Bruchem et al.(1997). It is not excluded that the digesta exchange between animals had some influence on N secretion along the small intestine. However, the accuracy of the estimations decreases progressively towards the end of the digestive passage and these preliminary values should be considered with some caution and verified in further experiments.

It is important for the proper course of this type of experiment with animals to ensure a similar course of digestion processes for all 3 animals during the whole trial. For this it is necessary not only to reach an identical feed and N intake for all 3 animals but also an exchange of digesta approximately synchronized in time and amount. These conditions were not totally fulfilled in our experiment as the N intake of animal No. 2 from the beginning of the exchange period was considerably lower than for both other animals, though they were similar during the labelling period. Therefore, a correction factor for percentage compensation was needed accepting assumption that the ratio of endogenous N:exogenous N will be constant for all three animals and will not be influenced by the food intake.

Absorption of total N and endogenous N in different sections of the digestive tract is usually calculated by the difference between the N input and the N output of the segment being examined. The quantity of truly absorbed N is mostly underestimated because the amount of endogenous N secreted into the lumen of this particular section and being absorbed before reaching its end is difficult to evaluate (Żebrowska et al., 1992). Such difficulty was avoided to a high degree in the presented experiment by estimating the true appearance and disappearance rate of ^{15}N labelled endogenous N of digesta passing through the particular intestinal section. Therefore, the secretion and absorption rates found in the experiment, espe-

cially those for reabsorption of endogenous N, are somewhat higher than those in earlier studies.

Another problem to be resolved is the assumption of nearly constant composition or even of approximately the same ¹⁵N level for all endogenous secretions along the intestinal tract (saliva, bile, pancreatic juice, ruminal and intestinal secretions). This is a simplification which is necessary for calculation of the endogenous part of N in the different sections of the digestive tract. This problem is relevant also for all the other methods for estimating endogenous N metabolism applying isotopic dilution methods. The possible error or deviation caused by this simplified assumption will be taken into consideration and quantified in further studies.

In summary, it may be concluded that the dynamics of metabolic processes during N digestion in ruminants are often underestimated. The combination of the ¹⁵N tracer technique and digesta exchange between labelled and unlabelled animals seems to be a suitable method for this purpose.

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STRESZCZENIE

Wydzielanie i wchłanianie azotu w różnych odcinkach przewodu pokarmowego owiec, oznaczone metodą wymiany treści między zwierzętami znakowanymi ^{15}N i nie znakowanymi

Badania prowadzono na trzech tryczkach o masie ciała około 25 kg z przetokami do żwacza i przetokami mostkowymi w początkowej części dwunastnicy oraz końcowej jelita biodrowego. Owca No.1 otrzymywała dożwaczowo w infuzji ciągłej ^{15}N mocznik (1 g/d 95% nadmiaru ^{15}N), natomiast owce No.2 i 3 takie same ilości mocznika nie znakowanego. Wszystkim zwierzętom podawano dziennie dawki paszowe zawierające 800 g SM, złożone z siana łąkowego i paszy treściwej w proporcji 40:60. Dawki zawierały 15,4% białka ogólnego i 15,3% włókna surowego. Paszę podawano w 6 jednakowych porcjach co 4 godziny. Po osiągnięciu stanu równowagi w poziomie ^{15}N u owcy No.1 oznaczano przepływ N ogólnego i ^{15}N przez dwunastnicę i jelito biodrowe oraz ich wydalanie w moczu i kale. W siódmym i ósmym dniu doświadczenia wymieniano treść wypływającą z dwunastnicy i jelita biodrowego między znaczonym izotopem zwierzęciem No.1 a nie znaczonymi No. 2 i 3, zgodnie z przyjętym schematem. Przepływającą w ciągu 48 godz. treść ważono i pobierano 3% próby do analiz na zawartość N i ^{15}N. Zawartość N i ^{15}N oznaczano również w kale, moczu i odbiałczonej plazmie krwi. Na podstawie uzyskanych wyników obliczono przepływ i ilość wchłanianego N egzogennego oraz wydzielanego i ponownie wchłanianego azotu endogennego w trzech częściach przewodu pokarmowego, a mianowicie na odcinku do początkowej części dwunastnicy, w jelicie cienkim i grubym.

Ilość przepływającego N ogólnego, egzogennego i endogennego zmniejszała się od dwunastnicy poprzez jelito cienkie do kału, ale udział N endogennego zwiększał się w tych odcinkach od 36 do 54%. Wydzielanie N było największe w pierwszej części przewodu pokarmowego (9,9 g/d), co stanowiło 60% N wydzielonego do całego przewodu pokarmowego, natomiast wchłanianie było najwyższe w drugim odcinku (14,1 g N/d = 46% N wchłoniętego). N pochodzenia endogennego stanowił 54% azotu zawartego w kale. Straty N endogennego w kale wynosiły 2 g/d, co stanowiło 12% ogólnej ilości azotu endogennego (16,5 g) wydzielonego do światła jelita. Całkowita reabsorpcja azotu endogennego wynosiła 88%. Uzyskane w doświadczeniu wyniki wskazują na wysoką dynamikę przemian azotu u przeżuwaczy.