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Studies on N-metabolism in different gastro-intestinal sections of sheep using the digesta exchange technique. 3. N secretion and reabsorption*

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ABSTRACT

Using a combination of fistulation, ^{15}N isotope technique and digesta exchange between labelled and unlabelled sheep, the flow rates of digesta (Sandek et al., 2001a) and the flow rates of endogenous N (Sandek et al., 2001b) were previously estimated. On the basis of these data N reabsorption in the stomachs, the small and large intestine as well as N secretion in these three sections were calculated and differences caused by variations in the crude fibre intake of the two feeding groups (Group 1: 89.7 g/d, Group 2: 119.4 g/d) were estimated.

Net N secretion into the forestomachs and abomasum varied considerably between the individual experiments (0.6-2.7 g N/d) but did not show clear differences between the groups. Daily N secretion into the small intestine was substantially higher in Group 2, amounting to 5.8 g in Group 1 and 7.7 g in Group 2 ($P<0.05$). In contrast, the daily N secretion into the large intestine was lower in Group 2 (2.3 g N vs 1.06 g N), corresponding to 30 and 12% of total postruminal N secretion, respectively.

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The daily net N absorption in the rumen and abomasum was 5.5 g N in Group 1 and only 2.9 g N in Group 2 ($P<0.10$). The reabsorption of postruminaly secreted N in the small intestine was 4.5 g N/d in Group 1 and 7.0 g N/d in Group 2 ($P<0.05$). Reabsorption per kg DMI in Group 2 were significantly enhanced when compared with Group 1 (14.7 vs 7.2 g/d; $P<0.05$) but there were no differences when N reabsorption was calculated as a percentage of the endogenous N entering the small intestine (77 vs 73%). Concerning N reabsorption in the large intestine (1.8 g N/d in Group 1 and 1.5 g N/d in Group 2) no differences were observed between the groups. The daily amount of postruminaly reabsorbed N was 6.4 g (Group 1) and 8.5 g (Group 2), which represents 75 and 84% of the total postruminal input of endogenous N, respectively. The greatest part of the postruminal endogenous N was reabsorbed during passage of digesta through the intestine.

KEY WORDS: sheep, digestive tract, digesta exchange, endogenous N, ^{15}N, N secretion, N reabsorption

INTRODUCTION

During digestion processes in the intestine fluid N-containing substances are secreted as protein or NPN by the intestinal wall and *via* bile and pancreas. Endogenous N is partly reabsorbed or excreted in the faeces. Neither the secreted nor the reabsorbed gross N amounts are known in sufficient detail.

Different methods were developed to determine N secretion in the individual sections of the intestinal tract. One possibility of determining the net secretion of N is the infusion of an N-free solution into isolated intestinal loops (Kay, 1969; Żebrowska and Kowalczyk, 1991; Skiba et al., 1995). These authors assumed that secretion is relatively constant over the entire intestine and throughout the day. Combination of the ^{15}N dilution technique with multiple fistulation of animals also enables the determination of N secretion. Van Bruchem et al. (1997) measured the entry of ^{15}N into the intestinal lumen at different positions after labelling the metabolic pool of sheep with ^{15}N amino acids. Other authors substituted digesta of ^{15}N labelled animals with pre-collected unlabelled digesta and studied the level of its labelling (Bergner et al., 1985; Siddons et al., 1985; Sommer et al., 1986). Assuming certain reabsorption rates, N secretion can be determined in this manner too. On the other hand, if ^{15}N-labelled chyme is given to an unlabelled animal, N reabsorption can be determined from the decreased ^{15}N passage. Through a combination of several techniques is necessary for simultaneous determination of N secretion and reabsorption.

Using a combination of fistulation, the ^{15}N isotope technique and digesta exchange between labelled and unlabelled animals, we estimated the flow rates of digesta and postruminaly secreted N (Sandek et al., 2001a,b). The present paper deals with the calculation of N secretion and N reabsorption in the stomachs and the small and large intestine.

MATERIAL AND METHODS

Details on modelling, animals, housing, feeding and the experimental protocol were recently described by Sandek et al. (2001 a,b). In brief, two groups of male growing sheep (Polish Merino, 20-25 kg BW), fitted with a cannula into the rumen, with re-entrant cannulas in the proximal duodenum and distal ileum and with a jugular vein catheter, were used for this experiment. In order to investigate the influence of crude fibre (CF) on postruminal N secretion and reabsorption, the following two dietary treatments were used:

Group 1 (experiments 1-3) low CF: 14.7% CF in DM; 16.3% CP in DM; 11 MJ ME/kg DM; 616 g DM intake × $sheep^{-1} \times d^{-1}$

Group 2 (experiments 4-6) high CF: 24.9% CF in DM; 15.7% CP in DM; 10 MJ ME/kg DM; 467 g DM intake × $sheep^{-1} \times d^{-1}$.

In each experiment three sheep were used. One of them (animal No. 1) was infused intraruminally with ^{15}N urea to label the metabolic N pool. After 6 d of labelling the duodenal and the ileal digesta were exchanged between the labelled animal and the unlabelled ones as follows:

Duodenal contents were exchanged:
from animal No. 1 (^{15}N labelled) ⇒ animal No. 2 (unlabelled)
from animal No. 2 (unlabelled) ⇒ animal No. 3 (unlabelled)
from animal No. 3 (unlabelled) ⇒ animal No. 1 (^{15}N labelled).
Ileal contents were exchanged:
from animal No. 1 (^{15}N labelled) ⇒ animal No. 3 (unlabelled)
from animal No. 2 (unlabelled) ⇒ animal No. 2 (unlabelled).
from animal No. 3 (unlabelled) ⇒ animal No. 1 (^{15}N-labelled)

Calculation of the secretion and reabsorption rates in the small and the large intestine was realised using the disappearing rate of ^{15}N in intestinal sections and the flow rate of endogenous N (Sandek et al., 2001b). Two experiments could be used for this calculation per group. One experiment in each group could not be used as a consequence of the incorrect positioning of the duodenal cannulas in one animal.

Calculation of N reabsorption

N reabsorption in the small intestine

N reabsorption in the small intestine was calculated by transfer of the disappearance rate of endogenous ^{15}N in the small intestine (100% - residue rate %) divided by the residue rate of the endogenous ^{15}N in the ileum as related to the amount of endogenous ^{15}N (nonmicrobial bound ^{15}N) in the duodenum of animal No. 3 (Equation 1).

$$\text{N reabsorption}_{\text{small intestine}}[\text{g/d}] = \frac{\text{endog. N}_{\text{ileum}}[\text{g/d}] \times 100[\%] - \text{residue rate of }^{15}\text{N}[\%]}{\text{residue rate of }^{15}\text{N}_{\text{duodenum}\rightarrow\text{ileum}}[\%]} \quad (1)$$

N reabsorption in the large intestine

For calculation of N reabsorption in the large intestine the disappearance rate of the endogenous ^{15}N during the passage from the ileum to the faeces and the residue rate of the endogenous ^{15}N in the faeces in percent of the endogenous ^{15}N in the ileum of animal 2 were used (Equation 2).

$$\text{N reabsorption}_{\text{large intestine}}[\text{g/d}] = \frac{\text{endog. N}_{\text{faeces}}[\text{g/d}] \times 100[\%] - \text{residue rate of }^{15}\text{N}[\%]}{\text{residue rate of }^{15}\text{N}_{\text{ileum}\rightarrow\text{faeces}}[\%]} \quad (2)$$

Calculation of N secretion

N secretion in stomachs

The digesta of unlabelled animals No. 2 and 3 was labelled with ^{15}N during the exchange period of the experiment, which was caused by exchanging of digesta between animals and by rumeno-hepatic N recycling. Thus the net N secretion into the rumen and the abomasum could be calculated using the quotient of ^{15}N enrichment in the duodenal digesta and the TCE soluble blood plasma of the animal No. 2 (Lammers-Wienhoven et al., 1998). The N secreted by bile and the pancreatic fluid (Sandek et al., 2001a) was subtracted from this value.

N secretion in the small intestine

N secretion in the small intestine was calculated according Equation 3:

$$\begin{aligned}\text{N secretion}_{\text{small intestine}}[\text{g/d}] = {} & \text{endogenous N flow into ileum [g/d]} \\ & + \text{N reabsorption in small intestine [g/d]} \\ & - \text{endogenous N flow into duodenum [g/d]}\end{aligned} \quad (3)$$

N secretion in the large intestine

N secretion in the large intestine was calculated according Equation 4:

$$\begin{aligned}\text{N secretion}_{\text{large intestine}}[\text{g/d}] = {} & \text{endogenous N in faeces [g/d]} \\ & + \text{N reabsorption in large intestine [g/d]} \\ & - \text{endogenous N flow into ileum [g/d]}\end{aligned} \quad (4)$$

Calculation of the N reabsorbility

N reabsorbility in the small intestine

The reabsorbed N in the small intestine presents the reabsorbed part of the endogenous N flow into the duodenum and additionally the N secreted into the duodenum. The N reabsorbility in the small intestine is calculated by Equation 5.

$$\text{N reabsorption}_{\text{small intestine}}[\%] = \frac{\text{N reabsorption in small intestine [g/d]} \times 100}{\text{N secretion in small intestine [g/d] + endog. N flow into duodenum [g/d]}} \quad (5)$$

N reabsorbility in the large intestine

The N reabsorbility in the large intestine is calculated analogously by Equation 6.

$$\text{N reabsorption}_{\text{large intestine}}[\%] = \frac{\text{N reabsorption in large intestine [g/d]} \times 100}{\text{N secretion in large intestine [g/d] + endog. N flow at ileum [g/d]}} \quad (6)$$

RESULTS

The calculated secretion rates are shown in Table 1. Net N secretion into the stomachs varied significantly between the individual experiments (0.6-2.7 g/d). These values represent a minimum quantity since the part of ^{15}N reabsorbed up to the beginning of the small intestine could not be determined. Concerning N intake, more N was secreted into the stomachs of Group 2 (higher fibre intake) than those of Group 1.

Daily secretion into the small intestine amounted to 6 to 8 g N. In comparison with Group 1 N secretion was considerably higher in Group 2, especially if considered in relation to the DM intake ($P<0.055$). Daily secretion into the large intestine was 0.9 to 2.9 g N. The variation between the experiments was high but the values tended to be higher in Group 1 than in Group 2 ($P<0.16$). In Group 1, N secretion in the large intestine was about 30% of the total postruminal N secretion, in Group 2 it was only 12%.

Related to DM intake the total postruminal N secretion in Group 2 was nearly 40% higher than in Group 1.

The net N absorption in the stomachs (forestomachs and abomasum) was calculated by addition of the ruminal N balance (N intake minus total N flow into

TABLE 1

Net N secretion into stomachs and N secretions in the intestine

	Group 1 (n = 2) CF intake: 89.7 g/d DM intake: 616 g/d N intake: 15.78			Group 2 (n = 2) CF intake: 119.4 g/d DM intake: 478 g/d N intake: 11.96		
	Experiment		Mean	Experiment		Mean
	1	2		4	6	
Net N secretion into rumen and abomasum						
g/d	0.64	2.50	1.57	2.69	2.15	2.42
g/kg DM intake	0.95	4.35	2.65	5.09	5.05	5.07
% of N intake	3.6	17.2	9.9	20.6	19.9	20.2
N secretion in small intestine						
g/d	5.77	5.76	5.77[a]	7.77	7.56	7.67[b]
g/kg DM intake	8.53	10.01	9.37[a]	14.69	17.75	16.05[b]
N secretion in large intestine						
g/d	1.75	2.87	2.31	1.18	0.93	1.06
g/kg DM intake	2.59	4.99	3.79	2.23	2.18	2.20
N secretion in postruminal tract						
g/d	7.52	8.63	8.08	8.95	8.49	8.72
g/kg DM intake	11.11	15.01	13.06	16.92	19.93	18.42

[a,b] significant differences between diet groups at $P<0.10$

duodenum) and net N secretion into stomachs (Table 2). As expected, net N absorption was enhanced in Group 1 in which higher feed intake and higher dietary N concentrations were observed than in Group 2. In relation to N intake it varied between 18 and 38%.

The reabsorption of N, postruminaly secreted in the small intestine, amounted to an average of 4.5 g/d (Group 1) and 7.0 g/d (Group 2). Reabsorption in Group 2 was clearly enhanced when compared to Group 1 ($P<0.05$). However, there was no difference if N resorption was calculated as a percentage of the input of endogenous N into the small intestine (73 vs 77%).

No difference was observed for N reabsorption in the large intestine between the two groups; average reabsorption was 1.8 g/d in Group 1 and 1.5 g N/d in Group 2, representing 30 and 18% of total N reabsorption in the postruminal section, respectively.

The daily amount of total N reabsorbed in the postruminal tract ranged from 6 to 9 g. This quantity represents 75 (Group 1) and 84% (Group 2) of the total postrumi-

TABLE 2

Net N absorption in stomachs and N reabsorption in the intestine

	Group 1 (n = 2) CF intake: 89.7 g/d DM intake: 616 g/d N intake: 15.78			Group 2 (n = 2) CF intake: 119.4 g/d DM intake: 478 g/d N intake: 11.96		
	Experiment		Mean	Experiment		Mean
	1	2		4	6	
Net N absorption in rumen and abomasum						
g/d	5.41	5.50	5.46^{a}	2.31	3.50	2.91^{b}
g/kg DM intake	7.99	9.57	8.78	4.37	8.22	6.30
% of N intake	30.6	37.9	34.2	17.7	32.3	25.0
N reabsorption in small intestine						
g/d	4.81	4.23	4.52^{a}	7.02	6.91	6.97^{b}
g/kg DM intake	7.10	7.35	7.22^{a}	13.27	16.22	14.74^{b}
%*	77.7	69.0	73.4	75.4	78.7	77.0
N reabsorption in large intestine						
g/d	1.29	2.38	1.84	1.93	1.13	1.53
g/kg DM intake	1.91	4.14	3.02	3.65	2.65	3.15
%*	41.2	49.9	45.6	55.6	40.4	48.0
N reabsorption in postruminal tract						
g/d	6.10	6.61	6.36^{a}	8.95	8.04	8.50^{b}
g/kg DM intake	9.01	11.50	10.26^{a}	16.92	18.87	17.90^{b}
%*	76.8	73.4	75.1^{a}	85.3	82.8	84.0^{b}

* N reabsorption [%] = N reabsorption in part of intestinal tract [g/d] / (N secretion in this part of intestinal tract [g/d] + flow of endogenous N into this part of intestinal tract [g/d]) × 100

^{a,b} significant differences between diet groups at $P<0.10$

nal input of endogenous N. Consequently, the largest part of postruminally secreted N was reabsorbed.

DISCUSSION

The total N secreted daily into the small intestine amounted to 5.8 to 7.8 g. These results are in line with those presented by Żebrowska and Kowalczyk (1991) who used the intestinal loop technique in 35-55 kg sheep. The authors infused Krebs-Ringer solution and estimated an N secretion of 7 to 10 g/d. Kay (1969) also determined a similar N secretion (7 g/d) using isolated intestinal loops of sheep. In multiply fistulated nearly adult sheep Voigt et al. (1996) and Van Bruchem et al. (1997) found higher secretion of protein-N (14 and 17 g/d). As to the metabolic weight the mean value of our study (0.67 g N/kg $BM^{0.75}$) was identical with that reported by Voigt et al. (1996) and only somewhat lower than the results of Van Bruchem et al. (1997) (0.83 g N/kg $BW^{0.75}$).

In comparison with Group 1, N secretion into the small intestine was increased in Group 2 (Table 1). This is probably caused by the higher CF intake. Lammers-Wienhoven et al.(1998) also found an enhanced N secretion by increase of fibre passage through the small intestine too. Voigt et al. (1996) and Van Bruchem et al. (1997) demonstrated a high correlation between the passage rate of ileal NDF and that of ileal endogenous protein N in sheep. Furthermore, Van Bruchem et al. (1989) reported that the passage of non-protein dry matter through the small intestine strongly influenced endogenous protein release in the small intestine. The studies of Żebrowska and Kowalczyk (1991) showed an infusion of cellulose into the small intestine to increase the secretion of total N but not that of urea N. Thus, in small intestine the passage of CF increases the N secretion.

The reabsorption of postruminally secreted N in the small intestine amounted to 4.5 and 7.0 g/d (Table 3). This resulted in a positive N balance across the small intestine (Table 3) and in an increased proportion of endogenous N of the total N towards the ileum.

Reabsorption in Group 2, with higher intake of fibre and lower intake of DM, was increased as compared with Group 1. This is a consequence of the increased N secretion in Group 2. On average, the endogenous N entering the small intestine was reabsorbed to 73 to 77% (Table 2).

These high reabsorption rates are in agreement with the regression analysis of Roy (1983), who reported that in the ruminating calf only a small loss of endogenous N occurred in the small intestine since this N was already reabsorbed before reaching the ileum.

The above reabsorption values are considerably higher than those observed by Voigt et al. (1996) and Van Bruchem et al. (1997) for protein N in the intestinal section between the duodenum and the ileum. These authors found average values of 50%. In the studies of Lammers-Wienhoven et al. (1998) the N reabsorbility amounted to 56%. These differences are likely due to the mode of calculation. The above authors calculated N reabsorption in the small intestine by the difference of the endogenous N flow at the distal duodenum and at the terminal ileum so that it represented the apparent reabsorption. In the present study N secretion into the small intestine was considered as well. The higher values of the N reabsorbility can thus be explained.

Daily N secretion into the large intestine amounted to 0.9-2.9 g. This range agrees with the high variation found in the literature. A considerable part of this N secretion is non-ammonia-N but several studies show that intestinal bacteria re-

TABLE 3

N balance in small and large intestine

	Group 1 (n = 2) CF intake: 89.7 g/d DM intake: 616 g/d N intake: 15.78			Group 2 (n = 2) CF intake: 119.4 g/d DM intake: 478 g/d N intake: 11.96		
	Experiment		Mean	Experiment		Mean
	1	2		4	6	
Small intestine						
N secretion g/d	5.77	5.76	5.77[a]	7.77	7.56	7.67[b]
N reabsorption g/d	4.81	4.23	4.52[a]	7.02	6.91	6.97[b]
N balance g/d	+ 0.96	+ 1.53	+ 1.25	+ 0.75	+ 0.65	+ 0.70
Large intestine						
N secretion g/d	1.75	2.87	2.31	1.18	0.93	1.06
N reabsorption g/d	1.29	2.38	1.84	1.93	1.13	1.53
N balance g/d	+ 0.46	+ 0.49	+ 0.48[a]	- 0.75	- 0.20	- 0.48[b]
Postruminal tract						
N secretion g/d	7.52	8.63	8.08	8.95	8.49	8.72
N reabsorption g/d	6.10	6.61	6.36[a]	8.95	8.04	8.50[b]
N balance g/d	+ 1.42	+ 2.02	+ 1.72[a]	± 0	+ 0.45	+ 0.23[b]

[a, b] significant differences between diet groups (P<0.10)

ceive their N supply from blood plasma urea (Dixon and Nolan, 1983). In contrast to N secretion into the small intestine, N secretion into the large intestine was higher in Group 1 than in Group 2. The reason is not clear.

As a whole, N secretion into the large intestine proved to be rather high, amounting to 30% and about 12% of the total postruminal N secretion in Groups 1 and 2, respectively. These results confirm the findings of Coelho da Silva et al. (1972) and Nolan et al. (1976) indicating that N metabolism in the caecum and colon of ruminants can be of considerable intensity. Under the present experimental conditions the values for N reabsorption in the large intestine were estimated to equal 1.3-2.4 g N, i.e. 41-56% of endogenous N entering the large intestine. Due to the high variation observed, no differences were evident between both groups.

However, in Group 1 large intestine N secretion exceeded N reabsorption, thus causing a positive N balance within the large intestine (Table 3) and an enrichment of endogenous N towards the faeces. In contrast, N secretion in Group 2 (higher CF- and lower DM- and N intake of the animals) was lower than the reabsorption of endogenous N. Thus, in this group of animals a relatively low amount of endogenous N flowed from the ileum to the caecum. These results contradict those reported by Voigt et al. (1985) who concluded from digestion experiments using the nylon bag method that the postruminal processes of digestion are nearly finished at the terminal ileum. In the experiments presented here large intestine digestion plays an important role in total postruminal N reabsorption, which averaged 75% in Group 1. In Group 2 it amounted to 84%, thus being 9% higher than in Group 1. Consequently the share of the large intestine in the postruminal reabsorption of N represents 29 and 18% in Groups 1 and 2, respectively.

Fermentation of undigested protein in the large intestine is inefficient for the animal since no appreciable absorption of amino acids occurs within the large intestine (Ulyatt et al., 1975; Nolan et al., 1976). The absorption of N in the large intestine occurs mainly in the form of ammonia, which after resynthesis to urea only slightly adds to the improvement of the N balance in the rumen (Kowalczyk et al., 1975a,b; Bergner et al., 1986; Dixon and Nolan, 1986).

In conclusion, our results illustrate the dynamics of endogenous N compounds in the different parts of the gastro-intestinal tract of sheep. Secretion and reabsorption are influenced by dietary factors such as fibre content. The major part of the secreted nitrogen compounds is reabsorbed in the small or large intestine. Thus, the amount of secreted N much exceeds the metabolic faecal nitrogen.

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STRESZCZENIE

Badania nad przemianą azotu w różnych odcinkach przewodu pokarmowego owiec przy zastosowaniu metody „wymiany treści". 3. Sekrecja i reabsorpcja azotu

W poprzednich dwóch pracach, przy zastosowaniu techniki izotowej z ^{15}N i wymiany treści pomiędzy znakowanymi i nieznakowanymi owcami, oznaczono tempo przepływu treści pokarmowej (Sandek i wsp., 2001a) oraz tempo przepływu azotu endogennego (Sandek i wsp., 2001b). Na podstawie otrzymanych danych oszacowano wielkość reabsorpcji N w przedżołądkach, jelicie cienkim i grubym oraz sekrecję N do tych odcinków przewodu pokarmowego owiec, a także wpływ ilości pobranego z paszą włókna (Grupa 1: 89,7 g/d, Grupa 2:119,4 g/d) na te wskaźniki.

Sekrecja netto N do żwacza i trawieńca różniła się między poszczególnymi doświadczeniami (0,6-2,7 g N/d), lecz nie stwierdzono wyraźnych różnic pomiędzy grupami. Dzienna sekrecja N do jelita cienkiego była istotnie większa (P<0,05) w Grupie 2 niż Grupie 1 i wynosiła odpowiednio 7,7 i 5,8 g, odwrotnie w jelicie grubym - w Grupie 2 była mniejsza niż w Grupie 1 (1,06 g vs 2,3 g N), co odpowiadało 12 i 30% całkowitej sekrecji N w przewodzie pokarmowym, bez uwzględnienia żwacza.

Dzienna absorpcja N netto w żwaczu i trawieńcu wynosiła 5,5 g w Grupie 1 i tylko 2,9 g w Grupie 2 (P<0,10). Reabsorpcja N w jelicie cienkim, wydzielanego w poprzednich częściach przewodu pokarmowego, wynosiła 4,5 g N/d w Grupie 1 i 7,0 g w Grupie 2 (P<0,05). W przeliczeniu na ilość pobranej suchej masy w grupie 2 była istotnie większa (P<0,05) niż w Grupie 1 (14,7 vs 7,2 g/d), jednakże nie stwierdzono istotnych różnic gdy reabsorpcję N wyrażono w procentach ilości N endogennego dochodzącego do jelita cienkiego (77 vs 73%). Ilość reabsorbowanego N w jelicie grubym także nie różniła się istotnie pomiędzy grupami (1,8 Grupa 1 vs 1,5 g/d Grupa 2). Ilość dziennie reabsorbowanego N w przewodzie pokarmowym, bez uwzględnienia żwacza, wynosiła w Grupach 1 i 2 odpowiednio 6,4 i 8,5 g, co odpowiadało 75 i 84% wydzielonego w tej części przewodu pokarmowego N endogennego. Największa część N endogennego (bez uwzględnienia żwacza) była reabsorbowana w czasie przechodzenia treści przez jelito cienkie.