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Secretion of nitrogen compounds into the isolated caecum and colon of sheep

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ABSTRACT

The experiments were carried out on 8 one-year-old rams of about 45 kg body weight, 4 with a surgically isolated caecum pouch (250 ml) and 4 with an approximately 1 m long isolated colon loop. The animals were fed a basal diet containing 11% CP or supplemented with urea to 14 or 17% CP. To study the influence of hypo- and hypertonic solutions on nitrogen compound secretion, the isolated caecum pouch was washed with antibiotics and filled with 0.45, 0.9, 1.8 or 2.7 % NaCl solutions. Samples were taken after 4h to determine secreted nitrogen compounds. Increasing the NaCl concentration from 0.45 to 1.8% had no effect, but at 2.7% it significantly raised the amount of total-N secreted into the caecum from 5.4 to 14.3; protein-N rose from 3.8 to 11.9 and urea-N from 1.5 to 2.8 mg/h for 0.45 and 2.7% NaCl, respectively. The influence of the CP level in the diet was studied at 0.9% NaCl solution in the caecum and colon. Increasing the level of CP in the diet from 11 to 17% caused an insignificant rise of total-N secretion into the caecum pouch from 5.6 to 6.1; protein-N from 3.4 to 4.7; urea-N from 1.6 to 1.7 mg/h and the blood urea-N level from 10.5 to 16.4 mg/100 ml, respectively. Animals fed diets with 11 or 14% CP secreted as follows into the colon loop: 3.8 and 4.3 total-N; 2.9 and 2.8 protein-N; 0.8 and 1.4 mg/h urea-N, with a concomitant blood urea-N level of 10.7 and 14.5 mg/100 ml, respectively for the diets. Injection of 40 ml 7.5 % urea solution into the jugular vein of each animal every hour for 5 h progressively increased the level of urea-N from 11 to 26 mg/100 ml. The respective values of urea-N secreted into the caecum pouch were 2 and 11 mg/h and into the colon loop 2.2 and 3.3 mg/h.

KEY WORDS: sheep, nitrogen, secretion, caecum, colon

INTRODUCTION

Information on the secretion of urea and other nitrogen compounds into the large intestine of ruminants is rather scarce and contradictory. It was demonstrated on heifers that the ammonia level in the caecum content increases after

intravenous infusion of urea (Kulasek, 1966 a,b) which could be a consequence of urea transfer from blood into the caecum and its hydrolysis to ammonia by urease of bacterial origin (Faichney, 1968). Their findings were corroborated by Nolan et al. (1976) who demonstrated rapid increase of enrichment with $^{15}N\%$ excess in the caecum content of sheep given ^{15}N-labelled urea into the blood. However, quantitative data defining the magnitude of nitrogen compound secretion into the large intestine are few and often discrepant.

The aim of this study was to estimate the amount and type of nitrogen compounds secreted into the caecum and colon of sheep depending on the nitrogen content in the ration and urea level in the blood.

MATERIAL AND METHODS

Animals

The experiments were carried out on 8 one-year-old rams of about 45 kg body weight. Four of them were provided with isolated pouches of the caecum with a cannula inserted into the end of the pouch according to Hecker (1974). The other 4 animals were prepared with an isolated loop of the spiral colon. An approximately 1 m long section of the spiral colon was cut at each end and equipped with T-piece cannulas. The proximal and distal end of colon were anastomosed end-to-end to allow digesta to pass. The isolated part of the caecum and colon were rinsed 3 times a day with 0.9% NaCl solution containing 0.33 g streptomycin, 0.33 g neomycin and 10 000 I.U. penicillin per litre. The animals were kept for a two-week recovery period in individual pens, fed meadow hay with free access to water.

Experiment 1

The rams with isolated caecums were given a basal diet containing 11% crude protein (Table 1) consisting of 700 g meadow hay and 400 g barley. The ration was distributed over two equal meals at 8.00 and 15.00 h and given for at least two weeks before the experiment started. The pouch of the caecum was filled with 250 ml solutions containing 4.5; 9.0; 18.0 or 27.0 g NaCl/l and 2 g PEG-4000/l. Each solution was introduced into the caecum after the morning meal during 5 consecutive days. Twenty milliliter samples of liquid were withdrawn 2 and 4 h after the solution was introduced and stored in deep freeze for analysis. The isolated caecum was rinsed with a 0.9% NaCl solution containing antibiotics and most of the solution was removed from the pouch by a syringe connected to soft tubing.

TABLE 1

Daily rations and chemical composition

Indices	Basal diet	Diets with urea	
	I	II	III
Meadow hay, g	700	700	700
Barley, g	400	400	400
Urea, g	–	10	20
Chemical composition, DM %			
organic matter	94.7	95.1	95.2
crude protein	11.1	14.1	17.1
crude fibre	24.8	24.8	24.8
N-free extractives	56.4	55.8	54.9

Experiment 2

The experiment was conducted in two periods: during the first period the animals with the caecum pouch and those with the isolated colon loop were fed as in Experiment 1. In the second period, the animals with the caecum pouch were given diet III consisting of 700 g meadow hay and 400 g urea-treated barley containing 20 g of urea. The animals with the colon loop received diet II of a similar composition but containing 10 g urea (Table 1).

During a 5-day period, 250 ml of 0.9% NaCl solution containing 2 g/l PEG were introduced into the isolated caecum after the morning meal and samples of 20 ml were withdrawn at 2 and 4 h afterwards. The isolated colon loops were perfused with solution as in animals with a caecum pouch by means of a peristaltic pump at the rate of 5 ml/min for 5 h. The perfusate was collected into a bottle kept on ice, measured every hour and stored for analysis.

Experiment 3

The experiment was conducted on animals with caecum pouches and colon loops given diet I as in Experiment 1, and the caecum pouches and colon loops were perfused as in Experiment 2. Forty ml of 7.5% urea solution were introduced into the jugular vein every hour for 5 h. Blood samples from the jugular vein were taken every 30 min after urea infusion. The samples of liquid from the caecum and colon were taken as in Experiment 2.

Analytical methods

Total nitrogen was estimated by the Kjeldahl method, protein-N by Bernstein, urea-N and ammonia by the Conway method (1954), PEG according to Hydén (1955).

RESULTS

Experiment 1

The secretion of nitrogen compounds into the caecum increased as the concentration of NaCl in the administered solutions rose (Table 2). The amount of total-N secreted during 1 h rose significantly ($P < 0.01$) from 5.41 to 14.3 mg at 0.45 and 2.7% NaCl solutions, respectively; this rise was due mainly to the increased amount of protein-N. The amount of urea secreted into the caecum was similar for 0.45; 0.9 and 1.8% NaCl solutions, but doubled when 2.7 % NaCl solution was given into the isolated caecum ($P < 0.05$).

TABLE 2

The amount of total-N, protein-N and urea-N secreted into the isolated caecum depending on NaCl concentration (Mean ± SD; n = 4), mg/h

	NaCl concentration, %			
Nitrogen fraction	0.45	0.90	1.80	2.70
Total-N	$5.41^{A} \pm 2.1$	$5.59^{A} \pm 0.5$	$7.90^{A} \pm 2.3$	$14.3^{B} \pm 7.7$
Protein-N	$3.79^{A} \pm 0.9$	$3.41^{A} \pm 0.2$	$6.36^{B} \pm 1.7$	$11.9^{C} \pm 2.3$
Urea-N	$1.49^{a} \pm 0.9$	$1.62^{a} \pm 0.3$	$1.48^{a} \pm 0.5$	$2.82^{b} \pm 1.2$

in rows: a, b – $P < 0.05$; A, B, C – $P < 0.01$

The movement of water across the wall of the caecum was affected by the NaCl concentration in the solution used (Table 3). About 20% of the water was absorbed from the caecum during 1 h when the intestine was filled with 0.45% NaCl, while greater concentrations of NaCl caused secretion of water into the lumen of the caecum, with water secretion increasing as NaCl concentrations rose.

TABLE 3

Changes of the amount of water (ml/h) and PEG concentration (%) in the isolated caecum at different NaCl concentration in administered solution (Mean ± SD; n = 4)

Concentration of NaCl	Changes in water content in the caecum	PEG concentration		
		0 h	2 h	4 h
0.45	−11.13 ± 8.4	0.21	0.22	0.23
0.90	+ 9.00 ± 1.4	0.21	0.20	0.18
1.80	+19.92 ±11.7	0.19	0.17	0.14
2.70	+31.42 ±13.9	0.19	0.15	0.12

TABLE 4

The amount of total-N, protein-N and urea-N (mg/h/250 ml) secreted into the isolated caecum and urea-N concentration (mg/100 ml) in blood (Mean ± SD; n = 4)

Nitrogen	Protein level in diets, %	
	11	17
Total-N	5.59 ± 0.5	6.11 ± 2.1
Protein-N	3.41 ± 0.2	4.68 ± 1.3
% of total-N	61	77
Urea-N	1.62 ± 0.3	1.73 ± 0.9
% of total-N	30	28
Urea-N in blood	10.45 ± 0.5	16.40 ± 5.1

Experiment 2

The amount of total-N, protein-N and urea-N secreted into the isolated caecum was not influenced significantly by the level of nitrogen in the diets ($P > 0.05$), however it did show an upward tendency (Table 4). The proportion of urea-N in total nitrogen in the effluent from the caecum was similar irrespective of the diet, but the proportion of protein-N rose from 61 to 77% with increasing crude protein level in the diet. The amount of total-N secreted into the colon loop rose from 3.8 to 4.3 mg as nitrogen level in the diets increased. This increase, however, was not statistically significant and was caused mostly by increased secretion of urea-N ($P < 0.05$). It was accompanied by increasing blood urea-N level (Table 5). Protein-N contribution in total-N in the effluent from the isolated colon decreased from 76 to 65% with increasing level of crude protein in the diet.

TABLE 5

The amount of total-N, protein-N and urea-N (mg/h/250 ml) secreted into the isolated colon and urea-N concentration (mg/100 ml) in blood (Mean ± SD; n = 4)

Nitrogen	Protein level in diets, %	
	11	17
Total-N	3.77 ± 1.3	4.32 ± 1.1
Protein-N	2.90 ± 1.1	2.75 ± 1.3
% of total-N	77	64
Urea-N	0.83^a ± 0.2	1.40^b ± 0.5
% of total-N	22	32
Urea-N in blood	10.70^a ± 0.5	14.50^b ± 2.1

a, b – $P < 0.05$

TABLE 6

The amount of total-N and urea-N (mg) secreted into the caecum filled with 0.9 % NaCl solution during urea infusion into the jugular vein, and the level of urea in blood (mg/100 ml) (Mean ± SD)

Time, h	Total-N	Urea-N	Urea-N as % of total-N	Urea-N in blood
0	20.5 ± 8.8	2.2 ± 1.3	10.7	10.6
1	29.9 ± 19.8	4.1 ± 2.6	13.7	13.9
2	40.8 ± 31.6	4.7 ± 2.6	11.5	17.0
3	45.2 ± 18.4	7.2 ± 2.7	15.9	19.1
4	56.0 ± 8.6	8.8 ± 2.5	15.7	20.7
5	65.2 ± 8.9	10.8 ± 2.3	16.6	23.7

Experiment 3

During infusion of urea into the jugular vein the amount of total and urea-N entering the caecum rose from 20.5 and 2.2 mg to 65.2 and 10.8 mg, respectively, and was accompanied by increased blood concentrations of urea-N (Table 6). The correlation coefficient between blood urea-N concentration and the amount of urea-N secreted into the caecum was $r^2 = 0.36$ ($P < 0.05$). Only traces of ammonia content were found in the samples from the caecum.

TABLE 7

The amount of total-N and urea-N (mg) secreted into the colon and the level of urea in blood (mg N/100 ml) during urea infusion into the jugular vein (Mean ± SD)

Time, h	Total-N	Urea-N	Urea-N as % of total-N	Urea-N in blood
0	–	–		11.7 ± 2.6
1	15.6 ± 2.5	2.2 ± 0.6	14.3	17.7 ± 2.8
2	8.7 ± 3.1	3.2 ± 1.1	36.8	18.4 ± 2.6
3	8.0 ± 2.7	2.7 ± 0.7	35.0	21.1 ± 2.2
4	7.6 ± 2.5	2.9 ± 0.5	38.8	25.4 ± 1.8
5	7.8 ± 1.9	3.3 ± 0.6	43.4	26.8 ± 2.7

In animals with isolated colon loops infusion of urea solution into the jugular vein raised the blood level of urea, similarly as in those animals with isolated caecum pouches, however secretion of urea into the loop increased only slightly (Table 7). The amount of total-N, protein-N and urea-N secreted during 24 h calculated using data of the Tables 4 and 5 and assuming that secretion of nitrogen compounds into the caecum and colon remained constant throughout the day, is presented in Table 8.

TABLE 8

Average calculated amount of total-N, protein-N and urea-N (mg/24 h) secreted into the isolated caecum and colon when the diets containing 11% or 17% crude protein was fed

	Caecum[1]		Colon[2]	
	11% CP	17% CP	11% CP	17% CP
Total-N	134.2	146.6	316.7	362.9
Protein-N	81.8	112.3	243.6	231.0
Urea-N	38.9	41.5	69.7	117.6

[1] mean capacity of isolated caecum was 250 ml

[2] assuming length of colon was 3.5 m

DISCUSSION

Studies on secretion of nitrogen compounds into the large intestine are difficult because of the high proteolytic activity of the microflora and degradation of urea to ammonia. Therefore in this study, the experiments were carried out on sheep with isolated caecum and colon devoid of digesta and washed with a solution containing antibiotics to stop development of microflora. Lack of microflora in the isolated caecum and colon was confirmed by presence of secreted urea and absence of ammonia in the liquid from these parts of the intestine. However, some adverse effects of antibiotic treatment on intestinal function have been reported. Studies by Madge (1969) and Coates (1973) have shown the thinning of the intestinal wall resulting from the antibiotics treatment, usually causing increased intestinal transport and cell permeability.

Factors influencing urea secretion into the small and large intestine are little explored. The results obtained in this study showed that the amount of urea secreted into the caecum depended on the NaCl concentration in the solution given into the isolated caecum. With concentrations of NaCl increasing from 0.45 to 2.7%, urea secretion increased almost twofold but intermediate concentrations did not markedly influence urea secretion. This may suggest that urea is secreted into the large intestine by simple diffusion. It is accepted that diffusion is the main process by which urea is transported to the rumen (Houpt, 1970; Harmeyer and Martens, 1980; Obara et al., 1991). Houpt and Houpt (1968) reported that increased concentrations of NaCl disrupted the epithelial cells and, as a consequence, urea transport rose significantly. It is possible that the mechanism of urea transport throughout the walls of other than rumen parts of the gastrointestinal tract is passive diffusion.

It has been assumed that urea secretion into the forestomachs of ruminants varies with the composition of the diet, but for most of the commonly used feeds it fluctuates between 45 to 60% of the total amount of urea secreted into the gastrointestinal tract (Kowalczyk et al., 1975; Harmeyer and Martens, 1980;

Kennedy and Milligan, 1980). Urea movement across the wall of the caecum (Nolan et al., 1976) and the small intestine was demonstrated to be quantitatively important and constituted 85% of urea secreted into the whole intestine in sheep given a hay and barley diet (Várady et al., 1979). Żebrowska and Kowalczyk (1991) reported that about 5.7 g/d of urea-N is secreted into the small intestine of sheep.

Our experiments have shown that changes of N-content in diets can only slightly modify the amount of nitrogen compounds secreted into the large intestine. Dixon and Nolan (1983) and Dixon and Milligan (1984) proved that less total-N was transported into the caecum and proximal colon when sheep were fed diets containing 10 than 23 g N/d. Other authors reported that addition of easily fermenting feeds into the caecum can increase urea transport into this part of intestine (Bergner et al., 1985; Sommer et al., 1986; Kijora et al., 1992). Siddons et al. (1985) reported that the level of nitrogen in the diet, varying from 11.0 to 19.5 g N/d, had no effect on urea transport into the whole gastrointestinal tract.

It is interesting to note that the amount of protein-N secreted into the isolated colon was independent of the nitrogen level in the diet, whereas the amount of urea-N rose significantly with increasing levels of dietary nitrogen. This may suggest that protein nitrogen originated mainly from shedding epithelial cells, while increased secretion of nitrogen into the colon was caused by greater urea transport across the intestinal wall. Dixon and Nolan (1983) suggest that the amount of nitrogen in the colon originating from epithelium cells is large and could reach 0.8 g N/d. Żebrowska and Kowalczyk (1991) have shown a similar dependence in their study on nitrogen compound secretion into the small intestine. It is difficult to explain why the higher level of nitrogen did not affect the amount of urea secreted into the caecum, although this was proved for the colon.

Our study clearly showed that the amount of urea-N secreted into the caecum and colon was related to the blood urea level, which is in agreement with results of Hecker (1971), Nolan and Leng (1972), Engelhardt et al. (1984) and Żebrowska and Kowalczyk (1991) indicating that a substantial quantity of plasma urea enters the post-ruminal part of digestive tract of sheep. Hecker (1971) demonstrated a close correlation between urea concentration in blood and ammonia, originating from endogenous urea, in the ileum and colon of sheep. Engelhardt et al. (1984) also found a high positive correlation between urea level in blood and urea secretion into the colon but the amount of urea secreted was low (0.1 to 0.3 mmol/h) suggesting that permeability of the colon epithelium for urea is rather low.

Assuming that secretion of urea into the large intestine is constant throughout the day, the approximate amount of urea-N secreted during 24 h into the isolated

part of caecum was estimated on the average only about 40 mg urea-N/250ml/d (Table 8). Nolan et al. (1976) estimated that urea-N secreted into the gastrointestinal tract was 5.3 g N/d but only 1.06 g was from the caecum. This discrepancy could result from the fact that Nolan's study referred to the whole intact caecum while our experiment was carried out on the isolated caecum with a capacity of 250 ml. However, even adjusting the estimated value of 40 mg to the volume of the whole caecum, which is usually about 1 l, an approximate value of 0.16 g urea-N is obtained, which is still about 6 times less than the above mentioned value given by Nolan et al. (1976). A value higher than 20 mg N/d secreted into the whole large intestine was reported by Dixon and Milligan (1987), but Fejes and Várady (1991) found a value of 0.25 g N.

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STRESZCZENIE

Sekrecja związków azotowych do jelita grubego owiec

Doświadczenie przeprowadzono na ośmiu 45 kg, jednorocznych tryczkach: 4 z izolowną petlą okrężnicy o długości około 1 m oraz 4 z izolowanym jelitem ślepym o pojemności około 0,25 l. Zwierzęta utrzymywano na dawce podstawowej zawierającej 11% lub uzupełnionej mocznikiem do 14 lub 17% białka ogólnego. Podanie hipo- i hipertonicznych, od 0,45 do 1,8% roztworów NaCl do przemytych roztworem antybiotyków izolowanej części jelita ślepego i okrężnicy miało niewielki wpływ na sekrecję związków azotowych do jelita, natomiast podanie 2,7% roztworu istotnie zwiększyło wydzielanie do izolowanego jelita ślepego N-ogólnego z 5,4 do 14,3; N-białkowego z 3,8 do 11,9 a N-mocznikowego z 1,5 do 2,8 mg/godz. Wpływ poziomu białka ogólnego w diecie na

sekrecję związków azotowych badano przy podawaniu do jelit 0,9% roztworu NaCl. Po zwiększeniu poziomu białka w diecie z 11 do 17% ilość azotu wydzielanego do izolowanego jelita ślepego wzrastała, odpowiednio dla diet: N-ogólnego z 5,6 do 6,1; N-białkowego z 3,4 do 4,7, a N-mocznikowego z 1,6 do 1,7 mg N/godz. przy wzroście poziomu N-mocznika we krwi z 10,5 do 16,4 mg/100 ml. Sekrecja do pętli okrężnicy przy skarmianiu diet o zawartości białka 11 i 14% wynosiła, odpowiednio: N-ogólnego – 3,8 i 4,3; N-białkowego – 2,9 i 2,8, N-mocznika – 0,8 i 1,4 mg/godz., przy poziomie N-mocznika we krwi 10,7 i 14,5 mg/100 ml. Wpływ poziomu mocznika we krwi na wydzielanie związków azotowych do izolowanych części jelita ślepego i okrężnicy badano podając zwierzętom dożylnie co godzinę przez 5 godzin po 40 ml 7,5% roztworu mocznika, zwiększając w ten sposób stopniowo jego poziom we krwi z 11 do 26 mg N/100 ml. Ilość wydzielanego do izolowanego jelita ślepego N-mocznika wzrastała w tym czasie progresywnie z 2 do 11 mg/godz., a do pętli okrężnicy z 2,2 do 3,3 mg/godz.