Studies on N-metabolism in different gastro-intestinal sections of sheep using the digesta exchange technique. 4. Whole body protein metabolism[*]

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ABSTRACT

Parameters of protein turnover were measured in sheep differing in postruminal secretion and re-absorption of nitrogen. The experiments were carried out with Polish Merino sheep (20-25 kg BW) fitted with rumen and re-entrant cannulas at the duodenum and the ileum. Two groups of animals (n=9) were fed with diets that were nearly isonitrogenous but differed in crude fibre (CF) content (CF in % dry matter (DM): Group 1, 14.7, Group 2, 24.9). As a result of the higher CF content, the intake of DM was lower in Group 2 than in Group 1 (616 vs 467 g x d⁻¹). In all carried out experiments (Sandek et al., 2001a) one of the three animals (No 1) was labelled with ^{15}N by intraruminal infusion of ^{15}N urea. Then duodenal digesta of this labelled animal was exchanged with digesta of an unlabelled animal (No 2) during a 48 h period. The N- and ^{15}N flow through the intestinal tract, the N and ^{15}N excretion in faeces and urine as well as the absorption rates were estimated in animal No 2 during that period. Using these data, kinetic parameters of protein turnover were calculated using the end-product method and the 3-compartment model.

Intake of N (16.1 vs 11.7 g x d^{-1} in Groups 1 and 2), net N absorption (12.3 vs 7.3 g x d^{-1}) and N balance (104 vs -56 mg x kg BW^{-1} x d^{-1}) were higher in Group 1 (P<0.10). No difference were found in flux (1666 vs 1458 mg N x kg BW^{-1} x d^{-1}), synthesis (1238 vs 1087 mg N x kg BW^{-1} x d^{-1}) or breakdown (1134 vs 1324 mg N x kg BW^{-1} x d^{-1}) of protein. However, the efficiency of protein synthesis (N balance/synthesis x 100) was significantly higher in Group 1 (8.8 vs -5.2%; P<0.10). The efficiency of protein synthesis correlated negatively with N secretion in the postruminal tract (r =-0.99; P<0.001) and with ileal flow of endogenous N (r =-0.95; P<0.01). In conclusion, a high intestinal N secretion adversely affects the efficiency of whole body protein synthesis in growing sheep.

KEY WORDS: whole body protein turnover, intestinal N secretion, efficiency of protein synthesis, ^{15}N

INTRODUCTION

Protein retention in the tissue of growing animals or humans is the result of two opposing, dynamic processes: protein synthesis and protein breakdown. Determination of such kinetic parameters of protein turnover as synthesis and breakdown may be of importance for animal as well as for human nutrition and enable to optimize protein gain or minimizing protein loss during growth. The efficiency of protein synthesis, i.e. the proportion of synthesized protein which is deposited, is considerably lower in the whole body than in some organs, e.g. muscles (Simon, 1989).

The reason for this are the much higher protein synthesis rates and low protein deposition rates in organs like liver or gastrointestinal tract. Secretion and partial reabsorption of protein in the gastrointestinal tract are part of whole body protein turnover. However, the secreted and excreted proteins are not measured as protein deposition. It can thus be assumed that protein secretion and the efficiency of whole body protein synthesis are related. Therefore the aim of this experiment was to study the whole body protein turnover in growing sheep differing in gastrointestinal secretion and reabsorption of nitrogenous compounds.

The experiments were carried out to estimate parameters of N metabolism in different gastrointestinal sections of sheep using the digesta exchange technique between ^{15}N labelled- and unlabelled animals (Sandek et al., 2001a,b, 2002). The data of N balances and ^{15}N balances estimated during the exchange periods were used to calculate the parameters of N kinetics.

MATERIAL AND METHODS

Animals and experimental design

Eighteen sheep (Polish Merino, 20-25 kg BW), fitted with rumen and re-entrant cannulas in the proximal duodenum and the distal ileum were divided in two groups. Group 1 (Experiments 1-3) received a ration containing 14.7 g crude fibre (CF)/100 g dry matter (DM), 16.3 g crude protein (CP)/100 g DM, and 11 MJ ME/kg DM, whereas Group 2 (Experiments 4-6) was fed a ration containing 24.9 g CF/100 g DM, 15.7 g CP/100 g

DM, and 10 MJ ME/kg DM. The DM intake was 616 g x d[-1] and 467 g x d[-1] in Group 1 and Group 2, respectively. The diets were offered as six meals per day.

Three sheep were included in each experiment. One of the three sheep (No 1) was labelled by continuous intraruminal infusion of 1 g ^{15}N urea (95 atom %, VEB Berlin-Chemie, Berlin, Germany) per day. After a 6-day labelling period the ^{15}N-labelled duodenal digesta of these animals was exchanged against the digesta of an unlabelled animal *via* the duodenal cannulas, so that the ^{15}N-labelled digesta passed into the digestive tract of animal No 2. During the two day digesta exchange period, whole body N balance as well as ^{15}N balance along the digestive tract of the animal were estimated. Using the end-product method and the 3-pool model of Sprinson and Rittenberg (1949) modified by Krawielitzki et al. (1989) these data were used to calculate the turnover rates of whole body protein metabolism. At the end of each experiment, the animals were slaughtered and the N content in whole body was estimated. For this purpose, the body was homogenised and the total N was estimated by the Kjeldahl procedure. More information on experimental design, materials and methods used is given in detail by Sandek et al. (2001a,b, 2002).

Three-pool model and calculation of N turnover

The 3-pool model used (Figure 1) is based on the assumption that the metabolism of the tracer (^{15}N) represents the metabolism of total N. The amount of ^{15}N is divided between protein synthesis and protein oxidation followed by urinary N excretion.
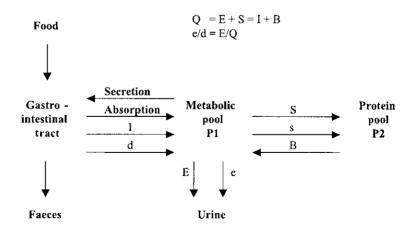

$$Q = E + S = I + B$$
$$e/d = E/Q$$

Figure 1. Model of protein turnover (Sprinson and Rittenberg, 1949, modified by Krawielitzki et al., 1989)

Q - N flux; I - net N absorption; E - urinary N excretion; S - protein synthesis; B - protein breakdown; d - postruminal absorbed ^{15}N; e - [15]N excretion in urine; s - [15]N incorporated in protein

Further assumptions for this model are that 1) during the measurement period no recycling of the tracer from the protein pool back into the metabolic pool occurs, 2) pool size and flow rates are constant, and 3) other pathways of the intermediate N metabolism except protein synthesis, breakdown, and oxidation followed by excretion are negligible.

During passage of the digesta through the small and the large intestine of animal No 2, most of the ^{15}N administered by digesta exchange at the duodenum will be absorbed. One part of this absorbed ^{15}N (^{15}N dose, *d*) will be excreted in urine (^{15}N excretion, *e*), the other part will be used for synthesis of body protein (^{15}N protein synthesis, *s*). Thus, the ^{15}N flux *(q)* entering or leaving the metabolic pool is defined as:

$$q \text{ [mg } ^{15}\text{N x d}^{-1}] = d \text{ [mg } ^{15}\text{N x d}^{-1}] = e \text{ [mg } ^{15}\text{N x d}^{-1}] + s \text{ [mg } ^{15}\text{N x d}^{-1}] \qquad (1)$$
$$^{15}\text{N flux} \quad = \quad ^{15}\text{N input} \quad = \quad ^{15}\text{N output}$$

Using the 3-pool model (Figure 1), knowing the urinary N excretion (E) and the quotient of *d/e* enable the calculation of N flux (Q), which is the sum of all N fluxes entering or leaving the metabolic pool:

$$Q \text{ [g N x d}^{-1}] = E \text{ [g N x d}^{-1}] \times d/e \qquad (2)$$

The ^{15}N dose *d* and the urinary ^{15}N excretion rate *e* are both estimated in animal No 2 for each experiment. The amounts of E and the net-N absorption I (I = N intake - N faeces) are calculated as the average of all three animals (No 1, 2, 3) of the individual experiments.

The rates of synthesis (S) and breakdown (B) for whole body protein can be estimated from the following equation (Waterlow et al., 1978):

$$Q \text{ [g N x d}^{-1}] = I \text{ [g N x d}^{-1}] + B \text{ [g N x d}^{-1}] = E \text{ [g N x d}^{-1}] + S \text{ [g N x d}^{-1}] \qquad (3)$$
$$\text{N flux} \quad = \quad \text{N input} \quad = \quad \text{N output}$$

The reutilization rate (R) which represents that part of the breakdown of N or AA used for more synthesis of body protein, can be computed as follows:

$$R \text{ [%]} = 100 \times S \text{ [g N x d}^{-1}] / Q \text{ [g N x d}^{-1}] \qquad (4)$$

Statistical analyses

N balance and N turnover data were subjected to analysis of variance using the one-factorial ANOVA procedure of SPSS (SPSS Inc., Vers. 10.07) at a 90% significance level. All results are expressed as means ± SEM. Linear regression analysis to analyse the relation between efficiency of protein synthesis and N secretion was done with the same software package.

RESULTS

The largest part of intraruminally ^{15}N administered as urea was absorbed during the passage up to the proximal duodenum (54±4.4%). The remaining amount was largely incorporated in microbial protein, which amounted to about 40% of the total digesta N passing to the duodenum. This ^{15}N labelled duodenal digesta of animal No 1 was exchanged against the unlabelled digesta of animal No 2 and passed the postruminal digestive tract of unlabelled animal No 2 up to excretion by the faeces.

The amounts of ^{15}N entering the duodenum with digesta to animal No 2, passing through the ileum, and excreted with faeces and urine, respectively, are shown for five experiments in Table 1. Data obtained for Experiment 3 (Group 1) were eliminated from calculations because the duodenal cannula in one of the animals was placed incorrectly.

TABLE 1

Parameters of intraruminal infusion and duodenal flow of ^{15}N of animals No 1 and flow and absorption of ^{15}N along various sections of the gastrointestinal tract of animals No 2 (mg x d[-1]) fed a low (Group 1) or high (Group 2) fibre diet[1]

	Group 1			Group 2	
	Exp. 1	Exp. 2	Exp. 4	Exp. 5	Exp. 6
Animal No 1					
intraruminal infusion	460.4	460.4	460.4	460.4	460.4
duodenal flow	251.7	181.8	187.3	270.9	173.8
Animal No 2					
duodenal input	244.1	176.4	181.7	261.8	168.6
ileal flow	66.6	65.6	68.2	105.1	60.3
small intestinal absorption	177.5	110.8	113.5	156.7	108.3
ileal input	64.6	63.6	66.1	101.9	58.5
faecal excretion	38.0	31.9	29.4	45.5	34.9
large intestinal absorption	26.6	31.7	36.7	56.4	23.6
postruminal absorption (d)	204.1	142.5	150.2	213.1	131.9
Urinary excretion (e)	58.3	32.4	34.5	61.7	33.0
d/e	3.5	4.4	4.4	3.4	4.0

[1] for details see text and Sandek et al. (2001a,b, 2002)

The apparent postruminal ^{15}N digestibility for both groups amounted to about 80%. Two thirds of the ^{15}N was absorbed in the small and one third in the large intestine, respectively. The ratio of intestinal absorbed ^{15}N to urinary excreted [15]N (d/e) was identical for both groups (Group 1, 3.95±0.45; Group 2, 3.93±0.29), indicating that three quarters of the ^{15}N dose absorbed during passage along the intestine was used for synthesis of body protein while the residual was directed to urinary excretion.

In comparison with Group 2, intake of N, net N absorption and N balance were significantly higher in Group 1 (P<0.10; Table 2). No difference could be observed in N flux, protein synthesis, protein breakdown or in the reutilization rate of N. However, the fractional growth rate (FGR) and the efficiency of protein synthesis (N balance/synthesis x 100) were significantly greater in Group 1 (P<0.10). In this Group fed a diet with a lower CF content, N secretion in the small intestine was significantly (P<0.10) lower than in Group 2 given a diet with a higher CF content (9.4 vs 16.0 g N x kg DMI⁻¹; Sandek et al., 2002).

DISCUSSON

Nitrogen retention or protein gain was significantly different between the groups (P<0.10). Ulbrich (1988) also found a negative influence of dietary crude fibre on protein gain in growing lambs. This gain is the result of protein synthesis and protein breakdown. The question is whether this lower N retention of Group 2 results from a reduced protein synthesis and/or an enhanced breakdown. Both synthesis and, in particular, breakdown of protein were insignificantly affected. This agrees with the findings of Davis et al. (1981) and Lobley (1993), who concluded that even small differences in protein synthesis or degradation result in large changes in protein gain.

The dynamic of intermediate protein metabolism is particularly demonstrated by the high synthesis rate, which was ten-fold that of the protein N gain in Group 1. Waterlow et al. (1978), Davis et al. (1981), Pahle et al. (1981) and Attaix et al. (1987) used a similar method to show that protein synthesis exceeds many-fold the amount of N gain.

Unfortunately, in this study a significant difference exists in the intake of DM and therefore in the consumption of N and energy. The net N absorption (I) in Group 1 (12.3 g N/d) was higher than that of Group 2 (7.3 g N/d), due to the smaller DM intake of this Group (Table 2). Despite the lower N absorption and energy intake in Group 2, protein synthesis was only marginally decreased and protein degradation was equivalent. This suggests that factors other than N and energy intakes affect protein turnover.

As shown in Figure 2, there is a significant negative relation between the efficiency of protein synthesis and N secretion in the postruminal tract (r=-0.99) or the ileal flow of endogenous N (r=-0.95). Hence, it can be concluded that the processes of postruminal N secretion and reabsorption influence whole body protein turnover significantly. Part of the total synthesized protein is secreted into the intestinal tract. The secretion and reabsorption of protein in the intestine are part of whole body protein turnover and cause unavoidable protein losses for maintenance.

The calculation of the kinetic parameters for protein metabolism using the pool model is correct only if the metabolic pool is homogenous, containing chemically

TABLE 2

Parameters of N balance and protein turnover in two groups of sheep fed a low (Group 1) and high (Group 2) fibre diet

	Group 1				Group 2				
	Exp. 1	Exp. 2	Mean	SEM	Exp. 4	Exp. 5	Exp. 6	Mean	SEM
N balance[1] (g x animal⁻¹ x d⁻¹)									
N intake	17.66	14.53	16.10ᵃ	1.57	13.08	11.20	10.83	11.70ᵇ	0.70
faecal N	3.66	3.89	3.78	0.11	5.14	4.05	4.06	4.42	0.36
net N absorption (I)	14.00	10.64	12.32ᵃ	1.68	7.94	7.15	6.77	7.29ᵇ	0.34
urinary N (E)	10.47	9.37	9.92ᵃ	0.55	8.18	8.78	8.62	8.53ᵇ	0.18
N balance	3.53	1.27	2.40ᵃ	1.13	-0.25	-1.63	-1.85	-1.24ᵇ	0.50
Protein turnover[2]									
whole body N (P) (g N x kg BW⁻¹)	26.0	25.5	25.8	0.21	25.9	23.8	25.6	25.1	0.7
N retention (G) (mg N x kg BW⁻¹ x d⁻¹)	156	53	104ᵃ	51	-10	-69	-88	-56ᵇ	23
N flux (Q) (mg N x kg BW⁻¹ x d⁻¹)	1614	1717	1666	51	1447	1284	1643	1458	104
synthesis (S) (mg N x kg BW⁻¹ x d⁻¹)	1151	1325	1238	87	1115	912	1233	1087	94
breakdown (B) (mg N x kg BW⁻¹ x d⁻¹)	997	1271	1134	137	1127	980	1324	1144	100
reutilization (R) (%)	73.3	77.2	74.3	2.9	77.0	71.1	75.1	74.4	1.7
efficiency of protein synthesis[3] (%)	13.5	4.0	8.8ᵃ	4.8	-0.9	-7.6	-7.1	-5.2ᵇ	2.1
FSR[4] (%xd⁻¹)	4.4	5.2	4.8	0.4	4.3	3.8	4.8	4.3	0.3
FBR[5] (%xd⁻¹)	3.8	5.0	4.4	0.6	4.4	4.1	5.2	4.5	0.3
FGR[6] (%xd⁻¹)	0.6	0.4	0.4ᵃ	0.2	-0.1	-0.3	-0.3	-0.2ᵇ	0.1

[1] mean value of animal No 1, 2, and 3 of the experiments
[2] animal No 2 of the experiments
[3] G/S x 100
[4] fractional synthesis rate = S/P x 100
[5] fractinol breakdown rate = B/P x 100
[6] fractional deposition rate = G/P x 100
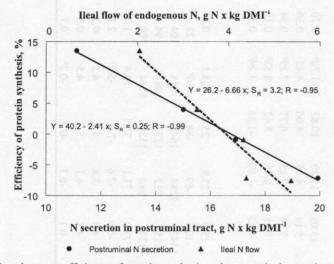[a,b] significantly different between Group 1 and Group 2 (P<0.10)

Figure 2. Relations between efficiency of protein synthesis and postruminal secretion of nitrogen respectively ileal flow of endogenous nitrogen

well-defined metabolites and does not change in size during measurement period (Garlick and Clugstone, 1981). But this is not quite true in reality. The metabolic pool is compartmented into intra- and extracellular spaces and also contains free amino acids and soluble NPN compounds, whose metabolism through specific pathways leads to different end-products of N metabolism (urea, other NPN, body protein) and the direct precursors of protein synthesis are amino-acyl t-RNAs, not free amino acids. The model is, therefore, a simplification of the very complex N metabolism. It follows that the absolute values of the kinetic parameters are also only approximate data, which can be over- or underestimated. However, the relative proportions for the main processes of intermediate N metabolism such as protein synthesis, protein breakdown, protein gain, and N excretion as well as reutilization between both feeding regimens are reflected sufficiently exactly by this method.

Some assumptions of the pool model must be discussed. The main condition, that the metabolism of the tracer (^{15}N) represents exactly the metabolism of the metabolic N of the animal, may be true. The substrates for protein synthesis in the intermediate metabolism are the absorbed amino acids, and their whole spectrum is labelled by ^{15}N due to the intensive activity of ruminal bacteria that produce ^{15}N labelled AA using the ^{15}N urea given intraruminally.

At the beginning of the tracer infusion the recycling of ^{15}N tracer from the protein pool back into the metabolic pool is relatively small but increases with the duration of infusion. The recycling of ^{15}N in ruminants reaches a maximum of 5% of the tracer amount (Lobley, 1993) and equals about 2% during the experimental time of 48 h, which seems to be negligible (Winkler et al., 1978). Alternative

pathways other than protein synthesis, breakdown, and oxidation are limited to 5% of the N flux and the flow rates from one pool to another oscillate during the day. Because of the short 4 h feeding intervals in this experiment it is assumed that the influence of alternative pathways is small.

CONCLUSIONS

In conclusion, the efficiency of whole body protein synthesis is significantly negatively influenced by N secretion in the postruminal tract. The higher the intestinal N secretion, the lower the efficiency of protein synthesis (N balance/synthesis). The N secretion is stimulated by dietary factors, like crude fibre content (Sandek et al., 2002) or intestinal passage of NDF (Żebrowska and Kowalczyk, 1991; Lammers-Wienhoven et al., 1998). Under practical feeding conditions this loss by N secretion should be take into account in protein evaluation systems for ruminants as indirectly done in the energy evaluation systems with the factor q (Van Es, 1975).

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STRESZCZENIE

Badania nad przemianą azotu w różnych odcinkach przewodu pokarmowego owiec przy zastosowaniu metody „wymiany treści". 4. Metabolizm białka w całym ciele owiec

Oznaczano parametry obrotu białka w organizmie owiec różniących się rozmiarem sekrecji i wchłaniania azotu w jelicie. Doświadczenia wykonano na tryczkach rasy merynos polski o m.c. 20-25 kg, z przetokami do żwacza oraz mostkowymi przetokami do dwunastnicy i jelita biodrowego. Zwierzęta podzielono na dwie grupy żywione dietami izoazotowymi, ale różniącymi się zawartością włókna surowego (CF): (Grupa 1-14,7 a Grupa 2 - 24,9% CF w s.m.). W wyniku większej zawartości włókna pobranie s.m. przez zwierzęta Grupy 2 było mniejsze niż w Grupie 1 (616 vs 467 g/d). Do obliczeń wykorzystano dane z naszych wspólnych doświadczeń (Sandek i wsp., 2001a), w których jedno ze zwierząt (Nr 1) było znakowane ^{15}N przez infuzję do żwacza ^{15}N mocznika. Treść dwunastnicy znakowanych owiec wymieniano z treścią owiec nie znakowanych (Nr 2) przez 48 godzin i oznaczano przepływ N i ^{15}N przez jelita; oznaczano również ilość N i ^{15}N wydalanego w kale i moczu oraz wchłoniętego z jelit w tym okresie. Wykorzystując te dane obliczono parametry kinetyki obrotu białka stosując metodę końcowych produktów przemiany i trój-przedziałowy model.

Pobranie N (16,1 vs 11,7 g/szt./d w Grupie 1 i 2), absorpcja N netto (12,3 vs 7,3 g/szt./d w Grupie 1 i 2) i bilans N (104 vs -56 mg/kg m.c./d w Grupie 1 i 2) były istotnie większe w Grupie 1 niż

2 (P<0,10). Nie stwierdzono różnic w tempie przepływu (1666 vs 1458 mg N/kg m.c./d), syntezy (1238 vs 1087 mg N/kg m.c./d) i degradacji (1134 vs 1324 mg N/kg m.c./d) białka. Jednakże wydajność syntezy białka (bilans N/syntezy x 100) była istotnie większa (P<0,10) w Grupie 1 niż 2 (8,8 vs 5,2%). Wydajność syntezy białka była ujemnie skorelowana z sekrecją N w jelitach (g/kg s.m. pobranej) (r=-0,99; P<0,001) oraz z przepływem N endogennego przez jelito biodrowe (g/kg s.m. pobranej) (r=-0,95; P<0,01). Uzyskane wyniki wskazują, że sekrecja N w jelitach wpływa ujemnie na wydajność syntezy białka w ciele rosnących owiec, a mianowicie im większa sekrecja azotu w jelitach tym mniejsza jest wydajność syntezy białka.