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Ammonia production, ammonia absorption, and urea recycling in ruminants. A review

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ABSTRACT

Relevant research on ammonia production, ammonia absorption, and urea recycling in ruminants was reviewed. Ammonia production and utilization in the rumen and post-ruminal digestive tracts are described in detail. Absorption of ammonia into portal-drained viscera, ammonia detoxification and urea synthesis in the liver, and urea degradation in the gastrointestinal tract are then discussed. The factors of affecting urea recycling and its pathways are also analysed. Suggested future research should focus on urea recycling dynamics and improvement of protein conversion efficiency, and on the development of an integrated mechanistic model to describe the digestion and metabolism of nitrogen-containing compounds in ruminants fed practical diets.

KEY WORDS: ammonia, urea, recycling, ruminant

INTRODUCTION

Ammonia and urea, in addition to amino acids (AA), peptides and microbial crude protein (MCP), etc., play an important role in nitrogen digestion and metabolism in ruminants. The feeding of non-protein nitrogen (NPN) supplements to ruminants is based on the knowledge that NH_3 is the major end-product of protein degradation in the rumen and on the belief, which appears to have been generally accepted, that most of the N utilized by rumen microbes comes from the NH_3 pool in the rumen (Nolan and Leng, 1972). Ruminants have been maintained on

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diets in which the only source of nitrogen was either NH_3 salts or urea, indicating that all of the AA that are essential for nonruminants can be synthesized by ruminal microorganisms. In ruminants, urea is an end product of N metabolism, but bacteria have the enzymatic capability to hydrolyze urea, thereby making urea-N available as NH_3. The objective of this paper is to focus on certain aspects of urea recycling that have been reported and to relate these to their potential nutritional significance in ruminants.

GENERAL OVERVIEW OF NH_3 PRODUCTION AND UREA RECYCLING

It is first necessary to understand the complex and dynamic process of N digestion and metabolism in ruminants. Usually, ruminants are much less efficient than nonruminants in utilizing high quality dietary proteins. A dominant feature of N digestion and metabolism is microbial conversion of some dietary protein to NH_3 in ruminants. Dietary intake protein (IP) is either degraded (DIP) in the rumen, with partial or total conversion to MCP, or passed from the rumen as undegradable intake protein (UIP). The DIP provides peptides, AA, and NH_3 to satisfy microbial requirements. In ruminants, NH_3-N concentrations in the rumen usually surpass the practical requirements for microbial growth in the rumen; therefore, excess N is absorbed as NH_3 and converted to urea by the liver. Urea synthesized in the liver can diffuse into the rumen, small intestine, and hindgut, or be secreted in saliva for utilization by ruminal microbes. Urea is also excreted by the kidneys and present in other secretions.

AMMONIA PRODUCTION AND LOSS IN THE GASTROINTESTINAL TRACT

Ruminants absorb substantial amounts of their dietary N as NH_3 and, for many diets, more N is absorbed as NH_3 than as α-amino N (Reynolds, 1992). Ammonia generation in the gut results from two main processes: one is microbial degradation of nitrogenous compounds within the gut lumen, the other is microbial hydrolysis of urea passing across the gut wall from the blood and intestinal fluids (Parker et al., 1995). The primary source of NH_3 within the rumen is dietary protein, except for ruminants consuming diets very low in protein. The UIP and indigestible intake protein (IIP) usually pass to the duodenum without affecting NH_3 production in the rumen. Degradable dietary NPN can be converted rapidly and quantitatively to NH_3, dissolved nucleic acids in the rumen are also degraded extensively (Leng and Nolan, 1984) by rapid action of bacterial peptidases and deaminases to produce NH_3. In addition, endogenous non-urea N and endogenous urea contribute to NH_3 sources of endogenous fermentable protein include sloughed mucosal cells and salivary proteins. Nolan (1975) indicated that 4.4 g of NH_3-N per day were produced from these endogenous sources in sheep. Endo-

genous urea can also serve as a significant source of NH_3 in the rumen after either passing from blood plasma into the rumen or being swallowed in saliva (Leng and Nolan, 1984). Other routes of NH_3 production in the rumen include NH_3 derived from protozoa and fixation of atmospheric N_2, although the latter is apparently negligible (Li Pun and Satter, 1975).

Routes of NH_3 loss from the rumen pool include NH_3-N incorporated into microbial cells, NH_3 outflow and NH_3 absorption. Al-Dehneh et al. (1997) noted that endogenous urea-N contributed 19.1 and 37.5% of the N in duodenal digesta and duodenal bacteria for lactating cows. Outflows of NH_3 depend on its concentration in the rumen and the fractional rate of fluid outflow. Duodenal NH_3 flow measured in cows and sheep represented 2 and 9% of N intake, respectively (Firkins et al., 1987; Song and Kennedy, 1989). NH_3 absorption from the rumen is mainly a function of the ruminal concentration of NH_3 and is also the primary pathway of NH_3 loss from the rumen. Absorption does not appear to be by active transport but occurs *via* passive non-ionic diffusion down a concentration gradient (Parker et al., 1995). High concentrations of ruminal NH_3 increase the flux of NH_3 into the blood. Diffusion of NH_3 across the rumen wall has been demonstrated *in vivo* and *in vitro* (Siddons et al., 1985; Bödeker et al., 1990; Rémond et al., 1993). Under normal physiological conditions, most of the NH_3 in the gut lumen will be in the ionized form because its pH ranges from 2 to 6.

Usually, concentrations of NH_3 in hind-gut digesta are substantial. The NH_3 in the post-ruminal digestive tract includes NH_3 outflow from the reticulorumen, NH_3 from deaminated AA, and NH_3 from hydrolysed endogenous urea. Of these, much of the NH_3 comes from endogenous urea N in the post-ruminal digestive tract. Routes of NH_3 loss include incorporation of NH_3 into MCP, absorption of NH_3, and elimination in faeces. Rémésy and Demigné (1989) found that NH_3 absorption from the caecum was increased in rats fed diets containing fermentable carbohydrates. Parker et al. (1995) concluded that this may in part be due to the increased entry of urea into the caecum and its hydrolysis by the caecal flora, it is also possible that the increased concentration of VFA in the caecal digesta had a more direct effect on NH_3 flux across the caecal wall. Meanwhile, it is also possible that bicarbonate has the ability to stimulate colonic NH_3 absorption in ruminants. Usually, bacteria in the digestive tract utilize NH_3 as their preferred source of N, and other forms of protein or AA are reduced to NH_3 before being used metabolically (Jackson, 1995).

UREA RECYCLING

Urea recycling is significantly related to NH_3 production and absorption in the gastrointestinal tract (GIT) of ruminants. All NH_3 absorbed from the rumen epithelium, small intestinal mucosa, and large intestinal mucosa travels *via* the portal

vein to the liver; body tissue NH_3 also enters the liver. Liver metabolism has a central role in the integration of body N metabolism. Ammonia in the liver is detoxified by conversion to urea, urea can then be recycled directly into the rumen, small intestine, or large intestine; it can enter the rumen in saliva, be excreted by the kidney, or be secreted in milk or sweat (Alio et al., 2000).

Although portal absorption rates provide an overall measure of NH_3 flux into the blood, a number of different techniques have been used to study the relative contribution of different sections of the digestive tract to total NH_3 absorption by PDV (Parker et al., 1995). Siddons et al. (1985) provided a dynamic model of NH_3-N transfer across different sections of the digestive tract. Seal and Reynolds (1993) probed the relationship between NH_3 flux in portal blood and dietary N intake; they found that portal NH_3 flux can represent as much as 0.65 of N intake and in many circumstances can exceed net α-NH_2-N absorption into portal blood. The NH_3 flux from different sections of the gastrointestinal tract can be measured using chronically-catheterized animals. Body tissue NH_3 flux into the liver can then be deduced, provided that the overall rate of urea synthesis from NH_3 is known.

HEPATIC DETOXIFICATION OF NH_3, UREA SYNTHESIS AND REMOVAL

Ammonia is extremely toxic in non-hepatic tissues, causing changes in cerebral metabolism that can result in tetany and death when circulating concentrations exceed 0.7 mM (Symonds et al., 1981). Under normal physiological and nutritional conditions, NH_3 absorbed into the portal vein is efficiently extracted by the liver and detoxified by conversion to urea or glutamine. Over a wide range of portal NH_3 concentrations and on a variety of diets, the liver is able to extract 70 to 95% of portal NH_3. As a result, hepatic NH_3 removal is on average slightly higher (4%) than portal absorption. Thus, arterial NH_3 concentrations remain relatively constant even when portal NH_3 absorption varies threefold (Parker et al., 1995). This ensures that any NH_3 which escapes conversion to urea in periportal hepatocytes is converted to glutamine in perivenous hepatocytes. Amide-N of glutamine is then removed and metabolized to urea by periportal hepatocytes during subsequent passages through the liver, and may also provide a mechanism to avoid a decrease in extracellular pH (Haussinger et al., 1992). Havassy et al. (1982) and Kowalczyk et al. (1982) found that urea nitrogen in the rumen was fixed transiently into plasma protein. Enrichment of ^{15}N of the bacterial matter and plasma protein exceeded that of individual amino acid indicating that urea nitrogen was utilized to a large extent for the synthesis of nitrogen compounds other than amino acids. Maltby et al. (1991, 1993b) reported that when urea was added to ruminant diets there was increased hepatic NH_3 uptake but glutamine uptake was either unchanged or slightly increased; however, net hepatic output of glutamate was decreased. The conversion of NH_3 to glutamine and glutamate

is not a major detoxification pathway under normal feeding conditions. Lobley et al. (1995) reported that 93.5 and 6% of portal $^{15}NH_4Cl$ is converted to ^{15}N-urea and ^{15}N-glutamine, respectively, when portal vein NH_3 concentrations were increased to 0.5 mM by intramesenteric vein infusion in sheep. The capacity of ruminant liver to remove NH_3 is apparently 1.2 to 1.5 μmol/min per gram (Symonds et al., 1981) and the potential contribution of extracted NH_3-N to hepatic urea-N formation ranges from 27 to 110%. Reasons for variation in the contribution of NH_3 to hepatic urea production are not clear, but Parker et al. (1995) considered the large range not to be an artifact and noted that animal factors and intake appeared not to be implicated. The major route of urea entry from blood to the rumen is *via* saliva.

UREA DEGRADATION IN THE RETICULORUMEN AND POST-RUMINAL DIGESTIVE TRACTS

Substantial amounts of recycled urea-N can be used by bacteria in the lumen of the gut for metabolic needs or reabsorbed as N in the forms of AA, nucleic acids, or NH_3 (Kowalczyk et al., 1975a; Nolan and Stachiw, 1979; Huntington, 1989; Reynolds, 1992). This provides a mechanism for salvage of urea-N by conversion into bacterial matter that can then be digested, yielding AA for use by the host (Sarraseca et al., 1998). Jackson (1995) concluded that urea-N retained in the body might, in principle, be converted into AA-N in one of four ways: absorbed as NH_3 and fixed in the liver through amination to form non-essential AA, e.g., as glutamate or glycine-serine; through wider transamination with the C skeleton of a transaminating non-essential AA, e.g., alanine and aspartate; through wider transamination with the C skeleton of a transaminating essential AA; by bacterial synthesis of an essential or non-essential AA.

The amount of urea-N transferred into the rumen is determined by the rate of salivary secretion and by the plasma urea concentration. Nolan and MacRae (1976) reported that 5.3 g of blood urea-N/d entered the digestive tract of sheep; 20% of this urea was degraded in the rumen, 25% in the caecum, and the remainder was apparently degraded elsewhere. There was evidence of urea degradation in the large intestine posterior to the caecum, and it was suggested that urea degradation and absorption of the synthesized NH_3 might also occur in the ileum.

Kowalczyk et al. (1975a,b) stated that only a small amount of blood urea nitrogen was utilized for microbial synthesis in the rumen, and the greatest part of postruminal endogenous nitrogen was reabsorbed during passage of digesta through the intestine (Sandek et al., 2002). Norton et al. (1978) noted that an average of 81% of the urea synthesized in the body was transferred to the digestive tract and degraded to NH_3 and carbon dioxide. Endogenous urea degraded in the rumen accounted for 7 to 13% of the total quantity degraded in the digestive tract, and the rate of urea transfer was not related to the rate of urea synthesis

in the body. The lower digestive tract was the major site of urea degradation in sheep given low protein diets, and the rate of urea transfer to this part of the digestive tract was linearly related to the rate of urea synthesis in the body. Koenig et al. (2000) and Newbold et al. (2000) reported that urea-N contributed 20% of rumen NH_3 flux in sheep offered either a forage-concentrate ration or pelleted dried grass, respectively. It was concluded that urea transferred from the blood to the reticulo-rumen and the hind gut is degradable, making NH_3-N available for use by microorganisms or for reabsorption and utilization by the body.

FACTORS AFFECTING UREA RECYCLING

All factors that influence the production, absorption, and transfer of NH_3 and urea will affect urea recycling in ruminants. Kennedy and Milligan (1980) reported that urea transfer to the rumen was inversely related to the rumen NH_3 concentration, and suggested that the NH_3 concentration was a factor regulating urea entry into the rumen. There was a marked reduction of urea transfer to the rumen when the ruminal NH_3 concentration was elevated by continuous NH_3 infusion into it. Rémond et al. (1993) concluded that NH_3 absorption seems to be mainly influenced by the NH_3 concentration in the rumen fluid, and by the rate of VFA absorption. Net NH_3 flux across the rumen wall is linearly related to both free NH_3 and to total NH_3 concentrations. Additionally, ruminal VFA may stimulate the uptake of NH_3. Bödeker et al. (1992) found that NH_3 absorption was stimulated by the presence of VFA in the mucosal buffer solution, either individually or as a mixture of acetate, propionate, and butyrate. Similar responses to additional butyrate on transfer of NH_3 into the ruminal vein of sheep have also been reported (Rémond et al., 1993).

Tracer studies have indicated that a supplemental energy source such as grain, starch, or dried beet pulp, significantly increased endogenous urea degradation in the gastrointestinal tract. It is possible that the rumen was the site of increased degradation because Kennedy and Milligan (1980) reported that dietary sucrose greatly enhanced the rate of transfer of urea to the rumen. Huntington and Reynolds (1986) pointed out that the effects of dietary energy density or fermentability of a substrate in the rumen on the rate and site of endogenous urea transfer to the gut were obvious.

On the other hand, urea transfer from blood to the GIT might not be controlled by the urea concentration in plasma alone. In sheep and cattle, the upper limits of the blood urea concentration above which urea transfer was no longer linearly related to plasma urea concentrations were 6.0 mM and 4.0 mM, respectively. Elevation of plasma urea above these concentrations did not further increase rumen NH_3. Norton et al. (1978) found that transfer of urea into the post-ruminal tract is correlated with both plasma urea concentration and its production rate.

Feed intake is an important factor that influences the return of urea to the GIT. Bunting et al. (1989) reported that net incorporation of blood urea-N into bacterial protein is inversely related to the protein intake of calves. Sarraseca et al. (1998) found that urea-N production in sheep increased with intake and exceeded digestible N at all intakes. Urea-N entering the digestive tract that was returned to the ornithine cycle remained constant across intakes but the absolute amount increased with N intake. Urea removed by the PDV, unaffected by intake, represented 32, 33, and 21% of the digested N. Meanwhile the reabsorption of endogenous nitrogen was significantly influenced by the dietary crude fibre level for growing sheep (Sandek et al., 2002).

Leng and Nolan (1984) reported that NH_3 concentrations in rumen fluid were positively correlated with the number of ciliate protozoa, and NH_3 concentrations in the rumen fluid of defaunated animals were lower than in those with protozoa. The absorption of NH_3 is also likely to be lower in defaunated animals. Additionally, Allan and Miller (1976) found that, at equal rates of urea production, lambs tended to maintain higher plasma urea concentrations and greater rates of urea degradation in the GIT than did wethers; urea degradation was related to plasma urea concentrations in lambs but not in wethers.

Lastly, there are other factors that can also influence urea recycling for ruminants, such as physiological conditions, osmolality in the GIT, gastrointestinal hormones, etc. (Kennedy and Milligan, 1980). Bödeker et al. (1991) found that HCO_3^- favoured NH_3 absorption across the ruminal epithelium and Rémond et al. (1993) noted that CO_2 insufflation resulted in a 16% increase in net transfer of NH_3 across the ruminal wall. Although blood flow to the sheep rumen was increased, increased osmolality after NaCl injection slightly decreased NH_3 absorption.

RESEARCH APPROACHES

Two approaches are often used to study the recycling of nitrogen-containing compounds. One involves use of labelled isotope tracers and the other employs chronic catheterization of venous and arterial vessels.

Single or continuous isotope tracer technique

First, it is necessary to assume that the animal is in a steady state; i.e. pool sizes remain constant and the rates of inflow and outflow are equal. Isotope tracer techniques generally include both single infusion and continuous infusion methods. Most of the metabolic studies made with ^{15}N have used single infusion rather than continuous infusion methods.

Analysis of isotope ratio with time yield curves for various primary compartments. The change in isotope ratio (Y_t) in a primary pool with time after a single injection of an isotope tracer is given by a multi-exponential curve of the form:

$$Y_t = \sum_{I=1}^{n} A_i e^{-m_i * t}$$

where t = time, A_i = ^{15}N-enrichment in the corresponding pool at the zero-time intercept of the i^{th} compartment, m_i = the fractional rate constant for the i^{th} compartment, n = the number of exponential compartment, i = the exponential compartment number, and Y_t = ^{15}N-enrichment in the corresponding pool at time t.

Parameter estimates from the fitted equations are then used to calculate ruminal NH_3-N pool size, total entry rate or flux, irreversible loss, and recycling. The relevant equations are as follows:

$$Q = D/\sum_{I=1}^{n} A_i$$

$$F = Q\{\sum_{I=1}^{n} a_i m_i\}$$

$$a_i = A_i/\sum_{I=1}^{n} A_i$$

$$L = D/\{\sum_{I=1}^{n} A_i/m_i\}$$

$$R = F - L$$

where Q = pool size, D = dose of ^{15}N, F = total flux rate, a_i is the fractional zero-time intercept of component A_i, L = irreversible loss rate, R = recycling rate.

The quantity of urea synthesized in the body, degraded to NH_3 in the digestive tract, and subsequently resynthesized into urea by the body can be estimated from the difference between the rates of irreversible loss of urea-C and urea-N from plasma, as estimated by using simultaneous injection of ^{14}C-urea and ^{15}N-urea. This is possible because ^{14}C from hydrolysed urea enters a very large bicarbonate pool with a rapid turnover; therefore, the return of ^{14}C into newly synthesized urea is negligible (Koenig et al., 2000). As for the continuous injection method, the irreversible loss rate of NH_3 from ruminal fluid is calculated by comparing enrichment of NH_3 at "plateau" enrichment with the rate of infusion of ^{15}N ammonium sulphate. The proportion of urea in plasma, or the bacteria-N in the ruminal fluid derived from this, is calculated as the ratio of the "plateau" enrichments of urea-N or bacteria-N to NH_3-N.

Recently, a different isotope tracer technique has been developed (Sarraseca et al., 1998). This method involves infusion of (^{15}N^{15}N)-urea, followed by isotope analysis of three species (^{15}N^{15}N), (^{14}N^{15}N) and (^{14}N^{14}N). The technique is based on the assumption that when urea enters the GIT as a (^{15}N^{15}N) molecule and then undergoes hydrolysis *via* bacterial urease action, this will yield two molecules of $^{15}NH_3$. If these $^{15}NH_3$ molecules are then reabsorbed and extracted by the liver then they may com-

bine with ^{14}N atoms (from aspartate) within the hepatic ornithine cycle to yield two ($^{15}N^{14}N$)-urea molecules. The chances of ($^{15}N^{15}N$)-urea returning to the system after entry to the gut, whether directly or indirectly by combination of two ^{15}N-containing molecules within the ornithine cycle, are considered negligible.

Arterial-venous difference techniques

This technique requires precise surgical interventions, liver and GIT metabolism can be separated and the latter can be further separated *via* careful catheterization; accurate determination of blood flows is required. Chronic catheters are usually inserted into the hepatic vein, the portal vein, a mesenteric vein, the ruminal vein and a jugular artery. Rates of NH_3 absorption and urea synthesis can be estimated but data on the fate of urea-N are not (Table 1). According to Table 1, the following relationships can be obtained between N intake (x_1 in g per day) or portal NH_3 absorption (x_2 in mmol per min) and hepatic urea synthesis (y in mmol per min):

Cattle:	$y = -116.8 + 2.94x_1$,	$r^2 = 0.77$,	$n = 20$
	$y = 13.0 + 1.53x_2$,	$r^2 = 0.77$,	$n = 20$
Cow:	$y = 1171.8 - 1.08x_1$,	$r^2 = 0.26$,	$n = 4$
	$y = -143.0 + 1.72x_2$,	$r^2 = 0.88$,	$n = 4$
Sheep:	$y = 29.0 + 0.60x_1$,	$r^2 = 0.06$,	$n = 10$
	$y = 11.1 + 1.23x_2$,	$r^2 = 0.10$,	$n = 10$

It was concluded that significant relationships exist between dietary N intake or portal NH_3 absorption and hepatic urea synthesis in cattle. In sheep, much weaker relationships are noted between N intake or portal NH_3 absorption and hepatic urea synthesis.

MANIPULATING PATHWAYS OF UREA RECYCLING

In ruminants, especially those in developing countries, protein nutrition becomes more important because protein resources are limited. In developed countries N in urine and faeces has sometimes become a serious environmental burden because of extensive use of high protein diets. Improvement of the utilization efficiency of dietary protein and reduction of N waste through rational formulation of diets has become very important. A considerable portion of N excreted in the faeces is endogenous material. Urinary N originates from inevitable losses related to maintenance, losses associated with the deposition of AA into skeletal muscle tissue, losses resulting from any imbalance between energy and protein supplied by the diet, and excretion of purine derivatives, degradation products of microbial

TABLE 1

Nitrogen intake (NI, g/d), portal NH_3 absorption (P-NH_3), hepatic NH_3-N uptake (H-NH_3) and urea-N output (H-Urea) (mmol/h) measured using the AV difference technique in ruminants fed a range of diets

Species	Diet constituents	NI	P-NH_3	H-NH_3	H-urea	References
Cattle	Grass nuts-flaked maize (70:30, w/w)	123	58	55	202	Wilton et al. (1988)
	Lucerne hay	162	291	290	366	Huntington et al. (1989)
	High concentrate	95	128	129	159	
	Grass nuts-flaked maize (50:50, w/w)	102	77	101	172	Fitch et al. (1989)
	Grass nuts	172	184	191	403	
	Maize silage	106	91	88	115	Maltby et al. (1991)
	Lucerne-ground maize (25:75, w/w)					Reynolds et al. (1991)
	low intake	98	143	148	235	
	high intake	174	250	260	491	
	Lucerne-ground maize (75:25, w/w)					
	low intake	133	186	194	354	
	high intake	209	340	353	593	
	Grass silage-grass nuts (70:30, w/w)	94	149	150	136	Maltby et al. (1993a)
	Barley-grass nuts (70:30, w/w)	79	71	77	119	
	Lucerne	153	253	259	363	Maltby et al. (1993c)
	Switchgrass hay:concentrate (73:27)	99	123	125	106	Huntington et al. (1996)
	Switchgrass hay:concentrate (63:37)	100	124	127	135	
	Chopped switchgrass:maize grain (37:63)	141	131	135	198	Whitt et al. (1996)
	Lucerne	197	245	248	346	
	High grain diets-different RDP					Krehbiel and Ferrell (1999)
	9.5% CP	122.1	79	—	—	
	11.5% + 0.72% urea	178.7	145	—	—	
	13.5% + 1.44% urea	204.3	163	—	—	
	11.5% + 250 g/d casein infusion	167.7	135	—	—	
	13.5% + 1.44% urea + 250 g/d casein infusion	202.5	211	—	—	
	Lucerne-ground maize-soyabean meal					Lapierre et al. (2000)
	low intake	58.5	90	95	150	
	medium intake	95.4	109	122	217	
	high intake	142.9	134	146	255	

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TABLE 1
continued

Species	Diet constituents	NI	P-NH_3	H-NH_3	H-urea	References
Cow	Maize silage:concentrate (60:40)					Reynolds et al. (1988)
	4 weeks postpartum	363	517	517	674	
	8 weeks postpartum	421	578	591	892	
	Meeting ME requirement (nonlactating)	139	121	—	—	Huntington and Reynolds (1987)
	2.8 × ME requirement (first lactation)	358	431	—	—	
	3 × ME requirement (lactating)	370	526	531	773	
	Lucerne hay : maize grain (50:50)	512	392	376	552	Whitt et al. (1996)
Sheep	Maize-soya-hulls-molasses-different N					Bohnert et al. (1999)
	urea	15.7	24.8	25.2	21.6	
	soyabean meal (SBM)	16.4	27.7	28.1	25.9	
	poultry by-product meal (PBM)	16.1	19.4	20.0	16.5	
	maize gluten and blood meal (BMCGM)	15.8	20.6	21.4	20.0	
	Maize-lucerne-soyabean meal					Burrin et al. (1991)
	ad libitum	24.6	25	28	101	
	maintenance	10.4	21	23	63	
	Bromegrass + no supplement	7.5	11.2	12.2	23.1	Krehbiel and Ferrell (1999)
	Bromegrass + SBM fed once every 24 h	21.2	38.0	38.7	54.9	
	Bromegrass + SBM fed once every 72 h	44.9	26.8	28.2	39.0	
	Grass pellets	21.4	25.8	30.1	41.9	Lobley et al. (1998)

nucleic acids absorbed from the small intestine (Van Bruchem et al., 1997). Excretion of endogenous N is considerably higher than ileal N flow or the quantity eliminated in faeces. These fractions only constitute part of the total quantity of endogenous protein produced because much endogenous protein is reabsorbed. Of these routes, urea recycling is one of the most important components of endogenous protein reabsorption.

The transport of urea N into the GIT is a normal process of great significance in the physiology of all mammals. A large amount of N passes through the urea pool daily and this provides a potential target for manipulation to improve its conversion to animal products. There are two main directions: either reduce the amount of dietary N converted to urea by reducing NH_3 absorption and AA catabolism, or improve the conversion of urea-N, produced in the liver and returned to the digestive tract, into microbial protein. Although many complicated relationships exist between N intake and hepatic urea-N (Table 1), Bunting et al. (1989) noted that net incorporation of blood urea-N into bacterial protein is inversely related to N intake; this implies that hepatic NH_3 production may be reduced by manipulating dietary N sources. For example, a less degradable source of dietary protein may provide a greater proportion of absorbable AA entering small intestines; this can reduce urea synthesis. Krehbiel and Ferrell (1999) noted that for cattle consuming high-grain diets, an optimal amount of DIP in the diets enhanced fermentation in the rumen, increased AA flow to the duodenum, and increased net portal appearance of AA, without influencing energy use by the PDV. When the dietary DIP requirement has been met, additional DIP will not be beneficial. For example Bohnert et al. (1999) demonstrated that N retention and efficiency were improved by increasing UIP from 40 to 60% of total CP when lambs were fed low energy diets.

On the other hand, supplementing diets with fermentable energy sources can enhance utilization of N for bacterial synthesis. Huntington (1989) reported that increased intake of readily fermentable carbohydrate increased the rate of endogenous urea transfer through the rumen wall, decreased salivary transfer of urea to the rumen, and decreased urea transfer to post-ruminal tissues. Thus, MCP production in the rumen can be increased. Obitsu et al. (2000) reported that abomasal infusion of glucose reduced urea production and urinary N excretion. This illustrates that increased glucose absorption from the small intestine may contribute to increased flow of AA to peripheral tissues and to reduced wastage as excretion of urinary N. As described above, it is necessary to maintain a suitable ratio of available energy and N to improve the utilization of recycled urea.

It is well known that protozoa in the rumen increase the degradation of dietary protein, producing a rapid release of NH_3. They also ingest and digest bacteria, recycling more N. Jouany (1996) concluded that defaunation may improve N utilization in ruminants by increasing AA supply to the intestines, by reducing

urea synthesis, and by reducing urinary N excretion and bacterial N turnover. In addition, Koenig et al. (2000) demonstrated that defaunation improved the intraruminal metabolism of N by increasing both the ruminal concentration of bacteria and the flow of bacterial N to the intestine.

It is also possible to manipulate the utilization efficiency of recycled urea by adjusting diet structure (i.e. the forage to concentrate ratio) and intake. Huntington et al. (1996) reported that, when fed diets with 20% or less concentrate, steers recycled 90% of hepatic urea production; the percentage of recycled urea decreased to 64 with 63% of the diet as concentrates, and to 51% when diets with 90% concentrate were fed. Increased urea recycling to the GIT may improve the overall efficiency of N utilization for maintenance and production. Under conditions of low or zero N intakes, urea-N production exceeds N intake in ruminants as body protein is mobilized when animals are in negative N balance.

FUTURE DIRECTIONS

Much data on NH_3 production, NH_3 absorption, and urea recycling in ruminants has been accumulated (Table 1); however, it is still difficult to utilize these data in feeding practice because few experiments have been conducted using practical diets. In the future, we propose that nutritional manipulations of N utilization must be tested on, and applied to, practical diets while the database on this topic continues to grow, i.e. while the optimal nitrogen intake, the ratio of dietary nitrogen and readily fermentable carbohydrate, are determined by the slow release technique for NPN in the rumen and the bypass technique for crude protein. After obtaining these practical data, these techniques or nutritional parameters will be organically conformed and applied in the practical diets of various animals. Further, considering the complexity of urea recycling, it is necessary to integrate the effects of the many dietary factors involved and to study their dynamics. This will involve the development and refinement of mechanistic metabolic models.

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STRESZCZENIE

Produkcja i wchłanianie amoniaku oraz recyrkulacja mocznika u przeżuwaczy. Praca przeglądowa

Omówiono ważniejsze badania dotyczące produkcji i wchłaniania amoniaku oraz recyrkulacji mocznika u przeżuwaczy. Opisano produkcję i wykorzystanie amoniaku w żwaczu i dalszej części przewodu pokarmowego. Przedyskutowano zagadnienie wchłaniania amoniaku do krwi żyły wrotnej, detoksyzację amoniaku i syntezę mocznika w wątrobie oraz rozkład mocznika w przewodzie pokarmowym. Analizowano czynniki wpływające na recyrkulację mocznika i jego szlaki. Sugeruje się, że dalsze badania powinny być ukierunkowane na dynamikę recyrkulacji mocznika i poprawę konwersji białka oraz opracowanie zintegrowanego mechanistycznego modelu opisującego procesy trawienia i metabolizmu składników azotowych u przeżuwaczy żywionych typowymi dietami.