

## THE ROLE OF SULPHUR IN RUMINANT NUTRITION. A REVIEW

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### ABSTRACT

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Some aspects of sulphur metabolism and its role in ruminant nutrition are presented in this text. In particular, the production of sulphide and its absorption from the rumen, the incorporation of sulphur into microbial protein, the metabolic interrelations of sulphur with other elements, the recycling and toxicity of sulphur, the excretion of sulphur, and the nitrogen and sulphur retention are reviewed.

### INTRODUCTION

Sulphur metabolism and nitrogen metabolism are closely associated in ruminants. The action of the rumen microflora may completely alter the dietary form of both of these elements; for instance, the degradation of dietary protein to yield ammonia and sulphide or the synthesis of microbial protein from dietary urea and inorganic sulphate. As ruminant metabolism combines a complex microbial system in both the rumen and large intestine with a mammalian metabolic system, any study of nitrogen and sulphur metabolism requires an understanding of the metabolic pathways in the microorganisms as well as in mammalian tissues.

A detailed and comprehensive coverage of many aspects of sulphur metabolism in microorganisms may be found in reviews by Peck (1962) and Trudinger (1969), in treatises by Roy and Trudinger (1970), Greenberg (1975) and Postgate (1979), and in symposia proceedings edited by Muth and Oldfield (1970) and by *Excerpta Medica* (1980). Similarly, the metabolic pathways of inorganic and organic sulphur that may occur in the rumen have been recently reviewed (Moir, 1970; Whanger, 1972; Schiff and Hodson, 1973; Bray and Till, 1975; Schiff, 1980).

### SULPHUR MODELS

There has been only a small number of models of sulphur metabolism in sheep reported in the literature (Kennedy and Siebert, 1975; Gawthorne and

Nader, 1976; Kennedy and Milligan, 1978; Doyle and Moir, 1979; Kandylis, 1981). The dietary sulphur intakes of the above models and the amounts of sulphur infused into the rumen, together with the sulphur flows from the reticulorumen and duodenum, have been used to develop compartmental balance models of sulphur metabolism in the stomach of the sheep. The recent model of Kennedy and Milligan (1978) looked at total organic sulphur flows in unavailable, protozoal and bacterial fractions, while the work of Doyle and Moir (1979) illustrates the importance of non-protein organic sulphur.

Compared with the information available for nitrogen, there is little information on flows and uptake of the digestion products of sulphur compounds in the intestines, particularly in the small intestine. In the hindgut, sulphide may be generated by bacterial activity and incorporated into bacterial protein or absorbed. The sulphur amino acids, absorbed from the small intestine, are incorporated into animal tissues as protein, or synthesized into wool, or hair. Models, on a whole animal scale, are needed to allow many of these interactions to be estimated.

#### DIETARY SULPHUR

Sulphur-adequate plants generally contain more sulphur amino acids and are presumably of better nutritional quality for animals than are sulphur-deficient plants. In addition, diets deficient in the sulphur-containing amino acids may cause a reduction in voluntary food consumption (Rees and Minson, 1978). Due to seasonal changes and species differences, sulphur intake of ruminants may drop to a level which causes a deficiency of sulphur for the rumen microorganisms; under such conditions no benefit will be obtained from supplementing the diet with urea and/or energy sources. Supplementation of such diets with some form of sulphur may be necessary to provide optimum dietary nitrogen to sulphur (N:S) ratios. The desirable dietary N : S ratio required for most efficient utilization by rumen microorganisms is about 10–13.5 : 1 for sheep (Moir et al., 1967–68; Bird, 1972c) and about 13.5–15 : 1 for cattle (Bird, 1974).

Because of their solubility, sulphates are present in most water supplies. Bray (1965) indicated the possibility that sheep drinking highly sulphated waters could consume up to 1.5 g of sulphur per day. However, the nutritional value of sulphur in drinking water has not been investigated yet, although it has been suggested that an animal's sulphur intake from this source may be large enough to produce adverse effects (Weeth and Hunter, 1971).

#### THE PRODUCTION OF SULPHIDE IN THE RUMEN

Because the rumen microorganisms can reduce oxidized forms of sulphur to forms which can be incorporated into organic compounds, ruminants have the ability to obtain their sulphur supply from inorganic sources of sulphur.

This is in contrast to non-ruminant animals which must have their dietary supply of sulphur in an organic form.

Sulphate reduction is known to occur in ruminants and there are two postulated mechanisms for the reduction of sulphate by microorganisms, the assimilatory and dissimilatory sulphate reduction (Peck, 1962). The dissimilatory sulphate reducing bacteria use sulphate as their terminal electron acceptor and produce large amounts of  $\text{H}_2\text{S}$ . The assimilatory bacteria, on the other hand, reduce sulphate to the sulphide level and incorporate the sulphur into cellular materials and normally do not produce  $\text{H}_2\text{S}$  in detectable amounts, unless from the fermentation of reduced sulphur compounds, or following death and autolysis of the microorganisms (Peck, 1962). Since rumen microorganisms can produce  $\text{H}_2\text{S}$  from sulphate and can incorporate sulphate sulphur into cellular materials (Anderson, 1956; Henderickx, 1961), it is postulated that both these pathways exist in rumen microbial metabolism. However, the high concentration of  $10^7$  sulphate-reducing bacteria per ml of rumen fluid found in sheep fed sulphate-containing diets (Huisingh et al., 1974) suggests that the dissimilatory sulphate reducing group makes a major contribution to the total sulphate reduced in the rumen of sheep. In the biological version presented in Fig. 1 the sulphate-reducing bacteria bypass assimilatory sulphate reduction and generate  $\text{H}_2\text{S}$  in sufficient amounts to support growth of the sulphide- and sulphur-oxidizing bacteria.

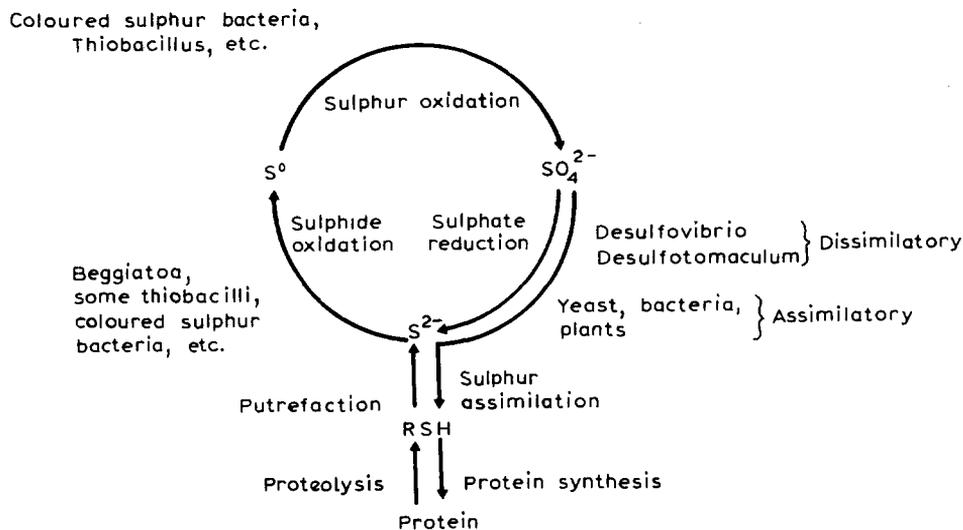


Fig. 1. The biological sulphur cycle. Sulphate ( $\text{SO}_4^{2-}$ ) is reduced to sulphide ( $\text{S}^{2-}$ ) by dissimilatory sulphate-reducing bacteria and provides substrates for sulphide-oxidizing bacteria who convert it, by way of elemental sulphur ( $\text{S}^0$ ) back to sulphate. In assimilatory sulphate reduction the sulphur of sulphate passes through the sulphide level of oxidation and becomes incorporated into an amino acid (RSH) before being built into plant as microbial protein. This is eaten by animals and the sulphur is eventually returned to the cycle as sulphide formed during the breakdown and putrefaction (by bacteria) of dead organisms (Postgate, 1979).

Various workers have shown a transient accumulation of sulphide in the rumen from sulphate administration or from various feeding regimens (Spais et al., 1968). The optimum pH for the reduction of sulphate was 6.5 (Anderson, 1956) but the reduction rate was not very sensitive to pH changes.

There is now substantial evidence to suggest that sulphate sulphur, when adaptation to give reduction is established, is an adequate source of sulphur for the rumen microorganisms. However, the utilization of dietary sulphur depends not only on the quantity and the nature of available sulphur, but also upon (1) the rate of sulphide production, (2) the uptake of sulphide by microorganisms, and (3) the loss of sulphide from the rumen (Moir, 1970).

The rate of sulphide production is rapid whether it originates from sulphate (Bird and Moir, 1971), from more reduced inorganic sulphur substrates, i.e. thiosulphate and sulphite (Henderickx, 1961) or from cysteine and cystine (Bird, 1972a).

#### ABSORPTION OF SULPHUR FROM THE RUMEN

In an experiment conducted by Anderson (1956), sulphide which was added to the rumen almost completely disappeared within 2 h of administration, and at the same time an increase in blood sulphate occurred. This suggested direct absorption of sulphide from the rumen, which has been confirmed subsequently by other workers with radiosulphur. Bray (1969 a,b) showed that there was very little absorption of  $^{35}\text{S}$ -sulphate, whereas the absorption of  $^{35}\text{S}$ -sulphide was very rapid when the normal contents of the rumen were replaced by a buffer solution. The pattern of sulphide disappearance from the rumen followed a first order reaction and the estimated half-life of rumen sulphide ranged from 10 to 22 min.

The size of the rumen sulphide pool is usually small, due to the rapid absorption of sulphide from the rumen (Bray, 1969a,b). The absorption rate is dependent on sulphide concentration and ruminal pH (Bray, 1969b; Bray and Till, 1975). The sulphate ion per se is apparently not absorbed from the rumen (Bray, 1969b). However, Gawthorne and Nader (1976) suggested that there may be some sulphate absorption from the rumen, but their evidence is inconclusive.

During periods of low fermentative activity in the rumen the sulphide produced would not be as rapidly incorporated by bacteria, and would therefore be lost by absorption from the ruminal pool (Bray, 1969b). However, all of the rumen sulphide is not available for absorption across the rumen wall. Bray and Hemsley (1969) reported that at rumen liquor sulphide concentrations of less than 1  $\mu\text{g}/\text{ml}$  most of the sulphide was unavailable for absorption from the rumen and held in the microbial fraction.

Doyle (1977) states that the absorption of organic sulphur from the rumen as sulphur amino acids would appear to be limited by the low concentration of free amino acids in the ruminal liquor. It is suggested that amino acids such as methionine and cysteine are poorly absorbed across the rumen wall (Leibholz, 1971).

## THE INCORPORATION OF SULPHUR INTO MICROBIAL PROTEIN

Rumen microorganisms can utilize both inorganic and organic sulphur to synthesize sulphur-containing amino acids in the production of microbial protein. Although it has been shown that a few rumen bacteria require amino acids which contain sulphur for growth (Pittman and Bryant, 1964), the current opinion is that sulphide is probably a major source of sulphur for bacterial protein synthesis and that amino acids containing sulphur are synthesized *de novo* from this substrate. Evidence in support of this view was provided by Nader and Walker (1970) who showed in rumen digesta studies *in vitro* a maximum of 11 and 1% direct incorporation of  $^{35}\text{S}$ -methionine and  $^{35}\text{S}$ -cystine respectively. In a later study, however, Gawthorne and Nader (1976) found in sheep that only 53–57% of the sulphur in microbial protein originated from the sulphide pool. They suggested that approximately half the sulphur amino acid content of microbial protein in ruminal digesta was synthesized *de novo* from sulphide, and the remainder resulted from the direct incorporation of amino acids from digested plant and salivary proteins, which indicates that direct incorporation of dietary thioamino acids into microbial protein may be at least equally important. However, Gawthorne and Nader (1976) were unable to account for 62–77% of the daily sulphate-sulphur turnover. More recently, Kennedy and Milligan (1978) used  $^{35}\text{S}$ -sodium sulphate with sheep and found that bacteria derived 52–67% of organic sulphur from rumen sulphide in sheep given brome grass, and approximately 45% of bacterial organic sulphur was derived from sulphide for sheep given lucerne. Protozoa derived approximately 90% of organic sulphur from bacteria.

Nolan and Leng (1972) suggested that around 30% of the ammonia continually being incorporated into ruminal microbial protein may have recycled through the amino acid and ammonia pools as a result of lysis of viable bacteria in the rumen due to bacteriophage activity or the engulfment of bacteria by protozoa. Walker and Nader (1968) using  $^{35}\text{S}$  for the estimation of microbial protein *in vitro* found that there was no reversibility of sulphide incorporation, i.e. there was no exchange of incorporated  $^{35}\text{S}$  with the sulphide pool. In a later study, Walker and Nader (1975) using  $^{35}\text{S}$  for the measurement *in vivo* of ruminal microbial protein synthesis in sheep did not observe distortion of the plot for decline of microbial  $^{35}\text{S}$  in the rumen after cessation of isotope infusion and suggested that sulphur recycling within the rumen is not a factor significantly affecting the results obtained. Recently, Kang-Meznarich and Broderick (1981) showed two exponents of  $^{35}\text{S}$  decline after plotting the ruminal protein-bound  $^{35}\text{S}$  concentration versus time. From this they concluded that the second slope may reflect intraruminal recycling of  $^{35}\text{S}$ , or possibly the turnover rate of protein-bound  $^{35}\text{S}$  which becomes indirectly incorporated into protozoa (whereas, the initial slope of  $^{35}\text{S}$  disappearance was used in estimation of bacterial protein turnover (synthesis) in the rumen). However, the internal recycling of sulphur within the rumen needs more investigation.

Walli and Mudgal (1978) have shown that sulphur plays an important role in the utilization of urea-based diets in cattle and buffaloes and its relative proportion to nitrogen in such diets is also equally important with special reference to protein synthesis in the rumen in general and the synthesis of thioamino acids in particular; out of the three N:S ratios studied, the 10:1 ratio seems to be adequate as regards protein and thioamino acid synthesis in the rumen. Recently, Harrison and McAllan (1980) reported a mean value (based on 31 observations) of 18.5:1 for mixed rumen bacteria, ranging between 8.6:1 and 30.8:1, and a mean value (based on 22 observations) of 21.6:1 for protozoa, ranging between 14:1 and 38:1. From this they concluded that a ratio of 20:1 between available N (either derived from non-protein nitrogen or from rumen degradable protein) and available S (either derived from organic S such as dietary sulphur amino acids or from inorganic S) should be adequate to meet the S requirements of rumen microbes. However, these workers suggested that a simple dietary N:S ratio is inadequate to express the minimum requirement because part of the N and part of the S may not be available for the microbes.

Little is known about the minimum concentrations of ruminal sulphide required for maximal microbial growth. By analogy with nitrogen, where a minimum required level of  $\text{NH}_3\text{-N}$  in rumen liquor of 50 mg/l was suggested (Satter and Roffler, 1976), for S a limiting level of approximately 1 mg/l sulphide-S was proposed (Bray and Till, 1975). Kandylis (1981) reported that the sulphide concentration required for maximal microbial growth was approximately 3.8 mg/l of rumen liquor, whereas the corresponding ammonia concentration was approximately 8.5 mg/100 ml (Kang-Meznarich and Broderick, 1981).

#### METABOLIC INTERRELATIONS OF SULPHUR WITH OTHER ELEMENTS

It has been well established that a metabolic interrelation between sulphate, molybdenum and copper exists, and the formation of a highly insoluble  $\text{CuMoS}_4$  complex was proposed by Dick et al. (1975). It has been suggested that molybdenum apparently exerts its limiting effect on copper retention in the presence of inorganic sulphate and neither molybdenum nor sulphate alone interfere with copper retention (Whanger, 1972). However, more recent research has revealed that both organic and inorganic S interfere with Cu retention, presumably because of the formation of insoluble  $\text{CuS}$  at sites beyond the rumen (Suttle, 1974).

Molybdenum inhibits the reduction of sulphate to sulphide in vitro (Huisling and Matrone, 1972) and in vivo (Gawthorne and Nader, 1976). However, it has been reported that additions of molybdate supplements (50 ppm Mo) increase the in vivo sulphide concentrations in the rumen of sheep (Mills, 1960) and cattle (Hartmans and Bosman, 1970). Huisling et al. (1975) found that dietary sodium molybdate (50 ppm Mo) significantly inhibited the production of sulphide from sulphate, but enhanced the produc-

tion of sulphide from methionine and suggested that the enhanced rumen sulphide concentrations measured by some workers were due, in part, to an increase in the rate of sulphide production from the sulphur amino acids.

Prentice and Matrone (1970) showed that sulphate was related to the formation of a Cu—Mo complex in vivo and in their data, copper was found to significantly decrease molybdate inhibition of sulphate reduction. Bishara and Bray (1978) observed that the intravenous infusion of high levels of molybdate inhibited tubular reabsorption of sulphate; similarly, infusion of high levels of sulphate inhibited molybdate reabsorption.

Various sulphur compounds have been shown to influence the metabolism of selenium by rumen microorganisms (Whanger, 1970). Cysteine and methionine inhibited the uptake of selenomethionine by rumen microbes more than did sulphite. However, conflicting reports have been presented on the effect of sulphur on selenium metabolism in the animal. The addition of sulphate to the diet was reported to decrease the effectiveness of dietary selenium as selenite in the prevention of white muscle disease (Hintz and Hogue, 1964), while other workers could not find evidence for sulphate contributing to white muscle disease (Whanger et al., 1969).

Somers and Underwood (1969) found that both nitrogen and sulphur retention were significantly lowered in zinc-deficient sheep; their results suggested impaired protein metabolism in zinc-deficient animals. Goodrich and Tillman (1966) reported that phosphorus retention was significantly reduced in lambs by sulphate in the presence of 100 ppm copper.

## RECYCLING OF SULPHUR

The recycling of sulphur to the rumen is a well-established phenomenon and has been reviewed in a number of papers (Moir, 1970; Bray and Till, 1975). Recently, however, Kandylis (1983) has published a detailed review on the transfer of sulphur from the blood to the rumen. From the data presented in these reviews it appears that recycling of total S and sulphate-S to the reticulorumen contributes approximately (mean  $\pm$  SD)  $7.44 \pm 2.55$  and  $3.55 \pm 1.63$  mg S/day/kg body weight, respectively.

From the available data, it appears that saliva is probably the major source of recycled sulphur to the rumen of sheep. The rate of transfer of sulphate from blood to the rumen is related to sulphate concentrations in blood and saliva (see Kandylis, 1983). The transfer of both urea and sulphate into the post-ruminal tract may seriously reduce the amounts available for recycling to the rumen and incorporation into microbial organic matter. Kennedy et al. (1975) found that sulphate recycling to the rumen of sheep was considerably less than for cattle, which could, at least partly, be explained by the greater need for sulphur amino acids in wool production in sheep as compared to the requirements in cattle.

## THE METABOLISM OF SULPHUR IN THE POST-RUMINAL TRACT

Bray and Till (1975) estimated that the digesta flowing into the intestines of sheep would provide the equivalent of 1–2 g of amino acid sulphur per kg organic matter intake. The combined bile and pancreatic secretions may contribute 142–245 mg sulphur per day (Bird, 1972b). Other major inputs of sulphur into the intestine are plasma proteins, which contribute about 80 mg sulphur per day (Campbell et al., 1961), mucous and the turnover of mucosal cells.

Bird (1971) suggested that sulphate infused into the duodenum and not absorbed in the small intestine may be reduced in the large intestine to hydrogen sulphide which is then absorbed. In vitro studies with sheep have indicated that the ileum is the most active and efficient site of amino acid absorption (Phillips et al., 1976). A recent review paper of Lindsay and Armstrong (1982) discusses the processes of digestion, occurring principally within the small intestine of ruminants, of the sulphur-containing amino acids methionine and cyst(e)ine.

Bray and Till (1975) observed that, under most circumstances, it is likely that the sulphide resulting from microbial degradation of various sulphur compounds in the hindgut would not be extensively used for protein synthesis but would be largely absorbed as such. However, the extent to which protein sulphur in the ileal digesta is degraded and the sulphide-sulphur either absorbed from the hindgut or converted into microbial protein is not known. Further data on the digestion in the intestines of dietary and microbial sulphur compounds and on the quantitative pathways of hindgut fermentation are necessary to establish the amount and form of sulphur that is absorbed and used for production processes.

## SULPHUR TOXICITY

Dougherty et al. (1965) suggested that the generation of large quantities of hydrogen sulphide in the rumen depress rumen motility, and cause severe nervous and respiratory distress if absorbed through the lungs during eructation. Bird (1972d) has shown that single ruminal infusions of sulphide (0.94 g S) solution resulted in temporary respiratory distress and collapse of sheep, while continuous ruminal infusions of sulphide (2.93 g S/day) solution resulted in a significant decrease in dry matter intake. No toxic effects of sulphur were reported by Gawthorne and Nader (1976) where 10 g of sodium sulphate per day were infused continuously into the rumen of sheep. However, Raisbeck (1982) reported an episode of cerebrocortical necrosis (polioencephalomalacia) in cattle fed high sulphate (> 2% sulphate) rations. In a recent study, Kandylis and Bray (1982) observed no toxic effects after the administration of 7.4 g of (<sup>35</sup>S) sodium sulphate into the rumen of sheep (2.4 g total S in ration plus 5 g carrier). Bird (1972d) states that 'intake by sheep of not more than 4 g sulphur/day, or the addition to ruminant diets of

0.2% sulphate sulphur or S-amino acid sulphur, should satisfy microbial and tissue sulphur requirements without adversely affecting feed intake.'

The very high levels of sulphide in the rumen in the work of Anderson (1956) did not result in any toxic symptoms, nor did the addition of sulphide to give rumen concentrations of  $330 \mu\text{g S}^{2-}/\text{ml}$  or  $113 \mu\text{g}/\text{ml}$ . Bray (1969b), however, observed respiratory difficulty in sheep when sulphide levels of approximately 330 and  $226 \mu\text{g}/\text{ml}$  were added to buffers replacing rumen contents, and sulphide could be smelled on the animals' breath in 10 to 15 min. As rumen concentration fell, the animals recovered without incident.

Sulphur toxicity was reported in a group of 20 yearling heifers which had consumed S mixed with corn (Julian and Harrison, 1975). The animals showed respiratory disease and abdominal pain. In a later study, Rumsey (1978) showed that the addition of 9.8 g/kg diet of sublimed S markedly reduced the feed intake and resulted in weight loss in steers fed high concentrate diets. Lower feed and water consumption, weight loss and diuresis were reported in growing heifers offered water containing 5000 ppm sulphate (Weeth and Hunter, 1971), while Digesti and Weeth (1976) concluded that 2500 ppm sulphate in drinking water represents a safe tolerance concentration.

Excesses of methionine or its hydroxy analogue adversely affect feed consumption by ruminants. Dietary supplements, ruminal infusions and abomasal infusions of these compounds can decrease dry matter intake by ruminants. Thus, in cattle, intraruminal infusion of D,L-methionine, 2.5% or more of dietary dry matter intake, resulted in a toxic effect on feed intake (Satter et al., 1975). Papas et al. (1974) reported that feed consumption by lambs was decreased from 1000 g to 786 g/day when methionine hydroxy analogue was included in the diet at a level of 1.2%. Recently, Doyle and Adams (1980) found that dry matter intake fell below the control level when 24 g/day or more of D,L-methionine was infused into the rumen of sheep, while one animal died when 30 g/day of the amino acid was infused.

Recently, Janowski and Chmielowiec (1981) reported a case of poisoning of cattle with sulphur from environmental pollution. Cattle within 1 km of a sulphur mine were exposed to sulphur dust, sulphur dioxide and hydrogen sulphide. Poisoning was associated with respiratory system and digestive system lesions.

#### URINARY AND FAECAL EXCRETION OF SULPHUR

Sulphur can be excreted in the urine as both organic and inorganic compounds. Urinary excretion of sulphate, the major end product of sulphur amino acid oxidation and inorganic sulphur metabolism in mammalian tissue, represents a major source of sulphur loss from the body. Generally, only trace amounts of amino acids appear in urine and ruminants, like monogastrics, excrete ester sulphates in the urine.

The major factors controlling the extent and rate of renal excretion of sulphate are plasma inorganic sulphate concentration, the tubular maximum reabsorptive capacity and the glomerular filtration rate. Inorganic sulphate in blood in excess of the tubular reabsorptive capacity is rapidly excreted (Bishara and Bray, 1978).

Variations in sulphur intake affect urinary sulphur excretion (Bray and Hemsley, 1969). Bird (1971) found that infusions of sodium sulphate (0–6g sulphur per day) into the rumen or duodenum significantly increased the excretion of total sulphur, ester sulphate, and inorganic sulphate in urine. Microbial activity in the hindgut may also affect the urinary excretion of inorganic sulphate. Bird and Thornton (1972) found that infusion of glucose into the hindgut decreased urinary sulphur excretion by reducing the output of sulphate.

The major portion of the faecal sulphur is organic (Bird, 1971; Bird and Hume, 1971) and is presumably derived from bacterial protein. The faecal excretion of total sulphur increases with sulphur intake and was also shown to be related to intakes of organic matter and digestible organic matter (Kennedy, 1974). Faecal neutral sulphur excretion by sheep may be increased when oral or ruminal supplements of sodium sulphate are given (Bird, 1972c). Bird (1971) suggested that the intake of sulphur and the supply of digestible energy to the fermentative rumen and hindgut regions primarily determine the amount of organic sulphur excreted in the faeces by affecting the synthesis of bacterial sulphur.

Bray (1969a) reported the faecal recovery of 12 and 19% of  $^{35}\text{S}$  from intravenous doses of  $^{35}\text{S}-\text{Na}_2\text{SO}_4$  and suggested that intravenously infused  $^{35}\text{S}$ -sulphate was secreted primarily into the post-ruminal tract in the form of sulphate esters or inorganic sulphate, and excreted as such in the faeces. However, Bird and Thornton's (1972) results show that these reducible sulphur or  $^{35}\text{S}$  fractions in the faeces were of minor significance.

#### NITROGEN AND SULPHUR RETENTION

The ratio of nitrogen retention to sulphur retention is determined by the amounts of nitrogen and sulphur deposited in body tissue. Generally, diets supplying more sulphur tend to result in higher retention of both nitrogen and sulphur, and oral supplements of sulphur given to sheep receiving diets low in sulphur also result in increased percentages of nitrogen and sulphur retained (Bray and Hemsley, 1969). Large doses of sulphur, as D.L.-methionine (Doyle and Bird, 1975) or  $\text{Na}_2\text{SO}_4$  (Bird, 1971), may tend to reduce nitrogen retention below that obtained at optimal levels of sulphur intake. Post-ruminal infusion of sulphur supplements result in more sulphur retained than with ruminal infusions (Bird, 1971).

Bray and Till (1975) used most of the published data for sheep to find a positive linear relationship ( $N=10.37 S-0.038$ ,  $r=+0.952$ ) between N-retention (g/day) and S-retention (g/day) in sheep, which shows the close rela-

tionship between nitrogen and sulphur metabolism. Bray and Till (1975) assumed that this linear equation also applied to N and S excretion. However, only limited data were available for the negative (excretion) region of the curve and it is evident that more negative balance trial studies are required to ascertain the accuracy of one equation describing both retention and excretion of N and S.

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## RESUME

Kandyliis, K., 1984. Le rôle du soufre dans la nutrition des ruminants: Revue bibliographique. *Livest. Prod. Sci.*, 11: 611–624 (en anglais).

Différents aspects du métabolisme du soufre et de son rôle dans la nutrition des ruminants sont présentés dans cet article et font l'objet d'une revue bibliographique. Sont essentiellement étudiés la production des sulfures et leur absorption au niveau du rumen, l'incorporation du soufre dans les protéines microbiennes, les interrelations métaboliques entre le soufre et les autres éléments, le recyclage et la toxicité du soufre, son excrétion et la rétention de l'azote et du soufre.

## KURZFASSUNG

Kandyliis, K., 1984. Die Bedeutung des Schwefels in der Wiederkäuerernährung. Eine Literaturübersicht. *Livest. Prod. Sci.*, 11: 611–624 (auf englisch).

Einige Aspekte des Schwefelstoffwechsels und seiner Bedeutung in der Wiederkäuerernährung werden in diesem Text vorgestellt. Es wird ein Überblick gegeben über die Produktion von Sulphiden und seiner Absorption aus dem Pansen, den Einbau von Schwefel in Mikrobeneiweiss, die metabolischen Wechselbeziehungen des Schwefels mit anderen Elementen, die Rückgewinnung und Toxizität des Schwefels, die Ausscheidung des Schwefels und die Retention von Stickstoff und Schwefel.