SULFUR: REQUIREMENTS FOR MOHAIR GROWTH, MILK YIELD AND BODY WEIGHT GAIN, AND EFFECTS ON NITROGEN, ZINC, COPPER AND MOLYBDENUM METABOLISM IN GOATS

By

KANHU QI

Bachelor of Science
Northwestern Agricultural University
Xi'an, China
1982

Master of Science
Beijing Agricultural University
Beijing, China
1985

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Thesis Approved:

L. M. Owens
Thesis Adviser

W. B Anthon

J Q Fitch

Elden C Nelson

Thomas C. Collins
Dean of the Graduate College

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CHAPTER I

INTRODUCTION

Sulfur is found in every body cell. Important body compounds containing S include specific amino acids (methionine, cysteine, cystine, homocysteine, cystathionine, taurine, and cysteic acid), thiamine, biotin, lipoic acid, coenzyme A, glutathione, chondroitin sulfate, fibrinogen, heparin, ergothionine, and estrogens. These compounds are involved in body and milk protein synthesis, lipid and carbohydrate metabolism, collagen and connective tissue formation through disulfide bonds between and within polypeptide chains, blood-clotting, enzyme synthesis, endocrine function, acid-base balance of intra- and extra-cellular fluids, and the detoxification process.

All of these S-containing compounds except thiamine and biotin can be synthesized in vivo from one essential amino acid -- methionine. Approximately 50% of the total requirement for sulfur-containing amino acids (SAA) can be provided by cystine. Inorganic S can be converted to organic S by microorganisms in the gastrointestinal tract. Both ruminants and nonruminants can use inorganic sulfate to form the sulfate esters in mucopolysaccharides. Although information about S metabolism from sheep and cattle

is extensive, research on S metabolism of goats has been limited. Goats have certain peculiar metabolic characteristics, e.g., higher S content in the milk (Haenlein, 1980), higher feed intake on a body weight basis, dedication of a greater proportion of their nutrient intake to growth, milk and fiber production (Larson, 1978), and absence of monoacylglycerol pathway for triacylglycerol synthesis in goat mammary gland (Hansen et al., 1986). Consequently, sulfur metabolism of goats may differ from that of sheep and cattle.

Hence, we conducted a series of trials with goats to 1) investigate S metabolism under different performance and physiological conditions; 2) determine the S requirements for growth, milk and fiber production; 3) evaluate effects of S supplementation on nutrient digestion and utilization, ruminal and blood metabolites and acid-base balance; and 4) explore the mechanisms behind the interactions between S and Zn, S and Cu, and among S, Cu and Mo.

Each chapter is prepared as a manuscripts in the style and form required by Journal of Animal Science to facilitate publication of experimental results.

CHAPTER II

REVIEW OF LITERATURE

This chapter will outline the literature relevant to the main topic of this dissertation.

This review will discuss S metabolism; S requirements for maintenance, growth, reproduction, lactation and fiber production; S function in cation-anion balance and its effect on blood acid-base balance of animals; S deficiency and toxicity; factors affecting availability of S such as dietary tannic acid, hydrogen cyanide and nitrate, chemical forms of S; and S interactions with Zn, Cu and Mo.

Sulfur Metabolism

Sulfur metabolism has been studied extensively in sheep and cattle, but not in goats. From such trials, the following points have been established (Bray and Till, 1975; Church, 1979; Moir, 1979; Goodrich and Garrett, 1986):

1. Sulfate is reduced to sulfide in the rumen before S is incorporated into organic molecules.
2. Many strains of ruminal bacteria can reduce $SO_4^{=}$ to HS^{-}.
3. Sulfide is absorbed from the rumen, duodenum and other parts of intestine.
4. Synthesis from $SO_4^{=}$ is more rapid for cysteine than for methionine.

5. Destruction in the rumen is slower for methionine than for cysteine.
6. Sulfide is the key intermediate between the breakdown of ingested and recycled S and its subsequent utilization and(or) loss from the system.
7. Sulfur-containing amino acids are absorbed from the small intestine.

Two pathways are used by ruminal microbes for the conversion of sulfate to sulfide. These are the assimilatory pathway and the dissimilatory pathway.

By the assimilatory pathway, the initial reaction, involving $SO_4^=$ and ATP, results in the formation of adenosine-5'-phosphosulfate (APS), an active form of sulfate. Adenosine-5'-phosphosulfate then is phosphorylated by another ATP to form 3'-phosphoadenosine-5'-phosphosulfate (PAPS). Reduction of $SO_4^=$ occurs as PAPS accepts two electrons from a donor protein and $SO_3^=$ is formed. The $SO_3^=$ is bound to a protein where an additional six electrons are accepted to form sulfide. By this pathway, sulfide can be transferred directly to serine to produce cysteine without release of free sulfide.

In the dissimilatory pathway, $SO_4^=$ initially reacts with ATP to form APS; APS-reductase then aids to convert APS to $SO_3^=$, AMP, and H^+. Cytochrome C_3 serves as the electron donor (Goodrich and Garrett, 1986). Free $SO_3^=$ is reduced to free sulfide (HS^-) by sulfite reductase.

The next step in S amino acid synthesis starts at sulfide. Sulfide can be incorporated into SAA by three pathways: 1) sulfide can react with serine to form cysteine; 2) sulfide can react with acetylhomoserine to form homocysteine, which is methylated to methionine; 3) sulfide can be incorporated into cysteine that further reacts with acetylhomoserine to form cystathionine. Cystathionine then can be hydrolyzed to homocysteine, and methylated to methionine. Cystathionine also can be hydrolyzed to form cysteine.

Moir (1979) concluded that the direct flow of sulfate-S across the rumen wall is so small (< 20 mg/d) as to be negligible. Sulfur (up to 200 mg/d in sheep) can return to the rumen through saliva. However, the concentration of sulfate in parotid saliva is low relative to that in plasma. Ester sulfates, and organic S also appear in the saliva, and contribute nutritionally to the ruminal S supply. The amount of S recycled in sheep is disproportionately low in comparison with N. The N:S ratio in saliva of sheep ranges from 70:1 to 80:1.

In cattle, a greater quantity of S is recycled via saliva (Moir, 1979). Per kg BW, cattle recycle ten times as much as sheep. Mixed saliva from cattle has a N:S ratio that ranges between 1.6:1 to 7:1. Hence, cattle may respond to NPN supplementation even with low S diets whereas sheep fed such diets would respond only to S supplementation.

Availability of S for recycling varies with the extent to which SAA are employed (e.g., wool or hair synthesis).

Excretion of fecal S has been related to intake of S, organic matter and digestible organic matter. Urinary S excretion varies with intake of S and organic matter (Church, 1979). The route of S administration does not markedly alter the route of S excretion.

Sulfur requirements of ruminants frequently are expressed as N:S ratios. Although ratios provide a convenient thumb-rule guide for supplementation, Goodrich and Garrett (1986) questioned the validity of a N:S ratio in diet formulation. If N is more available than S, the dietary ratio of N:S must be reduced. Conversely, if the form of S fed is more available than N, the dietary ratio of N:S can be increased and yet achieve a desirable N:S ratio at the tissue level. Thus, the N:S ratio has little practical use and may be misleading. Rather than thinking about an ideal N:S ratio, diets for ruminants should be formulated to provide adequate quantities of available S (Goodrich and Garrett, 1969).

Sulfur Requirements for Maintenance

The S requirement for maintenance of 28.6 kg sheep, based on metabolic urinary and fecal losses and S retained in wool, has been estimated at 300 mg/d (24.26 mg/BWkg$^{\cdot 75}$) of retainable S (Johnson et al., 1971). Langlands et al. (1973) studied the dietary S requirements of Merino sheep using fecal and urinary S excretions as indices. After

conducting 205 S balance trials with sheep fed fifty-one forage diets, they concluded that fecal S (FS, g/d) excretion varied with the S intake (SI, g/d), and organic matter intake (OMI, kg/d) as follows: FS = 0.124 * SI + 0.72 * OMI. This equation indicates that non-dietary fecal S excretion was 0.72 g S/kg OMI. Sulfur digestibility of forage S (SDIG) declined linearly with the reciprocal of dietary S content (HS, g S/kg OM) so that: SDIG = .844 - .681/HS (or as calculated from above, SDIG = .876 - .72 * SI/OMI), in which SI was S intake in g, OMI was organic matter intake in kg). Both urinary S (US) excretion and S retention varied with intakes of digestible S and digestible OMI. When digestible S intake was zero, and sheep were at zero energy balance, urinary S excretion was considered to equal endogenous urinary S excretion. Langlands et al. (1973) used regression analysis and calculated that endogenous urinary S excretion was 38 mg/d. Joyce and Rattray (1970) calculated that the daily S requirement for maintenance of 20 to 30 kg growing sheep was 540 mg/d.

Webster (1980) demonstrated that protein synthesis in the gut and skin is much more dominant than in muscle. Owens and Pettigrew (1989) suggested that requirements of amino acids for maintenance were more closely related to the amino acid composition of keratin than of muscle tissue. This might be expected because inevitable tissue losses include skin, hair or wool, intestinal mucosa and enzymes

which should have amino acid compositions similar to keratin. Keratin has a high content of SAA.

Sulfur Requirements for Growth

Only a very small amount of S in the body exists as sulfate. Practically all the S present is in protein, which in turn consists of SAA (cystine, cysteine, and methionine) or metabolic derivatives of these amino acids such as taurine, cystathionine, homocysteine, and cysteic acid). Sulfur in the mammalian body totals about .15% of body weight (NRC, 1980) or 1% of total protein (Church, 1979). Hansard and Mohammed (1968, 1969) presented information on the S content of various tissues of sheep and cattle. The S content of sheep (pregnant females) generally was between .22 and .36% of fresh tissue and that of cattle (pregnant females) from .20 to 40% of fresh tissue. Liver and heart tissues had the highest S concentrations. In fetal tissues of sheep, the liver, brain and pituitary tissues as well as some bones have high concentrations of S. The retention of S in the body varied with the age and body weight of sheep (Langlands and Sutherland, 1973). At the age of two weeks and 5 kg of body weight, S was .15% of body weight whereas an adult sheep with a body weight 55 kg contained .14% S. The S content of the sheep (Y, g) has been related to sheep age (X, months), live weight (Z, kg), and the interaction of age with live weight as:

$$Y = 0.351 * X + 1.474 * Z - 0.0104 * X * Z - 0.659.$$

$$(R^2 = 0.96).$$

Sulfur content of a specific protein is constant, but different proteins range from .3 to 1.6% S with a mean of 1% for total body protein (Church, 1979). Muscle protein contains about 0.25% S, and brain tissue contains about .5%. Following an intravenous dose of ^{35}S as sodium sulfate (Bouchard and Conrad, 1973c), radioactive S was particularly high in liver, kidney, spleen, and adrenal glands indicating that these were the sites of rapid turnover or of excretion.

Sulfur supplementation has increased feed efficiency with diets that contained an appreciable amount of urea in cattle (Goodrich et al., 1967). For growing beef steers, dietary S at .13% appeared adequate for supporting growth (Chalupa et al., 1973). Chalupa et al. (1971) fed Holstein bull calves a purified diet that contained various levels of S; they found that, besides the increase in N retention with S supplementation, calves fed S-deficient diet (.04% S) had high plasma concentrations of serine, citrulline, alanine, cystine and total non-essential amino acids, but low concentrations of glycine and tyrosine. Increasing dietary S linearly increased plasma methionine concentration. No changes in plasma concentrations of other essential amino acids were detected. Calves fed the low-S diet (.04% S) had a lower blood volume and lighter liver, spleen and testis but heavier brain and adrenal mass. Using the criteria of growth performance, N balance, plasma amino acids and tissue S levels to judge adequacy of dietary S level, bull calves

fed a purified diet required less than .3% elemental S in the diet (Chalupa et al., 1971).

Slyter et al. (1988) also studied the response to elemental S by calves and sheep fed purified diets. Sulfur deficiency in calves reduced the proportion of body weight that was rumen-reticulum tissue; in rams it reduced the proportion of body weight as gastrointestinal tissue and preintestinal tissue. Walli and Mudgal (1981) found that S supplementation of (from Na_2SO_4) a .175% S diet increased digestibility of crude protein and ruminal fluid concentrations of total protein and TCA-precipitatable protein in both cows and buffaloes.

Elliot and Armstrong (1982) reported that urea and urea plus sulfate supplementation increased microbial protein synthesis in the rumen of sheep fed a .061% N, .043% S diet (supplemented to 2.076% N, .035% S and 2.064% N, .229% S, respectively). The efficiency of microbial protein production (g bacterial total amino acid nitrogen/kg OM actually digested in the rumen) was increased by the addition of urea and still further by addition of SO_4 (11.1, 20.2 and 29.6 g/kg OM for basal diet, the basal diet plus urea, and the basal diet plus urea and sulfur, respectively). The proportions of cyst(e)ine-S in the rumen bacteria synthesized from the rumen sulfide pool were 8.8, 7.5 and 66.9% on the basal diet, basal diet plus urea and basal diet plus urea and S, respectively. Weston et al. (1988) observed that, besides increasing bacterial protein

production, S supplementation of a .070% S diet to .185% S tended to increase the concentration of SAA in ruminal bacterial protein of sheep.

Bray and Hemsley (1969) reported that for sheep fed a diet containing .058% S, S supplementation to .318% S increased retention of both N and S. In contrast, larger doses of S, as DL-methionine (Doyle and Bird, 1975), added to a .123% S diet or of Na_2SO_4 (Bird, 1971) added to .107% S diet, (providing the equivalent of .18% and .24% S, respectively) reduced N retention below that obtained at optimal levels of S intake. Despite this suggestion that an excess is detrimental, Bray and Till (1975), using most of the published data for growing and adult sheep, found that N retention (g/d) and S retention (g/d) ($N = 10.37 * S - .38$, $r = +.952$) were linearly related; this reflects the close relationship between N and S metabolism. This would imply that at typical N retentions of 6 to 20 g, the N:S ratio in retained tissue should be 10.2 to 10.4.

Sulfur Requirements for Reproduction

Langlands et al. (1973) studied the retention of S during pregnancy in sheep; they found that net storage of S (mg) in the uterus, membranes and foetus was related to time from mating (D) by a polynomial relationship:

Foetus: $S = 1.182 * D^{5.9} * 10^{-9}$

Membranes: $S = -10.74 * D + .298 * D^2 - .00133 * D^3$

Uterus: $S = 1.329 * D + .0295 * D^2$

Williams et al. (1988) reported that the ratio of N to S retained decreased as pregnancy advanced in the ewes, dropping from 8.8 in early (76 to 97 days after mating) to 4.2 late (110 days after mating) in pregnancy, and reaching 3 before parturition. According to Langlands and Sutherland (1973), S accumulated in the gravid uterus at a more rapid rate than N. This probably reflects an increasing concentration of cystine in the fetus, partially due to the growth of the fibers comprising the birthcoat. Williams et al. (1988) concluded that pregnancy does not greatly influence the availabilities of SAA; efficiency of utilization of supplemental SAA supplied at the abomasum appeared to be similar to that of non-mated sheep. In contrast, the efficiency of wool growth, as measured by wool growth per unit of DM intake, is lower during pregnancy (Oddy, 1985).

Sulfur Requirement for Lactation

Few reports have described the S requirements for lactation of dairy cattle; none is available for dairy goats. In work with dairy cows, Jacobson et al. (1967, 1969) concluded that diets containing .09% S (DM basis) were inadequate; but diets containing .13% were adequate. Adding S in the form of Na_2SO_4 to a semi-purified diet containing .10% S increased DMI and digestibility. A dietary N to S ratio of 12:1 was adequate to maximize feed intake in dairy cows. Regression analysis indicated that .12% S could maintain S balance but .18% was needed for positive S

balance in cows producing 8 to 37 kg milk per day (Bouchard and Conrad, 1973a). However, S supplementation of a diet composed of a hay (.13% S) plus grain (.28% S) mixture did not increase performance of dairy cows (Bougess and Nicholson, 1971). Sulfur supplementation (Na_2SO_4) of diets containing .11 or .13% S failed to increase feed intake or milk production in dairy cows (Grieve et al, 1973a,b). Several workers have failed to detect any response to S supplementation (Jacobson et al., 1967; Bougess and Nicholson, 1971; Grieve et al., 1973a,b); indeed, .30% S added (from double sulfate of potassium and magnesium) to a .05% S basal diet decreased DM intake (Bouchard and Conrad, 1974). NRC (1989) indicated that the S requirement for dairy cattle, though not well established, is approximately .20% S of dietary DM.

Haenlein (1980) reviewed the mineral nutrition of goats. He compared the compositions of the goat's milk with cow's milk and concluded that goat's milk was higher in S (.046%) than cow's milk (.03%, NRC, 1989). Because milk from various species differs in amount of several constituents, nutrient requirements may be different for different for different species.

Sulfur supplementation could alter rumen function or digestibility or SAA supply. Assuming that the effects of S supplementation result from changes in the SAA supply, the direct effects of SAA on milk production have been studied. Chandler (1970) calculated amino acid balance considering

the need for amino acids for milk protein production of cows. He ranked the limiting amino acids for milk production from highest to lowest as 1) methionine, 2) valine, 3) isoleucine, 4) tryptophan and 5) lysine. All amino acids should be adequate for the daily production of 10 kg of milk; but for 15 kg milk daily, methionine and valine supply would become limiting. Chalupa (1968) found that when plasma methionine and histidine were low, milk production was low. Broderick et al. (1970) infused 800 g of casein plus 24 g methionine per day into the abomasum of lactating cattle fed a 16% crude protein ration; milk protein content and protein yield were increased by 6.2% and 11.6%, respectively.

Recently, Schingoethe et al. (1988) studied the lactational responses of seventy-three high producing Holstein cows to ruminally protected methionine [15 g/(head.d)] with diets containing soybean meal, heat-treated soybean meal, and extruded soybeans. Methionine supplementation increased milk production when fed with soybean meal but not when fed with heat-treated soybean meal or extruded soybeans. Milk protein percentage and DMI were higher with supplemental methionine. Feeding rumen-protected methionine and lysine to cows also increased plasma concentrations of methionine, lysine, and milk protein. Supplemental lysine appeared to improve the utilization of methionine (Rogers et al., 1987). The effect of supplementation of DL-methionine on milk fat percentage

was quadratic whereas the response to methionine hydroxy analog was linear (Lundquist et al, 1985).

Intravenous infusion of methionine alone (Fisher, 1969; Teichman et al., 1969) or feeding only methionine treated to by-pass the rumen (Broderick et al., 1970; Williams et al., 1970; Martz et al., 1972) has failed to increase milk production. However, Griel et al. (1968) reported that milk production was increased by dietary methionine hydroxy analog (MHA). Polan et al. (1970) fed cows concentrates containing either 0, .2, .4 or .8% MHA and obtained a milk production response with peak production at 25 g of MHA daily. Kim et al. (1971) found that MHA supplementation (3.6 g/kg concentrate mix) increased milk fat production, but decreased N balance, with no effect on feed consumption, milk or SNF yields or N digestibility. Supplementation with MHA caused small but consistent increases in milk fat output with little or no change of milk yield or milk protein production (Oldham, 1980). Bishop (1971), in a field-study with 148 cows, found that feeding 30 to 40 g/d of MHA had positive effects on milk and fat yields. Ray et al. (1983) studied the effects of MHA on milk secretion and ruminal and blood variables of dairy cows fed a low fiber diet; supplementation with MHA increased milk fat by 6%; this was accompanied by an increased ratio of acetate to propionate in the rumen. Methionine hydroxy analog, via stimulating ruminal microbial growth, may increase cellulolytic activity and alter production of lipids by ruminal microorganisms

(Gil et al., 1973; Patton et al., 1970). However, Hutjens and Schultz (1971) reported no effect of MHA on the ratio of acetate to propionate. The increase of milk fat output may be due to some other function of MHA; methionine is essential for formation of phospholipids and lipoproteins; so a deficiency may inhibit transport of lipid in the blood (McCarthy and Porter, 1968). Under certain conditions, MHA supplementation increased concentrations of blood methionine (Belasco, 1980); this may increase transport of preformed lipid from the liver to the mammary gland. In other studies (Hutjens and Schultz, 1970; Polan et al., 1970), additions of MHA to the diet have not increased milk yield or milk fat production. Perhaps the nature of diet, the level of milk production, and the length of time that animals receive MHA are involved in obtaining positive responses. Once limiting amino acids are identified, titration experiments are needed to determine the amounts of each particular amino acid needed for lactation.

Because the goat is a proficient producer of milk with a high S content, the dairy goat may require more S than the cow; no research concerning the S requirement of goats for milk production has been reported. Further research with dairy goats is needed.

Sulfur Requirement for Fiber Production

Sulfur Content, Distribution and Function in Fiber. Animal fiber is largely keratin, a protein with 20 amino acids and a high S content. Sulfur content ranges from 2.7

to 5.4% of fiber weight. Most of the S in fiber is present as cystine, with smaller amounts as cysteine and methionine (Reis, 1979). Keratins are not homogeneous; keratin proteins are grouped as high S, low S and high tyrosine proteins. These three major protein groups are thought to be associated with different structural components of the cortical cells of the fiber; the low S proteins are concentrated in the microfibrils whereas the high S and the high tyrosine proteins are concentrated in the surrounding non-fibrous matrix. The epidermal scale of the fiber is richer in S than other parts of the fiber. Bradburg (1979), based on research on amino acids of the orth-cortex and para-cortex of fiber, concluded that the para-cortex is rich in high S proteins whereas the orth-cortex is rich in low S and high tyrosine proteins. The cardiac layer cells consist of low S proteins which contain very little or no cystine. High S content and the disulfide bond structure in fiber form the basis for the physical and chemical characteristics of a fiber. Sulfur-containing amino acids in a diet can markedly influence fiber yield, fiber elasticity, fiber strength and other textile criteria. Sulfur-containing amino acids in a fiber stabilize the tertiary and quaternary structures of wool protein molecules.

The Effects of Sulfur Supplementation on Fiber Growth.

1. Sulfur-Containing Amino Acids. Reis and Schinckel (1963) infused methionine and cystine into abomasum of sheep (fed chaff at 600 to 800 g/d. The basal diet supplied the

equivalent of 2 to 3 g cysteine daily). Infusing each sheep with 2 g L-cystine or its equivalent in S from DL-methionine (2.46 g) daily increased wool production by 35 to 130%. The S content of wool also was increased by 24 to 35%. This finding stimulated further research. Most researchers believe that the mechanism is as follows: infusing methionine into the rumen of animals fed low S diets can increase protein synthesis by rumen bacteria so animals have more high-quality protein for digestion in the intestines; in turn, an increased supply of SAA can stimulate the anabolism and weight gain (Reis and Schinckel, 1963).

Martson (1955) suggested that cyst(e)ine supply may limit keratin synthesis and that supplementation should increase the supply of cyst(e)ine for keratin synthesis. The increase in S content of the fibers must be differentiated from the increased rate of fiber growth. Although part of the fiber growth response is due to augmentation of substrate supply, this is not necessarily the primary or sole mechanism of action. Other mechanisms may include specific effects of cyst(e)ine, or of the S or sulfhydryl component of the cystine molecule on the follicle itself. It may stimulate mitotic activity in the follicle bulb; sulfhydryl groups are known to play a role in mitosis. Also, cofactors important in protein and energy metabolism may be increased. Cyst(e)ine is involved in synthesis of glutathione and coenzyme A. Cyst(e)ine may stimulate keratinization by providing sulfhydryl groups. In contrast

to cyst(e)ine, methionine could stimulate fiber growth in several ways beyond trans-sulphuration. Methionine plays roles in protein synthesis both as a chain initiator and as an amino acid transporter and may enhance the accumulation of other amino acids in cells (Reis, 1967). These peculiar effects of methionine on wool growth also may be related to S-adenosylmethionine, a methyl donor for many reactions and required for the synthesis of the polyamines spermidine and spermine (Pegg and McCann, 1982). Experiments with methionine analogues (ethionine and methoxinine) support the view that certain effects of methionine on wool growth are mediated via S-adenosylmethionine (Reis et al., 1990).

Hogan et al. (1979) summarized the research from different genotypes of Australian Merino on the conversion of nutrients to wool. At least half the cyst(e)ine absorbed was used for wool protein synthesis. This may be an underestimate because it seems unlikely that all the methionine absorbed from the intestine would be converted to cyst(e)ine as their calculations assume. Wool growth, even at the highest levels observed, was restricted by the supply of cyst(e)ine.

Williams et al. (1972) observed that sheep from a flock selected for high fleece weight were much more responsive in wool production and S output to infusions of cyst(e)ine or methionine than sheep selected for low fleece weight. The response in wool production indicates that the availability

of SAA can limit the productivity of animals with a high genetic potential for fiber production.

2. Inorganic Sulfur. Starks et al. (1953) found that lambs could utilize inorganic S, and that lambs fed a .062% S diet supplemented to .705% S retained more N than lambs receiving no S supplementation. Hale and Garrigus (1953), using isotope-labelled S, showed that sheep can synthesize cystine from elemental S and sulfate, and that microbes in the rumen utilized sulfate-S more readily than elemental S. When urea replaces some or all of the true protein in the ruminants' diet but S is not added, the efficiency of urea N utilization can be low due to a S deficiency (Allaway, 1970). Although non-ruminant animals need dietary SAA to grow, ruminants like sheep and goats can utilize inorganic S and N sources. These inorganic compounds are utilized via microorganisms in the rumen. Most bacteria in the rumen can use inorganic S to meet their requirements for growth; one bacterial strain, *Megasphaera elsdenii*, has been reported to be very efficient in utilization of inorganic S.

The dietary S requirement of sheep and goats can be met by inorganic or organic S, but the maximum utilization of inorganic S in the rumen is limited by the amount of protein synthesized by rumen microorganisms. Durand and Komisarczuk (1988) pointed out that the amount of S needed should be expressed on the basis of fermentable energy in the diet because S concentration in the rumen represents a balance between supply, absorption, rate of passage and microbial

utilization, the latter of which is altered by the supply of fermentable energy. Even if the ruminal need for S is met, the requirement for SAA for fiber production may exceed the supply from microbial protein; these can be met by additional postruminal SAA. Reis (1979) reviewed the effects of supplemental SAA on the growth and properties of wool. Dietary supplements generally were ineffective because they were degraded by ruminal microbes; however, SAA supplies in the abomasum, duodenum, parenterally, in a rumen-protected form or in drinking water markedly increased wool growth rate. The effectiveness of these SAA supplements was influenced by diet and the fiber-producing capacity of the animals. With sheep receiving moderate amounts of a roughage diet, maximal responses in wool growth were obtained from abomasal infusion of 2 to 3 g SAA per day. Amounts larger than 6 g methionine per day proved less effective or depressed wool growth (Reis et al., 1990). The mode of action by which SAA stimulate wool growth requires more study.

The Research of Sulfur Requirements for Sheep. Sulfur requirements have been proposed by four different groups. First, the ARC (1980) recommends that the need for S can be based on the supply of N; the minimum ratio of N:S in the ration should be 14:1. Secondly, the NRC (1985) suggests that diet DM should contain .14 to .18% S for adult sheep and .18 to .26% S for growing sheep; the minimum ratio of N:S should be 10:1. Thirdly, the Soviet Union National

Standard (Lu and Jiang, 1981) recommends a different S supply for various classes; for wool-meat type adult sheep, supply .30% S in dietary DM for a ratio of N:S of 5 to 6:1; for meat-wool type adult sheep, supply .25% S in dietary DM for a ratio of N:S at 6 to 7:1; for growing sheep, supply .24 to .31% S in dietary DM for a ratio of N:S of 8 to 9:1 because growing sheep require more N than adult sheep. Fourthly, In Australia, farmers are expected to spread S fertilizer to their grassland to increase the S content of the grass so that sheep get enough S to meet their needs. Chestnut et al. (1986) observed that with orchard grass, S fertilization not only increases the S supply, but also change the composition and apparent digestibility of phenolic constituents in the grass.

The Effects of Sulfur Supplementation on Fiber Quality and Fiber Sulfur Content. Both the rate of fiber growth and its S content are influenced by the availability of SAA. When supplemental cystine, methionine or casein were infused into the abomasum of sheep, both wool production and S content of wool were increased (Reis, 1979). The increase in wool S content is due to an increased yield of high S proteins. According to the two-stage theory of keratin synthesis in the wool follicles (Gillespie, 1983), the high S proteins of keratins are synthesized by the stepwise addition of S-rich peptides to precursors.

Qi (1989) reported that the S content of Chinese Merino wool with diameter at 22.3 μm was positively correlated with

wool strength, elongation at break, relative strength, work of rupture, initial modulus, white degree and crimp ratio. The S content also influenced the scouring yield, elasticity and resilience of the fiber.

Growth of wool has a higher priority than growth of muscle and other tissues (Langlands & Sutherland, 1973). Sheep in negative S and energy balance will mobilize body tissue in order to maintain wool growth. Hence, wool growth enjoys a priority for amino acids. Furthermore, when amino acids are supplemented, only the cyst(e)ine content of wool changes; other amino acids exhibit little change. The orth-cortex consists of low S proteins whereas the para-cortex consists of high S proteins; low S proteins had a constant cystine content, but high S proteins ranged from 2.9 to 4.2% S so that wool S content changes in response to the SAA supply.

Meeting Sulfur-Containing Amino Acid Requirements of Animals Through Genetic Engineering Methods. Animal geneticists may have found additional ways to provide more SAA to animals. Using modern genetic methods, scientists may be able to introduce novel metabolic pathways. In sheep, the pathway for the biosynthesis of cysteine from serine is under study (Ward, 1984; Ward et al., 1986; Ward et al., 1989). Cysteine is an essential amino acid because mammals lack the pathway for cysteine synthesis except by conversion from methionine. There are two key elements in the pathway for cysteine synthesis from serine:

(1) Serine + Acetyl-CoA ----------> O-Acetylserine + CoA
serine
transacetylase

(2) O-Acetylserine + H_2S ----------> Cysteine + Acetate
O-acetylserine
sulphydrylase

The genes that encode these two enzymes have been isolated from the bacterium E. coli (Boronat et al., 1984), sequenced and studied for transfer to sheep (I. V. Franklin, 1988, personal communication). Underlying these experiments is the hypothesis that these genes, when expressed in rumen epithelial cells, will enable cysteine to be synthesized from serine, hydrogen sulfide and acetyl-CoA, and that cysteine will be absorbed and transported to the wool follicles of the sheep to be used for wool growth.

In summary, the relationship between S nutrition and fiber production emphasizes the need for research that integrates the requirement of S for body growth and fiber production. Stimulation of fiber growth by organic and inorganic S-containing supplements illustrates that it is feasible for the animal industry to use low cost inorganic S sources in combination with organic S source. Differences in S requirements and responses to S supplementation between fiber-producing animals and breeds selected for meat might arise because fiber-growing animals grow slowly and mature later and have been specifically selected for fiber production, a form of animal production characterized by a high demand for SAA. We need to develop special nutritional

strategies to reap the greater production from our sheep and goat industry.

Sulfur in the Cation-anion Balance of Animals

Sulfur content of a diet can affect the acid-base balance of animals (Tucker et al., 1991). The dietary cation-anion balance can be calculated as meq[(Na + K) - (Cl + S)]/kg of dietary DM. Oetzel (1991) analyzed the nutritional risk factors for milk fever in dairy cattle. He found that prepartum dietary S level had the greatest influence on the incidence of milk fever. Increasing the dietary S concentration lowered the risk of developing milk fever.

Sulfur Toxicity in Animals

Sulfur toxicity occasionally occurs in animals (Kandylis, 1984). In some regions of the world, the surface and(or) ground water contains enough sulfate to be toxic to animals that consume large quantities of water. High sulfate water exists in Colorado making S toxicity to animals a primary concern there (A. P. Knight, 1990, personal communication). NRC (1980) sets the maximum tolerable level of S at .4% of dietary DM for sheep and cattle. Certain feedstuffs contain more than .4% S (e.g., molasses and syrup at .60% S; NRC, 1989).

Signs of acute S toxicities in cattle include muscular twitching, restlessness, diarrhea, dyspnea, and recumbency. Breath that smelled of hydrogen sulfide was evident in sheep suffering from acute S toxicity; postmortem examination

revealed severe enteritis, peritoneal effusions, darked kidneys, and generalized hemorrhage (White, 1964). Accumulation of sulfide in the rumen has adverse effects on animal health because some of the sulfide passes directly into the blood. High S content of the diet also can affect metabolism of Mo, Cu, Se and Zn (Grace and Suttle, 1979; Ademosum and Munyabuntu, 1982). The optimum S content in the diet is one that satisfies the requirements of animals but is not excessive to the point that it has adverse effects on animal health or survival.

Doran and Owens (1987) suggested that elevated sulfate from gypsum (calcium sulfate), and double sulfate of K and Mg increased ruminal thiamin destruction so as to cause a thiamin deficiency and polioencephalomalacia (PEM) in animals. Raisbeck (1982), Sadler et al. (1983) and Gooneratne et al. (1989) also have related PEM incidence to a high sulfate-S content of ruminant diets. However, toxicity occurs only under extreme cases and is rare.

Sulfate toxicity can be treated by injecting glucose-saline, followed by glycerine and bismuth carbonate by mouth, or with bismuth carbonate mixed into the feed for animals willing to eat (White, 1964). These treatments reduce absorption of sulfide from the rumen by increasing rumen pH; alkalinity reduces the amount of non-ionized sulfide, the form absorbed most rapidly (Bray and Till, 1975).

Sulfur Deficiency in Animals

According to Tabatabai (1986), regions of S deficiencies are found everywhere in the world. Most S in feeds is in the form of SAA. Church (1979) suggested that the total S content of most proteins varies from .3 to 1.6% so that the N:S ratio ranges from 53:1 to 10:1, averaging 16:1. Most protein feeds, although high in N content, have a N:S ratio above 20:1 (Table 1). As shown in Table 1, we can find that when these protein are fed to satisfy the protein requirement of animals, we may exacerbate a S deficiency. Sulfur deficiency under field conditions in the U.S. has been reported by Beaton (1971) and Beaton et al. (1971).

Signs of S deficiency in ruminants include reduced appetite, weight loss, hair loss, weakness, excessive lacrimation, profuse salivation, cloudy eyes, dullness, emaciation, and death (Kincaid, 1988).

Sulfur deficiency may directly affect ruminal fermentation (Whanger, 1972). Ruminal microorganisms from sheep fed a S-free purified diet formed more acetate, propionate and lactate than did microbes from sheep fed a S supplemented diet. The latter microorganisms formed more butyric and higher acids. D-lactate accumulated in the rumen of sheep fed a S-free purified diet whereas only traces of D-lactate were found in the rumen of the control sheep (Whanger and Matrone, 1966). In vitro studies indicated that added sodium sulfide (31 mg sulfide-S per 100 mL fluid) decreased methane production and the molar ratio

of carbon-dioxide to methane increased from 1.98 to 4.49. Bray and Till (1975) reviewed the metabolism of S in the gastrointestinal tract of ruminants. They concluded that sulfide was the key intermediate between the breakdown of ingested, absorbed S and its utilization and(or) loss from the rumen. They suggested that the plasma sulfate concentration may regulate SAA catabolism; this concept deserves further study.

Factors Affecting Availability of Sulfur

Dietary Factors. Goats prefer oaks containing tannic acid to other plant species (Lu, 1988) and have a high tolerance for tannin bitterness. Mcleod (1974) found a negative correlation between tannin content and ruminant total tract protein digestibility; this is because tannic acid forms a complex with protein and reduces protein digestibility. As most S in plants is present in protein as SAA, tannic acid-containing plants may provide inadequate amounts of available S. This has been demonstrated in the acacia aneura (mulga) in which much of the S is unavailable; it exacerbates a marginal S deficiency (Gartner and Hurwood, 1976). With range goats that liberally graze and browse tannin-containing plants, S supplementation is particularly critical. Wheeler et al. (1985) indicated that S also is deficient in forage sorghums which contain cyanogen. Hydrogen cyanide is liberated after forage is ingested; S is used in detoxification of hydrogen cyanide which exacerbates a S deficiency in the animal. Spears et al. (1977) also

found that dietary nitrate increased the amount of S required for optimum cellulose digestion. This may be because both nitrate reductase and sulfide oxidase require Mo (Anke et al., 1985) and Mo interacts with S. The sulfate reduction and nitrate reduction by ruminal microorganisms counteract each other (Takahashi et al., 1981). Glenn and Ely (1981) studied the effects of sulfate and nitrate supplementation of sheep fed tall fescue. They concluded that fertilization of fescue to reduce NPN and increase nonprotein S increased utilization of tall fescue.

Ruminal ammonia concentration, which relates to dietary degraded protein level, affects S utilization because sulfide incorporation into the microbial protein parallels ammonia incorporation.

Chemical Form of Sulfur. Various S chemicals have been used to study S nutrition and metabolism. Bouchard and Conrad (1973) found that supplemental sulfates of sodium, calcium, potassium, and magnesium sustained optimum utilization of S when fed at .20% S of the diet for cows producing as much as 35 kg of milk per day. Goodrich and Garrett (1986) reviewed S supplementation research and concluded that calcium sulfate was soluble in ruminal fluid and readily available for microbial protein synthesis.

In contrast to the sulfates, elemental S was only 8% as efficient as S from L-methionine for wool growth (Hale and Garrigus, 1953) and approximately 30% as efficient for body weight gain (Goodrich and Garrett, 1986). Low solubility of

elemental S may impair its utilization by ruminal microorganisms (Muntifering et al., 1984). Nevertheless, Slyter et al. (1988) have used elemental S instead of sodium sulfate to avoid excesses of dietary Na in purified diets. Hale and Garrigus (1953) reported that the efficiency of sodium sulfate for wool growth in lambs was 68% that of L-methionine. Similarly, Bouchard and Conrad (1973) indicated that the relative efficiency of S from calcium sulfate was only 70% that of methionine. In summary, relative to methionine, sulfates are 70% as available and elemental S is less than 30% as available.

Sulfur Interactions with Zinc, Copper, and Molybdenum

Dietary Zn, Mo, Cu concentrations affect S availability in ruminants in a complex fashion (Suttle, 1991). These interactions have attracted more attention than direct studies of the requirements for each individual element.

Zinc, required at every stage of the life cycle (NRC, 1980), functions in a large number of Zn metalloenzymes. Zinc requirements of ruminants are poorly defined (NRC, 1981, 1984, 1985, 1989). Inconsistency in responses to Zn supplementation in ruminants suggests that Zn requirements are affected by many dietary or physiological factors (Spears, 1991). Sulfur and Zn interact at two locations. Firstly, Zn reacts with sulfide in the rumen or in tissues to form ZnS; this precipitate renders Zn and S unavailable to animals. Secondly, Zn is absorbed by facilitated diffusion in the duodenum and upper jejunum (NRC, 1980).

Sulfur-containing amino acids are the facilitating agent (Ruth and Kirchgessner, 1985) so that diets rich in SAA have greater absorption of Zn. Thirdly, SAA may act as chelates to enhance absorption of many divalent minerals.

Copper is used in hemoglobin formation, pigmentation of hair, bone and connective tissue formation, myoglobin synthesis, iron absorption from the small intestine and iron mobilization from tissue stores. Copper also is involved in reproduction and heart functions. Numerous oxidative enzymes require Cu (NRC, 1980). Cupric sulfide formed in the rumen will decrease Cu absorption; this is detrimental if S or Cu supply is low, but useful if Cu approaches toxic concentration.

Molybdenum is a component of several enzymes in the animal body: xanthine oxidase, aldehyde oxidase and sulfide oxidase (Ward, 1991). A Mo deficiency that could be corrected by Mo supplementation has been described in human patients (Mills and Davis, 1987). Although Mo deficiency is rare, in one area of China , a high incidence of esophageal cancer proved to be associated with foods of low Mo content (Luo et al., 1982). Anke et al. (1985) determined that goats required .1 ppm Mo in dietary DM. Important symptoms of Mo deficiency in goats include infertility and a high abortion rate. In practice, Mo toxicity is more common than Mo deficiency. The potential for Mo toxicity relates partly to its interaction with Cu and S.

Copper, Mo and S all ınteract in ruminants (Huisingh et al., 1973; Spears, 1991). Due to the complex nature of their three way interaction, no unified mechanism for Cu-Mo-S interactions has emerged. Copper can become biologically unavailable in three ways: 1) interaction with molybdate to form cupric molybdate, 2) formation of insoluble cupric sulfide and 3) formation of Cu thiomolybdate complexes in either the rumen, intestine or tissues (Kincaid and White, 1988). Molybdate may either aggravate or alleviate the Cu deficiency symptoms observed in ruminants, depending on the Cu status of the animal and the level of sulfate in the diet (Suttle, 1974). Possible mechanisms for this interaction are: 1) molybdate competition with the sulfate membrane carrier system (Mason and Cardin, 1977), and 2) molybdate inhibition of the sulfate-reducing system, decreasing ruminal H_2S level. Sulfate has been shown to either enhance or relieve Cu deficiency depending on the Cu status of the animal and the level of dietary molybdate (Miller et al., 1970; Suttle, 1975). This phenomenon can be attributed to: 1) formation of copper sulfide or 2) sulfate competition with molybdate for the carrier that transports sulfate and molybdate across membranes of either the intestinal mucosa for absorption or the distal tubules of the kidney for excretion.

In predicting the post-ruminal availability of Cu, Bird (1970) regressed the soluble Cu outflow (Y, mg/d) from rumen to the omasum against the ruminal concentration of sulfide

(X, mg/L) in sheep fitted with omasal and ruminal cannulae. The fitted regression equation was:

$$Y = 5.57 - 2.36 * X + .49 * X^2 - .0333 * X^3$$

$(R = .95; P < .0001)$

According to this equation, when ruminal $S^=$ concentration ranges from about 3 to 6 mg/L, ruminal outflow of soluble Cu is approximately constant.

Suttle and McLauchlan (1975) used data from 10 repletion experiments with sheep fed semipurified diets varying from 0.08 to .40% S diets and from 0.5 to 16.5 ppm Mo to predict the effects of S and Mo on the decimal fraction of true availability (A) of dietary Cu. They found the following equation:

$$\text{Log (A)} = - 1.153 - .0019 * \text{Mo} - .0755 * \text{S} - .0131 * (\text{S} * \text{Mo})$$

$(R^2 = .857, P < .001, df = 28)$

This equation implies that S exerts a dominant and independent effect on Cu availability, whereas Mo has a lesser and S dependent effect but a very small independent effect. Responses to dietary S and S * Mo were exponential rather than linear, indicating that S increments at the lower end of the normal range markedly depressed Cu availability.

Suttle and McLauchlan (1975) validated their prediction equation by using the publishing data of Todd (1972). The equation predicts a high Cu availability (5.9%) for cereal-

rich diets which are associated with susceptibility to Cu poisoning (Todd, 1972).

In the absence of data from natural foodstuffs, an equation from semi-purified diets was used by ARC (1980) as a provisional means to predict the effects of Mo and S on Cu requirements of ruminants; it has been used by others to predict the absorption of Cu from herbage and brassicas grazed by cattle (Suttle, 1981).

Some workers have found that the validity of this equation is affected by diet type. Therefore, a separate equation was developed for summer pastures (Suttle, 1981). This equation is:

$$\text{Copper absorption (\%)} = .075 - .0303 * Mo - .0134 * S + .0083 * (S * Mo)$$

$$(R = .76, df = 6)$$

(Values calculated from this equation are about 1% expected values: therefore, we suspected that the Cu absorption had a decimal fraction unit rather than % reported)

Suttle (1983, as cited by NRC, 1985) revised this equation for summer pasture as:

$$\text{Copper absorption (\%)} = 5.71 - 1.279 * S - 2.785 * \text{Log}_e Mo + .227 * (S * Mo)$$

where S and Mo are herbage concentrations of S in g/kg and Mo in ppm.

This equation differs substantially from that describing the effects of S and Mo on Cu availability in semipurified

diets and may prove more appropriate for estimating the absorption of Cu from summer pasture.

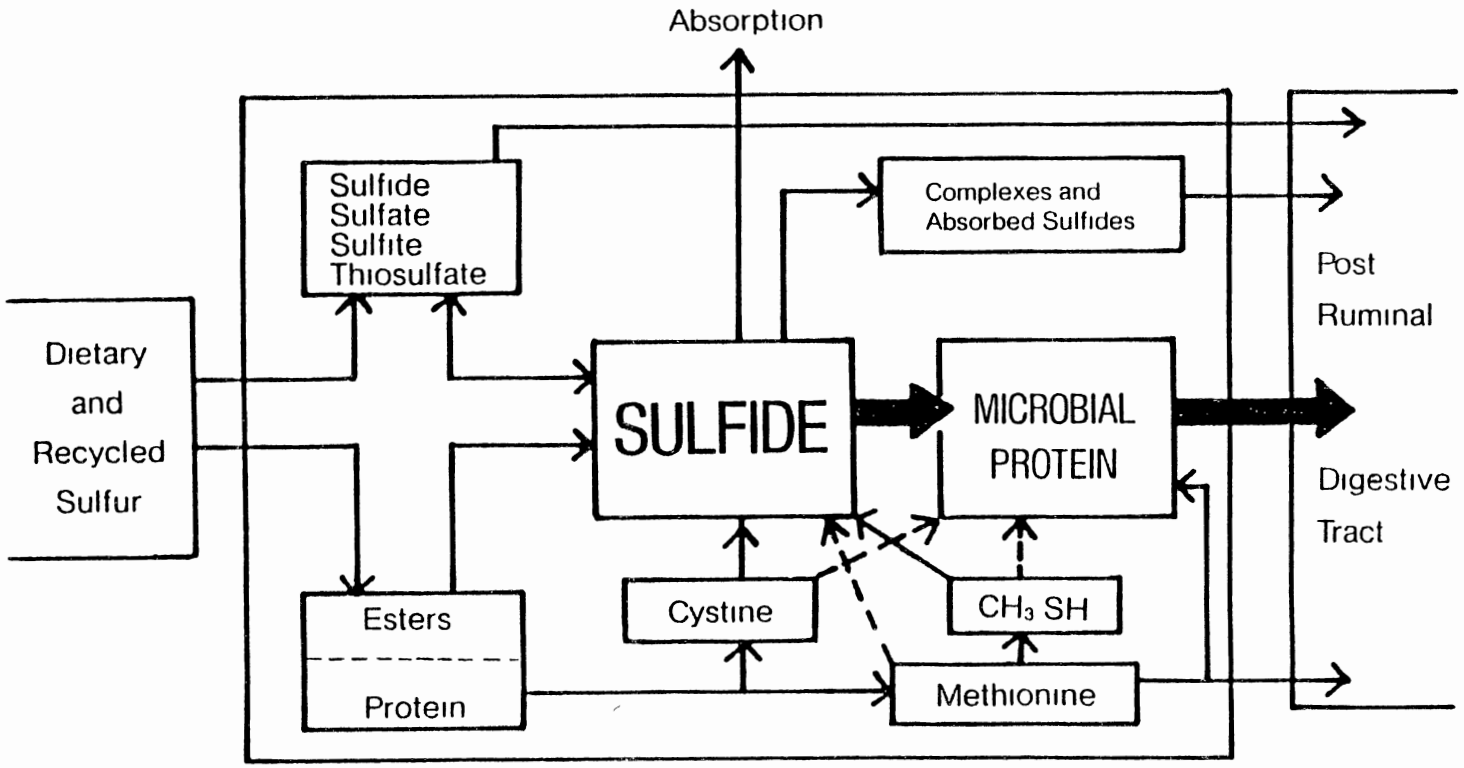

Figure 1 The major pathways of sulfur metabolism in the rumen.

Table 1. The sulfur contents and N:S ratios of the common protein feedstuffs[a]

Feed Name	International Feed Number	Protein Content (%)	Nitrogen Content (%)	Sulfur Content (%)	N:S Ratio
Alfalfa meal	1-00-023	18.9	3.02	.24	12.6
Alfalfa hay	1-00-050	23.0	3.68	.33	11.15
Cotton seed meal	5-07-873	48.9	7.82	.34	23.01
Fish meal	5-02-009	66.7	10.67	.49	21.78
Blood & bone meal	5-00-387	50.2	8.03	.28	28.69
Meat bone meal	5-00-388	54.1	8.66	.27	32.06
Peanut meal	5-03-649	52.0	8.32	.29	28.69
Safflower meal	5-07-959	46.9	7.5	.22	34.11
Soybean seeds	5-04-610	42.8	6.85	.24	21.53
Soybean meal	5-20-637	49.9	7.98	.37	21.58

[a]Protein and sulfur contents are adapted from NRC (1989). The nitrogen contents are calculated as protein divided by 6.25.

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CHAPTER III

SULFATE SUPPLEMENTATION OF ANGORA GOATS: METABOLIC AND MOHAIR RESPONSES

K. Qi[1,2], C. D. Lu[1], F. N. Owens[2], and C. J. Lupton[3]

Langston University[1], Langston, OK 73050

Oklahoma State University[2], Stillwater 74078; and

Texas Agricultural Experiment Station[3], San Angelo 76901

ABSTRACT. Eight castrated male Angora goats (4-5 years of age) were used in a repeated, simultaneous 4 X 4 Latin square design to evaluate metabolic and mohair responses of Angora goats to sulfate supplementation. Goats had ad libitum access to isonitrogenous diets containing .16% (basal), .23%, .29%, or .34% S (DM basis) giving N:S ratios of 12.7, 8.3, 6.8, or 5.5:1. Feed intakes were not affected ($P > .20$) by dietary S level. Quadratic increases ($P < .05$) to S supplementation were observed in grease and clean mohair production, grease and clean staple strength, and staple length. Mohair diameter, med fiber, kemp fiber, S, and cysteine contents were not affected ($P > .05$) by supplemental S. Averaged across the pre-feeding, 2, 4 and 6 h postprandial sampling times, ruminal pH, ammonia N, total

S, organic S, protein S, and plasma urea N, organic S concentrations were quadratically increased ($P < .05$) by supplemental S. Ruminal sulfate S, total sulfide S and plasma sulfate S were linearly increased ($P < .05$) by supplemental S. Retention of N and mohair S yield exhibited quadratic increases ($P < .05$), but S retention exhibited a linear increase ($P < .001$) to increased S intake. Calculated by regression, the optimum dietary S concentration for maximum clean mohair production was .267% of dietary DM for a N to S ratio of 7.2:1; this indicates that the National Research Council recommnendation of a N:S ratio of 10:1 is inadequate for Angora goats. The optimum level of digestible S was calculated to be .18% of diet DM.
KEY WORDS: Goat, Sulfur, Mohair, Metabolite, Nitrogen.

Introduction

The importance of S for animals has been broadly reviewed for general livestock (Goodrich and Garrett, 1986), and for ruminants (Whanger, 1972; Kandylis, 1984). Effects of S supplementation on feed intake, BW gain, organ development and digestibilities of nutrients in sheep and cattle have been reported (Slyter et al., 1988; Morrison et al., 1990). Sulfur supplementation stimulates wool growth (Weston et al., 1988) and improves wool quality in sheep (Qi, 1989). Because mohair protein is homologous to wool protein (Parris and Swart, 1975), supplemental dietary S may increase mohair production via increasing the supply of S-containing amino acids. Typical Angora goats are smaller

than average wool producing sheep, but produce twice as much fiber as sheep (Gallagher and Shelton, 1972). All these results lead us to hypothesize that Angora goats may require more S for fiber growth than sheep. However, we found limited information pertaining to S requirements of Angora goats for mohair growth and metabolic responses in blood or in the rumen of goats with S supplementation. Therefore, an experiment was conducted with Angora goats to 1) measure the effects of S supplementation on mohair N and S yields, 2) estimate the dietary S requirement of Angora goats for mohair growth, and 3) evaluate the metabolic responses in the rumen and in blood to S supplementation.

Materials and Methods

Animals and Diets. Eight castrated mature Angora goats weighing 47.8 $\pm$ 2.6 kg were blocked into two groups according to BW and used in a 180-d experiment. A repeated, simultaneous 4 X 4 Latin square design (Cochran and Cox, 1957) was adopted. The eight goats had ad libitum access to one of the four treatment diets each period. These diets differed only in S content that resulted from addition of $CaSO_4$. Calcium carbonate was used to balance the Ca contributed by $CaSO_4$. Silicon dioxide was added to equalize dietary nutrient contents. Each diet was mixed completely (Weigh-Tronix, Fairmont, MN), and feed sorting by goats was minimal. Compositions of the four treatment diets are presented in Table 1. Urea N accounted for one-third of the total N in the diet. All chemical compositions except ME

were measured. Feed, urinary and fecal gross energy were measured; methane energy was calculated from energy digestibility (Blaxter and Clapperton, 1965). Values for ME were calculated by difference. Goats were housed in individual pens in a metabolism room with a constant temperature (23 $\pm$ 2°C). Diets were fed once daily and water was available ad libitum. Before initiation of the experiment, we allowed goats to adapt to their diets for 2 wk and then sheared. Each period lasted 4 wk with a 2-wk interval between successive periods to reduce carryover effects of the previous diet and to permit the goats to adapt to their next diet.

Mohair Yield and Quality Evaluation. To measure differences in the rate of fiber growth and its S content in sheep, one standard method is to clip wool samples at regular intervals from a defined area of skin. This method is subject to errors due to several factors (Downes and Sharry, 1971). First, it is difficult to clip the wool from precisely the same area and at the same height above the skin surface each time. Second, exposure of the skin on this area to low temperature reduces blood flow and fiber length growth rate. Third, fiber diameter may change during the emergence time (the time required for the newly keratinized portions of fiber to move out of the follicles to the point of clipping); hence, changes in fiber diameter cannot be detected until the newly synthesized fiber appears above the skin surface. Fourth, residual effects of

previous diets can affect fiber growth for at least one week (Cobon et al., 1988). Because this experiment was designed to measure the S and N content and yield in mohair as affected by sulfate supplementation, two additional problems arise. Firstly, total mohair production during each period was sought. It is imprecise to calculate the whole fleece weight from weight of a sample from a defined area. Secondly, the reticuloruminal system for sulfate reduction requires a period of time to adapt to dietary sulfate (Lewis, 1954). To circumvent these problems, the following approaches were adopted. Firstly, all animals were kept indoors at 23 $\pm$ 2^{o}C. Secondly, a period of at least 2 wk was allowed for adaptation to diets before the experiment and between successive periods. Thirdly, fiber growth during this adaptation period was clipped and discarded. Fourthly, 4 wk of mohair growth in each period was allowed and the whole fleece was sheared with an animal clipper (Model EW610, Sunbeam, Milwaukee, WI). Mohair was weighed and evaluated for grease fleece weight, laboratory scoured yield (laboratory scoured yield = clean, dry mohair weight * (100 + 13.87)/grease mohair weight, in which 13.87 is the standard moisture regain of mohair; ASTM, 1990a), clean fleece weight, staple length (ASTM, 1990b), med and kemp fibers (med fiber is defined as a medullated animal fiber in which the diameter of the medulla is less than 60% of the diameter of the fiber; kemp fiber is a medullated animal fiber in which the diameter of the medulla is over 60% of

the diameter of the fiber; the medulla in mammalian hair fibers is the cellular marrow inside the cortical layer in most medium and coarse fibers; medullated fiber is an animal fiber that in its original state includes a medulla; ASTM, 1990c). Because med and kemp fibers do not retain dye, high levels result in price discount for a fleece. Average mohair diameter and distribution was measured on a random sample of fibers representing each whole fleece using a Peyer Texlab FDA 200 (Siegfried Peyer AG CH-8832, Wollerau, Switzerland). Grease and clean staple strength were determined on random staple samples representative of each whole fleece using an Agritest Staple Breaker System (Agritest Pty, Sydney, Australia). Staple strength of grease and clean mohair was analyzed as the maximum load (Newtons, N) needed to break a staple. To correct for differences in the size of the staple being tested, these measures were standardized by the linear density (grams/centimeter = Kilotex) of grease or clean mohair. Sulfur content (Mottershead, 1971) and cysteine content (Gaitonde, 1967) of dry (0% moisture regain), clean mohair from the whole fleece sample were measured.

Sample Collection and Analyses. Daily feed intake was monitored on individual goats for each period (4 wk) and feed samples were collected weekly and composited by period. Feces and urine were collected for 7 d during the wk 3 of each period. Feed, feces, and urine were analyzed for DM,

total S, N, and GE. Feed and feces also were analyzed for ADF and ash to calculate OM.

Blood samples were taken via jugular venipuncture before feeding as well as 2, 4, and 6 h postprandially during the wk 4 of each period. At least 30 mL of blood were collected. Blood plasma was harvested immediately after blood sampling and stored frozen until analysis.

Ruminal samples were procured via stomach tube at the same time as blood was sampled. The first 20 to 30 mL of ruminal fluid were discarded to reduce salivary contamination; at least 50 mL of fluid were collected subsequently for analysis. One milliliter of saturated $HgCl_2$ solution was added to each collected sample to kill the microbes and to stop metabolic reactions. Ruminal fluid pH was determined using a pH meter (SA-720, Orion Research, Boston, MA) immediately after sampling and a 20-mL subsample was transferred to a culture tube; 1 mL of 2 *M* zinc acetate was added to preserve this subsample for total sulfide-S (including S in H_2S, HS^-, and $S^=$) analysis (Fresenius et al., 1988). In addition, ruminal nonionized but volatile sulfide-S (H_2S-S) was calculated according to Henderson-Hasselbalch equation. The formula developed was as follows:

$$H_2S\text{-}S = \text{Total sulfide-S}/[1 + \text{antilog}(pH - 6.74)$$

where 6.74 is the pK_a of sulfide-S (H_2S ==> HS^- + H^+; K_a = $1.8 * 10^{-7}$; Bray and Till, 1975). The H_2S-S was an estimate of the amount of sulfide-S that can be volatilized and lost easily by eructation.

Goats were weighed after shearing, before feeding in the morning at the start and the end of each period, as well as before and after the collection phase at the third week.

Dry matter, OM, ash, and N were determined by standard procedures (AOAC, 1990). Gross energy was determined with an adiabatic bomb calorimeter (Parr Instrument, Moline, IL), and ADF was determined according to Goering and Van Soest (1970). Urinary energy was determined on lyophilized samples. Feed contents of Ca, P, Cu, Zn and Mo were analyzed using a plasma emission spectroscope (Spectrospan V, Beckman Instruments, Irvine, CA).

Total S was analyzed according to Mottershead (1971). Sulfate S was analyzed by the method described by Bird and Fountain (1970). Organic S was the difference between total S and sulfate S (Bird and Fountain, 1970). Ruminal samples were centrifuged at 1000 X g for 5 min to remove feed particles and protozoa (Merchen and Satter, 1983). Ruminal and plasma samples were deproteinized using 20% TCA (1:1, vol/vol) as described by Cline et al. (1958). The supernatant fluid was used for analysis of sulfate-S; S in the precipitate was considered to be protein-S and was analyzed according to Mottershead (1971).

Ruminal VFA were analyzed according to Erwin et al. (1968). Plasma urea N was analyzed according to Chaney and Marbach (1962). Total ruminal ammonia N (RAMN) was analyzed by using the method of Broderick and Kang (1980). In addition, ruminal free, nonionized ammonia N (FAMN) was

calculated according to Visek (1968). The FAMN was an estimate of the amount of the total RAMN which can be readily absorbed across the ruminal epithelium and into the portal circulation. The amount of FAMN is a function of both ruminal pH and RAMN concentration. Ruminal and plasma L-lactic acid concentrations were determined using Sigma Kit 826 (Sigma Diagnostic, St. Louis, MO).

Statistical Analysis. Data were subjected to ANOVA for a repeated, simultaneous 4 X 4 Latin square. Orthogonal polynomial contrasts were used to determine the linear, quadratic and cubic effects across the treatment diets by assuming that the dietary S levels were equally spaced (Steel and Torrie, 1980). Analyses were performed according to the GLM procedure of SAS (1985). Body weight at the end of each period was tested using beginning weight as a covariate, whereas the average of the beginning and the ending BW of each period was used for calculating metabolic BW.

Ruminal and plasma data having repeated measurements were analyzed as a split-plot in time (Steel and Torrie, 1980). Square effect was absorbed into animal effect because no square by diet interaction ($P > .20$) existed for the criteria analyzed. The statistical model included the effects of period, animal, diet, animal by diet interaction, sampling time, period by sampling time interaction, animal by sampling time interaction, diet by sampling time interaction, and the residual error. The effects of period,

animal, and diet were tested using the mean square of the animal by diet interaction. Effect of sampling time was tested using the mean square of animal by sampling time interaction. Other effects were tested by the residual mean square. Orthogonal polynomial contrasts also were used to examine the linear, quadratic and cubic effects for S content of the diets and time of rumen and blood sampling using appropriate error terms. Because none criteria analyzed exhibited a diet by sampling time interaction ($P > .25$), time course data with each diet are not presented.

Determination of Sulfur Requirement. After a guadratic increase of clean mohair yield with S supplementation was confirmed, sulfur requirement of Angora goats for mohair growth was determined by fitting a parabolic equation between clean mohair yield (Y, g/period) and dietary S contents (X, %) as: $Y = a + bX - cX^2$. The maximum value of Y should occur at the optimum value of $X = b/2c$ (Cochran and Cox, 1957).

According to the law of diminishing return (Lancaster, 1973), the marginal efficiencies of intake S and retained S for each increased supplemental S also were calculated and tested by orthogonal polynomial contrasts. When linear decreases in marginal efficiencies for each increased S supplementation were confirmed, linear equations were fitted between marginal efficiencies of intake S and retained S for mohair growth for each increased S supplementation (Y, %) and midpoints of dietary S contents (X, %) as: $Y = a - bX$.

Then, the zero marginal efficiency should be at the optimum value of X = a/b.

Results and Discussion

Body weight, BW change, and DM intake of goats were not affected (P > .20) by S content of the diet (Table 2). The digestibilities of DM, OM, GE, and ADF were not altered (P > .20) by S content of the diet. Morrison et al. (1990) gave Merino sheep ad libitum access to a poor-quality tropical grass hay of low sulfur content (.4 g/kg DM) supplemented with all essential minerals but S. When the diet containing urea was supplemented with Na_2SO_4 at a N:S ratio of 10:1, feed intake by sheep doubled (P < .05) and apparent digestibility of OM was increased (39.3 vs 30.6 %; P < .05). Disagreements between our results and those of Morrison et al. (1990) might be due to the differences in basal diet composition and in animal species. Ash digestibility increased linearly (P < .05) with S supplementation. This presumably was due to the addition of SiO_2 to the low S diet to make all diets isocaloric and isonitrogenous. The calculated digestibility of ash was similar among diets if one subtracts the indigestible dietary SiO_2 from the total ash. Intake of ME expressed as per unit of metabolic BW was similar across all diets, averaging 102.6 $\pm$ 4.1 Kcal/KgBW$^{\cdot 75}$ (Table 2). Dry matter intake averaged 2.5% of BW or 66.5 g/KgBW$^{\cdot 75}$.

Mohair production responded quadratically (P < .01) to dietary S intake, both in grease and clean mohair weight

(Table 3). This was attributed mainly to an enhanced staple length ($P < .01$). Mohair diameter was not affected ($P > .10$) by supplemental S. Mohair quality criteria, grease, and clean staple strengths increased quadratically ($P < .05$) with increased S intake. Staple strength of mohair is related to processing performance. Mohair of low strength generally will suffer more breaks during processing and produce a top with lower mean fiber length (Blakeman et al., 1990). Laboratory scoured yield, med fiber, and kemp fiber of mohair were not altered by diet ($P > .20$). Sulfur and cysteine contents of mohair were not affected by added S ($P > .20$). The N:S ratio of mohair averaged 5.4 $\pm$ .09 and was not changed with S supplementation. Williams et al. (1972) supplemented sheep with S-containing amino acids and found that wool growth was increased more for high wool-producing sheep than for low wool-producing sheep. Williams et al. (1972) also noted wool S content was increased and the wool N:S ratio was decreased. Qi (1989) reported that the major criteria for evaluating wool quality (strength, elasticity and resilience) were highly correlated with the wool S content in wool of a given diameter (22.3 $\pm$ .14 μm). However, mohair is different from Merino wool in that mohair contains a higher percentage of medullated fibers, and the medulla layer contains a very low concentration of S-containing amino acids (Qi, 1988). Therefore, S content might be lower in mohair than in wool (N:S ratio of 3.0 to 6.4). In summary, mohair production, staple length and

strength responded quadratically to the addition of S to the diet whereas other measured parameters were unaffected (Table 3).

Using clean mohair production as a dependent variable (Y, g) and dietary S percentage as an independent variable (X, %), the parabolic equation relating the two variables was: $Y = 43.9 + 1448.7\ X - 2712.6\ X^2$ ($R^2 = .85$; $Sy.x = 27.47$; $P < .0001$). Solving this equation for maximum clean mohair production, the optimum S content of the diet was .267%. Based on this value and the dietary N content (1.92%), the optimum dietary N:S ratio was calculated to be 7.2. These values for the optimum S content and the optimum N:S ratio in the diet are higher than NRC (1981) recommendation (N:S of 10), which is adopted from research in sheep. Angora goats are smaller than most of the fiber-producing sheep. Furthermore, nutrient partitioning toward fiber growth is higher in Angora goats than in sheep because Angora goats grow twice as much fiber as sheep (Gallagher and Shelton, 1972). Huston et al. (1971) suggested that requirements of Angora goats for macrominerals might be slightly higher than those of other species because they had a higher basal metabolic rate. Because goats have less body fat, a higher proportion of their BW is physiologically active. This might cause nutrient and energy requirements to be higher for goats than for sheep.

The disposition of S in goats was evaluated in order to examine specific effects of dietary treatments. No increase

in fecal S ($P > .20$) was apparent as intake of S increased (Table 4). Digestibility of S exhibited a linear ($P < .001$) response to S supplementation. Urinary S output exhibited a linear increase ($P < .01$) with increased S intake. These results suggest that the route of excretion of added S was mainly through urine. Total S digestibility was linearly partitioned into digestibilities of basal dietary S vs supplemental S (data not shown). At the lowest level of S supplementation (Diet 1 to Diet 2), added S had a digestibility of 83.2%, at the next level (Diet 2 to Diet 3), added S had a digestibility of 77.0%; at the highest level (Diet 3 to Diet 4), added S had a digestibility of 73.9%. Combined by linear regression, sulfur digestibility was higher for supplemental S than for S in the basal diet (78.1% vs 59.9%, $P < .01$). Mohair S yield exhibited a quadratic response ($P < .01$), primarily due to higher mohair production (Table 3). Apparent S retention increased linearly ($P < .01$) with S intake (Table 4). This increase might be due partly to an increased loss of sulfide-S from eructation ($H_2S \Longrightarrow HS^- + H^+$, $pK_a = 6.74$; Bray and Till, 1975). Ruminal fluid pH was approximately 6.4 (Table 6); therefore, H_2S was dominant compared with HS^-. Hence, sulfide-S loss from eructation is inevitable. Because sulfide-S loss was not measured in this experiment, it became part of apparent S retention. Ruminal microorganisms reduce sulfate to sulfide (Durand and Komisarczuk, 1988) and use $S^=$ for synthesis of S-containing amino acids

(methionine, cystine, cysteine, and cystathionine). Sulfur also is used for vitamin synthesis (thiamine and biotin). There are two known main pathways of microbial sulfate reduction: assimilatory, which does not release free sulfide into the medium, and dissimilatory, which does. The amount of free sulfide formed depends on the relative activities of these two pathways (Bray and Till, 1975). Because most ruminal bacteria use sulfide derived from the dissimilatory pathway (Moir, 1979), gaseous loss may explain a large loss of S (in the form of H_2S) from the medium (Durand and Komisarczuk, 1988). In summary, for maximum mohair growth, the diet should contain .267% S when 40% was from supplemented sulfate. Digestibility of S averaged 76%, and apparent efficiency of absorbed S for mohair growth averaged 40% (Table 4).

The marginal efficiencies of S utilization for mohair growth were calculated both on the basis of marginal S intake and marginal S retention (Table 4). The marginal efficiency of retained S used for mohair growth dropped linearly ($P < .01$) as S retention increased. Regression equation of marginal efficiency of retained S used for mohair growth (Y, %) from midpoints of dietary S percentage (X, %) was: $Y = 132.96 - 495.15\ X$ ($R^2 = .97$, $Sy.x = 7.537$, $P < .11$). From this equation, the calculated requirement of dietary S percentage (X, %) for zero marginal efficiency of retained S for mohair growth (Y, %) was .269%, which was close to the value .267% previously calculated from equation

for maximal clean mohair yield. Similarly, the regression equation of marginal efficiency of intake S for mohair growth (Y, %) to midpoints of dietary S percentage (X, %) was: $Y = 18.11 - 71.47\ X$ ($R^2 = .91$, $Sy.x = 1.964$, $P < .20$). From this equation, the calculated requirement of dietary S percentage (X, %) for zero marginal efficiency of intake S (Y, %) was .253%, which was lower than the value obtained previously. This can be attributed to a higher residual error for intake S than for retained S.

Nitrogen metabolism data are summarized in Table 5. Although N intake, N digestibility, fecal and urinary N outputs were not different ($P > .15$) across the treatment diets, N absorption ($P < .07$) and N retention ($P < .05$) exhibited quadratic increases to supplemental S. Presumably, the added S improved the N utilization. Allaway (1970) suggested that if a diet contains a wide nitrogen to sulfur ratio, the animal will adjust to this ratio by wasting N. Therefore, efficiency of feed protein utilization decreases when S is deficient. The percentage of absorbed N retained was more than 5% higher ($.10 < P < .20$) in goats fed the .29% S diet than in goats fed other diets. Mohair nitrogen yield exhibited a quadratic increase ($P < .01$) with S supplementation. The percentage of retained N used for mohair growth averaged 20.5 ± 4.2 and did not differ ($P > .20$) among the treatment diets.

Total ruminal fluid VFA concentration ranged from 76.7 to 79.1 m*M* (Table 6) and was not affected ($P > .20$) by

added S. Ruminal acetate, propionate, isobutyrate, and butyrate concentrations were not altered ($P > .20$) by added S. Ruminal isovalerate, valerate concentrations were increased quadratically ($P < .05$) by S supplementation. The acetate to propionate molar ratio (A/P ratio) was numerically higher ($P = .1862$) for goats fed the basal diet than for those fed the S supplemented diets.

Ruminal fluid pH increased quadratically ($P < .05$) with increased S intake (Table 7). Edman (1988) indicated that the optimal range of pH for cellulose digestion is 6.4 to 6.8. Mean ruminal pH was above 6.4 for all diets with the highest value for goats fed .23% S diet. Weston et al. (1988) also found that a low dietary S concentration depressed fiber digestibility in sheep. Ruminal ammonia N (RAMN) and ruminal free, nonionized ammonia N (FAMN) exhibited quadratic increases ($P < .01$) to dietary treatments peaking with the .23% S diet. Plasma urea N increased quadratically ($P < .10$) with increased S intake (Table 7). A higher plasma urea N may increase ruminal ammonia N by increasing the amount of N recycled to the rumen via saliva and the ruminal epithelium (Nolan and Leng, 1972). However, a higher ruminal ammonia concentration decreases the amount of N recycled to the rumen via the ruminal epithelium (Wallace et al., 1979). According to Mehrez et al. (1977), the maximal rate of fermentation was observed when the ruminal ammonia N concentration was 23.5 mg/dL in the ruminal fluid, somewhat below the value we

measured. A higher ruminal ammonia N concentration may increase bacterial protein synthesis (Hume et al., 1970). Because urinary N output was similar across diets and because N balance increased quadratically with S intake (Table 5), the levels of ruminal ammonia N and free ammonia N in this trial appeared to be adequate for activity of ruminal bacteria.

Ruminal L-lactate concentration was numerically lower in goats fed the basal diet than in goats fed the S supplemented diets ($.10 < P < .20$). Plasma L-lactate concentration was not affected ($P > .20$) by S supplementation. Whanger (1972) reported that lactate (not specify L- or D-lactate) accumulated in the rumen of sheep fed sulfur-deficient diets while only traces of lactate are found in the rumen of their control sheep. The reason for this discrepancy is not known.

Ruminal fluid total S concentration exhibited linear ($P < .0001$) and quadratic increases ($P < .05$) with S supplementation (Table 8). Ruminal sulfate S concentration exhibited a linear increase ($P < .01$) with added S. Organic S ($P < .05$) and 10% TCA precipitated protein-S ($P < .01$) concentrations increased quadratically with added S. Hungate (1966) stated that because proteolytic activity did not vary across natural diets, any difference in protein concentration in the rumen fluid could be considered to be microbial protein. Protein-S should follow a similar pattern. The quadratic effect of dietary S on protein-S

suggests that microbial growth and microbial protein synthesis was greatest with the .23 and .29% S diets. Passing to the intestine, microbial protein will supply more S-containing amino acids to enhance mohair growth. Stimulation of microbial protein synthesis by S addition has been observed in vivo with semipurified diets containing a high proportion of urea (Elliott and Armstrong, 1982) and with natural diets in 23 different reports summarized by Durand and Komisarczuk (1988).

Ruminal total sulfide-S concentration increased linearly ($P < .01$) with S supplementation (Table 8). Ruminal nonionized, volatile sulfide-S exhibited a similar trend as total sulfide-S. According to Kandylis (1984), when the ruminal sulfide S concentration is below 3.8 mg/L, bacterial growth depressed. Our values were about 3 times of this estimate that should be sufficient for microbial protein synthesis. Low ruminal sulfide-S concentration also can reduce the S-containing amino acid content of ruminal microbes (Weston et al., 1988).

Sulfide derived from the reduction of inorganic S sources or from the dissemination of S-amino acids (Moir, 1979), which has not been used for protein synthesis, is absorbed very rapidly through the ruminal wall and some is lost by eructation (Kandylis and Bray, 1982). Absorption from the rumen is much faster for sulfide than for ammonia and is a function of sulfide concentration. Sulfide absorbed into blood is oxidized in blood and liver to

sulfate for excretion via urine and recycling to the rumen via saliva (Bray and Till, 1975). The sulfur metabolism models presented by Doyle and Moir (1979) show that up to 40% of dietary S with an alfalfa diet and most of the supplemental dietary methionine S is not used by the microbes. The observed range of ruminal fluid sulfide S concentrations is .6 to 288 mg/L (Bray and Till, 1975). Because many factors can affect ruminal sulfide S concentration, the optimal ruminal sulfide S level has not yet been determined. Nevertheless, the ruminal sulfide S concentration (1.0 mg/L) proposed to limit bacterial growth or fermentation as reported by Bray and Till (1975) for sheep, is very low and should be considered the lower limit for estimating the S requirement of ruminant animals as suggested by Durand and Komisarczuk (1988).

Plasma total S and sulfate-S concentrations increased linearly ($P < .01$) with added S. Plasma organic S was increased quadratically ($P < .001$) by added S, mainly because plasma sulfate S concentration was elevated with increased S intake.

Implications

The dietary S level required to maximize mohair production calculated from data in this experiment was .267% of dietary DM giving an ideal N:S ratio of 7.2. Based on marginal efficiency of retained S for mohair growth, the optimal diet would contain .269% S. Both values were higher than the NRC (1981) recommendation for a N:S ratio of 10:1.

Mohair quality also was improved at this level of dietary S supplementation. Apparent digestibility of the basal dietary S was 60%, whereas apparent digestibility of added $CaSO_4$ was 78%. The optimal level of digestible S for mohair production was .18% of the dietary DM.

Table 1. Composition of experimental diets[a]

Item	Diet 1	2	3	4
Ingredient				
Bermuda grass hay	19.20	19.20	19.20	19.20
Ground peanut hulls	57.50	57.50	57.50	57.50
Ground corn	18.15	18.15	18.15	18.15
Urea	1.50	1.50	1.50	1.50
$CaCO_3$	.82	.55	.27	-
Calcium phosphate[b]	.80	.80	.80	.80
$CaSO_4$	-	.42	.85	1.25
Trace mineralized salt[c]	1.00	1.00	1.00	1.00
Vitamin A,D,E[d]	.60	.60	.60	.60
SiO_2	.43	.28	.13	-
Chemical Composition[e]				
ME, Mcal/kg	1.58	1.51	1.58	1.53
CP, %	11.9	11.9	12.2	11.8
ADF, %	41.3	42.2	41.5	41.1
S, %	.16	.23	.29	.34
Sulfate S, %	.06	.13	.19	.24
Organic S, %	.10	.10	.10	.10
Ca, %	.69	.67	.68	.66
P, %	.36	.35	.34	.35
Cu, ppm	8.75	8.74	8.83	8.76
Zn, ppm	26.04	29.10	30.65	31.10
Mo, ppm	1.00	.98	1.01	.97
N:S Ratio	12.7	8.3	6.8	5.5

[a]DM basis.

[b]A chemical mixture of monocalcium and dicalcium phosphate containing 17% Ca, 21% P.

[c]Containing (percentage): NaCl, 95.5 - 98.5; Mn, > .24; Fe, > .24; Mg, > .05; Cu, > .032; Co, > .011; I, > .007; Zn, > .005.

[d]Contained 2,200 IU of vitamin A; 1,200 IU of Vitamin D_3; 2.2 IU of vitamin E per gram.

[e]All except ME were measured. Feed, fecal, and urinary energy were measured, but methane energy was estimated (Blaxter and Clapperton, 1965) for calculating ME.

Table 2. Means of intakes, digestibilities and body weight

Item	Sulfur, %				SE	Probability <		
	.16	.23	.29	.34		Linear	Quadratic	Cubic
BW, Kg	44.4	43.9	44.6	44.5	.32	.4861	.6026	.2334
BW change, g/d	5.0	20.4	14.9	5.9	13.32	.5840	.2459	.5640
Intake								
DM, g/d	1,106	1,132	1,213	1,117	56.0	.6568	.2903	.3666
GE, kcal/d	4,837	5,032	5,330	4,942	247.9	.5872	.2552	.4854
ME, kcal/d	1,694	1,790	1,834	1,761	72.1	.4552	.2558	.8420
ME, kcal/(kgBW$^{.75}$.d)	97.3	104.3	103.9	105.0	4.15	.2392	.4785	.6328
Digestibility, %								
DM	42.7	42.6	42.4	43.4	.91	.6253	.5875	.7351
ADF	20.2	23.3	22.8	22.1	1.42	.8484	.9656	.4245
OM	43.6	43.1	43.8	43.6	.99	.9079	.5294	.8180
Ash	31.4	36.1	37.9	41.5	2.71	.0165	.8477	.7095
GE	42.9	43.4	42.4	43.6	.96	.7829	.7086	.4206

Table 3. Means of mohair yield and quality evaluation

Item	Sulfur, %				SE	Probability <		
	.16	.23	.29	.34		Linear	Quadratic	Cubic
Grease mohair, g/d	12.3	14.3	14.4	12.8	.38	.3441	.0003	.8255
Clean mohair, g/d	10.1	11.6	11.7	10.5	.30	.3251	.0004	.9401
Staple length, mm/d	1.02	1.09	1.01	.99	.011	.0110	.0002	.0050
Mohair diameter, μm	37.9	37.3	38.5	36.6	.50	.2500	.1930	.1299
Grease staple strength[a]	64.3	71.6	64.6	62.9	2.02	.2345	.0396	.0421
Clean staple strength[a]	78.5	88.3	79.4	76.7	2.80	.2683	.0399	.0617
Yield[b], %	82.0	81.1	81.4	82.0	.62	.9309	.2602	.7616
Med fiber, no./1000	16.8	15.5	16.5	14.3	2.85	.6162	.8627	.6712
Kemp fiber, no./1000	1.1	.8	1.9	.8	.67	.9999	.5822	.2263
Sulfur[c], %	2.95	2.99	3.00	2.97	.054	.8289	.5805	.9915
Cysteine[c], %	10.15	10.27	10.29	10.20	.186	.8315	.5797	.9976
N:S Ratio	5.5	5.4	5.4	5.5	.09	.9833	.3307	.7506

[a]Newton/Kilotex;
[b]Mohair yield (%) = Clean, dry mohair weight * (100 + 13.87)/Grease mohair weight, in which 13.87% is the standard moisture regain for mohair;
[c]Dry means mohair moisture regain = 0%.

Table 4. Sulfur metabolism, mohair sulfur yield and marginal efficiencies

Item	Sulfur, %				SE	Probability <		
	.16	.23	.29	.34		Linear	Quadratic	Cubic
Intake, g/d	1.71	2.61	3.54	3.86	.195	.0001	.1557	.4724
Fecal output, g/d	.68	.65	.80	.78	.095	.3300	.9628	.4134
Urinary output, g/d	.50	1.13	1.57	1.81	.107	.0001	.0887	.9792
Apparent digestibility, %	59.93	74.54	77.99	80.29	2.964	.0001	.0499	.4611
Retention, g/d	.53	.83	1.17	1.27	.142	.0008	.4923	.6753
Mohair sulfur yield, g/d	.26	.30	.31	.27	.008	.2899	.0001	.9362
Efficiency of S Utilization, %								
Intake S for mohair[a]	15.72	11.87	9.22	7.83	.825	.0001	.1537	.9886
Retained S for mohair[b]	52.48	41.16	34.78	26.16	5.360	.0022	.8047	.7678
Marginal Efficiency of S Utilization, %:								
Intake of S for mohair[c]	-	3.44	1.13	-5.27	11.160	.6894	.9212	-
Retention of S for mohair[d]	-	33.59	10.37	-26.34	11.401	.0013	.6342	-

[a]Calculated as [mohair S yield/(S intake)]*100.
[b]Calculated as [mohair S yield/(S retention)]*100.
[c]Calculated as [marginal mohair S yield/(marginal S intake)]*100.
[d]Calculated as [marginal mohair S yield/(marginal S retention)]*100.

Table 5. Nitrogen metabolism, mohair nitrogen yield and efficiency of nitrogen utilization

	Sulfur, %					Probability <		
Item	.16	.23	.29	.34	SE	Linear	Quadratic	Cubic
Intake, g/d	21.08	21.78	23.54	21.27	1.041	.6243	.1706	.2891
Fecal output, g/d	6.88	6.92	7.32	6.84	.450	.8966	.5618	.5435
Absorbed, g/d	14.20	14.86	16.21	14.43	.616	.4656	.0633	.1807
Urinary output, g/d	6.05	6.03	5.75	5.47	.460	.3421	.7808	.9073
Digestibility, %	67.45	68.03	69.06	67.87	.625	.4205	.1744	.3559
Retention, g/d	8.15	8.83	10.46	8.96	.516	.0955	.0489	.0940
Mohair N, g/d	1.42	1.63	1.64	1.48	.043	.3251	.0004	.9401
Absorbed N retained, %	57.58	58.47	63.78	57.55	2.781	.6782	.2170	.2155
Retained N for mohair growth, %	18.21	20.68	16.65	26.39	4.218	.2912	.4007	.2967

Table 6. Means of ruminal fluid volatile fatty acid contents (m*M*)

	Sulfur, %					Probability <		
Item	.16	.23	.29	.34	SE	Linear	Quadratic	Cubic
Total VFA	77.1	78.0	79.1	76.7	2.74	.9786	.2442	.5762
Acetate	53.8	53.5	54.1	52.2	2.19	.4111	.4791	.4912
Propionate	13.3	14.3	14.5	14.2	1.07	.2153	.2244	.8526
Isobutyrate	.57	.59	.60	.56	.051	.9870	.2779	.7658
Butyrate	8.26	8.32	8.45	8.51	.552	.4945	.9941	.9136
Isovalerate	.49	.52	.59	.46	.077	.8896	.0468	.1788
Valerate	.75	.81	.84	.75	.060	.8041	.0274	.5367
A/P Ratio[a]	4.20	3.95	3.98	3.89	.285	.1862	.5791	.5247

[a]Calculated as Acetate(m*M*)/Propionate(m*M*).

Table 7. Means of ruminal fluid pH, ammonia N, L-lactate, plasma urea N, and L-lactate concentrations

Item	Sulfur, %				SE	Probability <		
	.16	.23	.29	.34		Linear	Quadratic	Cubic
Rumen								
pH	6.45	6.54	6.47	6.41	.050	.1160	.0089	.1049
Ammonia N, mg/dL								
Total	33.13	39.64	35.94	30.98	3.494	.3113	.0041	.2665
Nonionized	.10	.13	.11	.08	.020	.0621	.0054	.2262
L-lactate, mg/dL	9.99	10.89	10.98	10.89	.882	.1508	.3087	.7115
Plasma								
Urea N, mg/dL	9.70	9.95	9.96	9.39	.392	.3097	.0585	.7048
L-lactate, mg/dL	21.13	20.23	19.67	19.18	2.487	.2665	.8747	.9656

Table 8. Means of ruminal, and plasma sulfur metabolite concentrations (mg/L)

Item	Sulfur, %				SE	Probability <		
	.16	.23	.29	.34		Linear	Quadratic	Cubic
Rumen								
Total	44.00	55.11	60.68	58.98	4.723	.0001	.0143	.8719
Sulfate	36.60	40.89	45.50	45.44	3.613	.0012	.2442	.5451
Organic	7.40	14.21	15.17	13.53	3.383	.0197	.0223	.6719
Protein	6.03	13.04	14.43	10.82	2.705	.0178	.0010	.9215
Sulfide	9.13	10.84	11.57	12.59	1.282	.0011	.6005	.6576
H_2S^2	5.99	6.75	7.45	8.56	.844	.0003	.6918	.8021
Plasma								
Total	29.55	36.58	45.63	51.93	10.794	.0055	.9463	.8466
Sulfate	27.65	31.07	39.02	49.88	10.074	.0039	.4696	.9437
Organic	1.89	5.51	6.61	2.05	1.019	.5026	.0001	.1871

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CHAPTER IV

SULFATE SUPPLEMENTATION OF ALPINE GOATS: EFFECTS ON MILK YIELD AND COMPOSITION, METABOLITES, NUTRIENT DIGESTIBILITIES, AND ACID-BASE BALANCE

K. Qi[1,2], C. D. Lu[1], and F. N. Owens[2]

Langston University[1], Langston, OK 73050 and
Oklahoma State University[2], Stillwater 74078

ABSTRACT. Effects of sulfate supplementation on milk yield and composition, ruminal and blood metabolites, acid-base status, and nutrient digestibilities were determined using 30 multiparous lactating Alpine does. Goats were fed ısonitrogenous diets containing .16% (basal), .26%, or .36% S (DM basis) durıng a 13-wk lactation trial that coincided with wk 3 to 15 of lactatıon. During wk 16 to 17, in a metabolism trial nutrient digestibility and balance were measured using four does from each treatment. Feed intake, yield of 4% fat-corrected milk and milk S content were not affected by added S, but the goats fed the .26% S diet tended to have ($P < .20$) higher persistency of lactation. During wk 10 and 15 of lactation, milk solids-not-fat

percentage was highest (P < .10) for does fed the .26% S diet. Sulfur supplementation resulted in quadratic decreases in ruminal ammonia N (P < .05) during wk 15, in plasma urea N during wk 10 and 15 (P < .05), but linear increases (P < .05) in ruminal protein S concentrations throughout the experiment. Added S had little impact on blood acid-base status. Apparent digestibilities of DM, OM, ash, ADF, and GE were increased linearly (P < .10) by added S. Milk N:S ratio remained constant. Increasing S from .16 to .26% of diet DM was beneficial to lactating Alpine goats during early lactation.

Key Words: Goat, Lactation, Sulfur, Metabolite, Acid-Base Status, Digestibility.

Introduction

Sulfur requirements of lactating ruminants have received limited research attention. The National Research Council (1989) indicated that the S requirement for lactating dairy cows was not clearly established, although a .20% S of dietary DM was suggested. The National Research Council (1981) indicated that no information was available for the S requirement of lactating goats.

Sulfur may alter acid-base balance (Tucker et al., 1991). Dairy goats have certain peculiar metabolic and physiological characteristics; for example, on a body weight basis, high-producing dairy goats consume twice as much feed as dairy cows and dedicate a greater proportion of their energy consumed to milk production (Larson, 1978).

Furthermore, goat's milk generally contains more S than cow's milk (Haenlein, 1980; NRC, 1989). Hence, extrapolation of the results from cattle to goats may be inadequate. Therefore, an experiment was conducted to 1) evaluate the effects of S supplementation on milk yield and composition, 2) measure the effects of S supplementation on ruminal and blood metabolites, acid-base status of lactating goats, and 3) quantify the impact of S on feed intake, DM, OM, and ADF digestibilities. Ultimately, we seek to establish the optimal concentration of S in the diets of lactating goats.

Materials and Methods

Animals and Diets. Thirty multiparous lactating Alpine does (X $\pm$ SE BW = 65.3 $\pm$ 1.5 kg) were used in a lactation trial. Goats were allowed ad libitum access to a standard lactation diet (14% CP and 65% TDN) for 2 wk postpartum. Animals were blocked according to parturition date (X $\pm$ SD = 14 $\pm$ 4 d postpartum) and assigned to one of three treatments based on pretreatment milk yield, BW, and DMI. Six does were assigned to each of the five time blocks in a randomized complete block design (Cochran and Cox, 1957). Animals had ad libitum access to experimental diets starting at wk 3 of lactation, and daily milk production was recorded from wk 3 to wk 15 of lactation. Diets (Table 1) were isonitrogenous and isocaloric, containing .16% (basal), .26%, or .36% S (DM basis). Calcium sulfate served as the

source of supplemented S, and was included to achieve N:S ratios of 14.2:1, 8.7:1, and 6.3:1. Calcium intake from $CaSO_4$ was balanced by addition of $CaCO_3$; SiO_2 was added to equalize nutrient density among diets. Each diet was completely mixed (Weigh-Tronix, Fairmont, MN) to minimize particle size separation and to reduce sorting. Urea nitrogen accounted for one-third of total nitrogen in the diet. The forage to concentrate ratio of the diet was 43:57. The dietary cation-anion balance, expressed as meq((Na + K) - Cl)/100 g of diet DM (DCAB) or meq((Na + K) - (Cl + S))/100 g of diet DM (DCAB:S) (Tucker et al., 1991), was calculated. Does were fed once (0830) and milked twice (600 and 1800) daily. Water was available at all time. Calan gates (American Calan, Northwood, NH) were used to monitor individual feed intake but allow animals to interact (six goats per pen and two per each treatment in each 20 m^2 pen). Animals were housed in a closed barn equipped with infrared heating and forced air ventilation.

In order to quantify digestibilities of DM, OM, ADF, ash, and balances of N and S, four does from each treatment were placed in metabolism crates for total collection of feces and urine in a completely randomized design (Cochran and Cox, 1957) during wk 16 to 17 of lactation.

Sample Collection and Analyses. Feed samples were collected weekly and composited every 3 wk for analysis. Goats were weighed on two consecutive days at 14-d intervals during the lactation trial, and at the beginning and the end

of the collection phase of the metabolism trial. Milk production was measured with a computerized flow metering device (Westfalia Systemat, Elk Grove, IL). Composites of milk collected at consecutive morning and afternoon milking during wk 5, 10, and 15 of lactation were prepared. Ruminal samples, obtained via stomach tube, and blood samples, obtained via jugular venipuncture, were procured 4 h postprandially during wk 5, 10, and 15 of lactation. The first 20 to 30 mL of ruminal fluid was discarded to reduce salivary contamination. Thereafter, at least 50 mL was collected for analysis. Ruminal fluid pH was determined using a pH meter (SA-720, Orion Research, Boston, MA) immediately after sampling. Then, one milliliter of saturated $HgCl_2$ solution was added to the 50 mL sample to inhibit microbial fermentation.

Twenty milliliter subsamples of rumen fluid were mixed with 1 mL of 2 *M* zinc acetate to preserve them for total sulfide-S (sum of H_2S-S, HS^--S, and $S^=$-S) analysis (Fresenius et al., 1988). Ruminal nonionized, volatile sulfide-S (H_2S-S) was calculated according to Henderson-Hasselbalch equation (Boyer, 1986). The formula used was as follows:

$$H_2S\text{-}S = \text{Total sulfide-S}/[1 + \text{antilog}(pH - 6.74)$$

where 6.74 is the pK_a of sulfide-S ($H_2S \Longrightarrow HS^- + H^+$, $K_a = 1.8 * 10^{-7}$; Bray and Till, 1975). The H_2S-S was an estimate of the amount of sulfide-S that could volatilize and be lost through eructation.

Total feces, urine, and milk were collected for 7 d and composited for chemical analysis. Dry matter, OM, ash, and nitrogen of feed, feces, and urine were determined (AOAC, 1990). Feed, fecal, and urinary GE were determined using an adiabatic bomb calorimeter (Parr Instrument, Moline, IL). Urinary samples were frozen and then slowly lyophilized at 20 ^{o}C and less than 100 millitorr without losing any DM (Virtis, Gardiner, NY). Urinary energy was determined on these lyophilized urinary samples. Methane energy loss was calculated according to Blaxter and Clapperton (1965). Acid detergent fiber (Goering and Van Soest, 1970) was determined by standard procedures.

The GE digestibilities of experimental diets measured during the metabolism trial were used to calculate DE intake during the lactation trial. The ratio of ME to DE determined during the metabolism trial was similar across diets; the average (.857) was used to calculate ME intake during the lactation trial.

Total S contents of feed, feces, urine, milk, ruminal fluid, and plasma were determined according to Mottershead (1971). Sulfate-S contents of plasma and ruminal fluid were analyzed by the method described by Bird and Fountain (1970). Organic S was calculated as the difference between total S and sulfate S (Bird and Fountain, 1970). Ruminal samples were centrifuged at 1000 X g for 5 min to remove feed particles and protozoa (Merchen and Satter, 1983). Ruminal fluid and plasma samples were deproteinized using

20% tricarboxylic acid (TCA, 1:1, vol/vol) as described by Cline et al. (1958) and the supernatant fluid was analyzed for sulfate-S. Sulfur in the precipitate, considered to be protein-S, was measured (Mottershead, 1971).

Blood samples for acid-base analyses were collected anaerobically into 10-mL evacuated blood collection tubes containing sodium heparin. Tubes were placed on ice and analyzed within 2 h for blood pH, bicarbonate (HCO_3^-), pCO_2, pO_2, base excess, base excess in extra-cellular fluid, total CO_2 content, standard bicarbonate and oxygen saturation using a blood gas analyzer (System 1304, Instrumentation Laboratory, Lexington, MA).

Ruminal VFA were measured according to Erwin et al. (1968). Plasma urea N was determined according to Chaney and Marbach (1962). Total ruminal ammonia N (AMN) was analyzed by the method of Broderick and Kang (1980). In addition, ruminal free, nonionized ammonia N (FAMN) was calculated according to Visek (1968). Ruminal fluid L-lactate was determined using Sigma Kit 826 (Sigma Diagnostics, St. Louis, MO).

Composites of morning and afternoon milk samples were analyzed via infrared spectrophotometer (Multispec 2, Multispec, Wheldrake, York, UK) for fat, protein (N X 6.38), solids-not-fat and lactose contents. Feed was analyzed for Na, K, Ca, P, Cu, and Zn by emission spectroscopy (Spectrospan V, Beckman Instruments, Irvine, CA). Chloride

was analyzed by a volumetric procedure (AOAC, 1990) using standard solutions (Fisher Scientific, Plano, TX).

Statistical Analyses. Statistical analyses were conducted according to GLM procedure of SAS (1985). Data for the lactation trial were averaged and analyzed per each week (Steel and Torrie, 1980). Average 4% fat-corrected milk (FCM) yield for the entire lactation trial was analyzed; pretreatment milk measurements (wk 1 to 2) served as a covariate. The model included the effects of block, diet, block X diet interaction and the residual error. The residual mean square was used as the error term. Orthogonal polynomial contrasts were used to detect linear and quadratic effects of treatments. Data for the metabolism trial was analyzed for the effects of diets. Significance was declared at level of $P < .10$, while $P < .20$ was interpreted to indicate a trend. The exact probability values are presented in all Tables.

Persistency of lactation was analyzed using linear regression of weekly FCM yield in each goat by the week of lactation. Intercepts and regression coefficients were tested as above.

Results and Discussion

Lactation Trial.

During the 13-wk lactation trial (wk 3 to 15 of lactation), BW and BW change, intakes of DM, OM, GE, DE, ME, and intake of ME per metabolic BW (Table 2) were not affected ($P > .20$) by S supplementation. Sulfur intake

increased linearly ($P < .0001$) with S supplementation. The overall FCM yield of goats was not affected ($P > .20$) by added S, although the FCM yield of goats receiving the .26% S diet was numerically higher than those fed the other two diets. Persistency of lactation was calculated by regressing weekly FCM yield over weeks of lactation. The slope was -.183, -.077 and -.170 for diets containing .16, .26 and .36% S, respectively, indicating that a trend was apparent ($P < .20$) for a quadratic response.

Milk protein content (Table 3) during the lactation trial tended to be higher ($P < .20$) for does fed the .26% S diet. Milk fat content averaged across the three sampling times also was numerically higher ($P > .20$) for does fed the .26% S diet. Lactose content increased linearly ($P < .10$) with added S during wk 10 of lactation. Solids-not-fat content was increased quadratically ($P < .10$) with S supplementation during wk 10 and wk 15 of lactation. However, milk S content and milk N:S ratio were not altered ($P > .20$) by added S. Garrigus (1970) summarized research on N and S contents of goat milk and found that N:S ratio ranged from 15.7 to 17.9. The milk N:S ratio during the lactation trial averaged 16.9 $\pm$ 1.8, which was within this range.

Total VFA, and acetate concentrations in ruminal fluid (Table 4) were not affected ($P > .20$) by S supplementation when averaged across the entire lactation trial. Except for a quadratic trend ($P < .20$) during wk 15, ruminal propionate

was not affected (P > .20) by S supplementation. Isobutyrate was increased linearly (P < .05) by added S during wk 15, but no responses were detected during wk 5 and 10 of lactation. Butyrate was increased linearly (P < .10) during wk 15, but no response was detected during wk 5 or 10 of lactation. Isovalerate increased quadratically (P < .05) during wk 5, and increased linearly (P < .10) during wk 15, and tended to increase quadratically (P < .20) during wk 10 of lactation by S supplementation. Except for a quadratic trend (P < .20) during wk 10, valerate was not affected (P > .20) by added S. The acetate to propionate molar ratio was not affected by added S during wk 5, but there were trends toward quadratic decreases during wk 10 and 15 (P < .20) of lactation.

Ruminal fluid pH (Table 5) was not affected (P > .20) with S supplementation. Ruminal fluid ammonia N tended to decrease (P < .20) during wk 5, and decreased quadratically with added S during wk 15 (P < .05) of lactation. Ruminal fluid free, nonionized ammonia N followed a similar pattern (P < .10). According to Mehrez et al. (1977), fermentation was maximal when the ruminal ammonia N concentration was 23.5 mg/dL, somewhat below the value we measured. A higher ruminal ammonia N concentration increases bacterial protein synthesis (Hume et al., 1970). The ruminal fluid ammonia N concentration in goats fed .26% S diet was very close to the optimal value in Angora goats fed similar diet (Qi et al., 1992). Plasma urea N decreased quadratically during wk 10

($P < .01$) and wk 15 ($P < .05$) of lactation with S supplementation. The quadratic decreases in ruminal ammonia N and plasma urea N concentrations can be interpreted to suggest that .26% dietary S might have enhanced ammonia N utilization by ruminal bacteria. This suggestion was further confirmed by increases in ruminal protein-S (Table 6) with S supplementation.

Ruminal fluid L-lactate (Table 5) was not affected in wk 5 ($P > .20$), but increased linearly in wk 10, and quadratically in wk 15 ($P < .01$) of lactation with S supplementation. Whanger (1972) reported that D-lactate accumulated in the rumen of sheep fed S deficient diets, but he found only traces of D-lactate in the rumen of sheep fed supplemental S. We only measured L-lactate in this experiment.

Ruminal fluid total S, sulfate-S, and organic S concentrations (Table 6) all were increased linearly ($P < .10$) by added S during the each week of the lactation trial. Sulfur precipitated by 10% TCA (protein S) also was increased linearly ($P < .05$) by added S. Qi et al. (1992) observed that ruminal protein S was increased in Angora goats by adding S to a .16% S diet. Hence, the higher protein S with goats fed the S-supplemented diets can be interpreted to suggest that microbial growth and microbial protein synthesis were increased by S supplementation. Total sulfide-S and nonionized sulfide-S (H_2S-S) concentrations were not affected ($P > .20$) by added S during

wk 5 and 10, but were increased quadratically during wk 15 ($P < .05$) of lactation by S supplementation. Microbes reduce inorganic sulfate to sulfide (Bull, 1984; Durand and Komisarczuk, 1988) and incorporate sulfide into S amino acids. A higher concentration of total sulfide S might enhance bacterial utilization of S, whereas a higher concentration of nonionized, volatile sulfide-S should increase sulfide-S loss to eructation (Kandylis and Bray, 1982; Durand and Komisarczuk, 1988). With more than 80% of the sulfide-S in the nonionized (H_2S-S) form in this experiment, eructation loss would be expected to be high.

Plasma total S and sulfate-S concentrations (Table 7) were increased linearly ($P < .001$) by S supplementation during wk 5 and 10, and tended to increase linearly ($P < .20$) during wk 15 of lactation. Organic S increased quadratically ($P < .01$) with S supplementation when averaged across the entire lactation trial due mainly to the higher sulfate-S concentration in goats fed higher dietary S.

Blood pH (Table 8) was not affected ($P > .20$) by added S when averaged across the lactation trial. Blood HCO_3^- tended to decrease ($P < .20$) during wk 5 and 15 with S supplementation, but was not affected ($P > .20$) during wk 10. The blood HCO_3^-, base excess, PCO_2, and PO_2 values were similar to values for lactating does reported by Fredeen et al. (1988). Tucker et al. (1991), feeding supplemental S from the double sulfate of potassium and magnesium to decrease DCAB:S from 30 to 0, detected no change in blood pH

in dairy cows. However, they noted that blood HCO_3^- and urinary pH decreased with S supplementation. In their study, milk production and milk fat yield were increased ($P < .01$) by a low level of S supplementation (15 meq added S/100 g of diet DM, increasing S from .30 to .54% S of dietary DM). In our experiment, though not changing DCAB, S supplementation decreased DCAB:S approximately 6 meq per 100 g of diet DM (Table 1). This was smaller than the changes introduced by Fredeen et al. (1988) and Tucker et al. (1991); in our study, the decreases induced only small numerical changes in HCO_3^- concentration. Consequently, S supplementation in this experiment did not affect acid-base status of lactating goats. No abnormal behavior or signs were apparent from added S during the entire experiment. The quantitative information about base excess in extracellular fluids, total CO_2 content, standard bicarbonate, and oxygen saturation in lactating does under defined dietary DCAB and(or) DCAB:S conditions was included in Table 8 to permit a full evaluation of dietary effects on metabolic acid-base status of lactating goats as suggested by Fredeen et al. (1988).

Metabolism Trial.

Body weight, BW change and intakes of DM, GE, DE, ME, and intake of ME per metabolic BW (Table 9) were not affected ($P > .20$) by treatments. Qi et al. (1992) also detected no change with S supplementation of Angora goats.

Apparent digestibilities of DM, OM, ash, ADF and GE (Table 10) were increased linearly ($P < .10$) by added S. The ash digestibility increase may be due partially to addition of more SiO_2 to the low S diet; calculated on a SiO_2-free basis, this difference was reduced. The increase in ADF digestibility accounted for 78% of the increase in OM digestibility. Bull (1984) reviewed several studies and concluded that S supplementation of diets fed to ruminants increased fiber digestibility. In our experiment, ADF digestibility increased by 9.2 percentage unit from the .16% S diet to the .26% S diet, but ADF digestibility only increased by 3.2 percentage unit from the .26% S diet to the .36% S diet. Apparent digestibility of CP was quadratically decreased ($P < .20$) by S supplementation. This decrease in CP digestibility presumably reflects lower digestibility for bacterial protein than urea-N. However, the retention of apparently absorbed N would be higher for bacterial N than urea-N, a trend we observed (Table 11).

Apparent digestibility of dietary S increased (linear, $P < .0001$; quadratic, $P < .01$) with S supplementation. Apparent digestibility of S was partitioned by regression into digestibility for the basal dietary S vs the supplemental S. Digestibility of S in the basal diet was 48.6 vs 95.8% for the supplemental S. In a previous study using similar feedstuffs, Qi et al. (1992) calculated values of 59.9 and 78.1 for digestibilities of S in the basal diet and S from $CaSO_4$.

Numerical values (g/d) for N metabolism were not affected by added S (data not shown). Expressed as a percentage of N intake, fecal N increased quadratically ($P < .10$) whereas urinary N decreased quadratically ($P < .10$) with S supplementation (Table 11). The percentage of absorbed N retained was not affected by added S, but the value was numerically highest for the .26% S diet. Qi et al. (1992) observed that efficiency of N utilization in Angora goats was increased when S was added to a .16% S diet.

Although S intake increased linearly ($P < .0001$) with added S, fecal total S output was similar ($P > .20$) among treatments (Table 12). Garrigus (1970) concluded that fecal S concentration was fairly constant in ruminants because it was affected mainly by basal dietary S digestibility. In contrast, urinary excretion of S was more responsive to S intake (linear increase, $P < .05$). Apparent S retention increased linearly ($P < .01$) with added S. The increase in apparent S retention with increased S intake can be ascribed partially to gaseous sulfide-S losses. These losses were not quantified in this experiment; hence, they became part of S apparently retained. Milk S output was not affected by supplemental S ($P > .20$).

Implications

Manipulation of dietary S level appeared to enhance ammonia N utilization by ruminal bacteria and to increase solids-not-fat content of milk produced by lactating goats.

Added S had little impact on blood acid-base status of lactating goats. The S requirement for lactation of dairy goats during early lactation appears to be greater than .16% but less than .36% of dietary DM.

Table 1. Composition of experimental diets[a]

Item	Diet 1	Diet 2	Diet 3
Ingredient			
Chopped bermuda hay	21.50	21.50	21.50
Ground peanut hulls	21.50	21.50	21.50
Ground corn	48.73	48.73	48.73
Soybean meal	3.00	3.00	3.00
Urea	1.60	1.60	1.60
$CaCO_3$	.57	.27	-
Calcium phosphate[b]	1.20	1.20	1.20
$CaSO_4$	-	.45	.87
Trace mineralized salt[c]	1.00	1.00	1.00
Vitamin A,D,E[d]	.60	.60	.60
SiO_2	.30	.15	-
Chemical Composition[e]			
ME, Mcal/kg	2.11	2.12	2.27
CP, %	14.4	14.0	14.3
ADF, %	21.6	21.2	21.4
S, %	.16	.26	.36
N:S Ratio	14.2	8.7	6.3
Ca, %	.49	.51	.50
P, %	.53	.50	.54
Na, %	.48	.50	.51
K, %	.88	.85	.86
Cl, %	.58	.58	.58

Cu, ppm	4.8	4.4	4.8
Zn, ppm	28	24	26
DCAB[f], meq/100 g	27.13	27.34	27.88
S, meq/100 g	5.06	8.02	11.35
DCAB:S[g], meq/100 g	22.07	19.32	16.50

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[a]DM basis.

[b]Mixture of monocalcium and dicalcium phosphate containing 17% Ca; 21% P.

[c]Containing (%): NaCl, 95.5 to 98.5; Mn, > .24; Fe, > .24; Mg, > .05; Cu, > .032; Co, > .011; I, .007; Zn, .005.

[d]Contained 2,200 U.S.P. Units of vitamin A; 1,100 U.S.P. units of vitamin D_3; 2.2 IU of vitamin E per gram.

[e]All except ME were measured. Feed, fecal, and urinary energy were measured, but methane energy was estimated to calculate ME.

[f]Dietary cation-anion balance was calculated as meq((Na + K) - Cl)/100 g of diet DM.

[g]Dietary cation-anion balance was calculated as meq((Na + K) - (Cl + S))/100 g of diet DM.

Table 2. Average body weight, body weight change, intakes of nutrients, and milk yield of Alpine goats during the lactation trial

	Sulfur, %				Probability <	
Item	.16	.26	.36	SE	Linear	Quadratic
BW, kg	62.8	64.6	62.5	3.0	.9351	.4912
BW Change, g/d	-51.6	-39.5	-58.4	20	.7047	.2938
Nutrient intake						
DM, Kg/d	2.59	2.55	2.52	.22	.7773	.9884
OM, Kg/d	2.40	2.39	2.35	.20	.8448	.9600
GE, Mcal/d	11.10	11.10	10.95	.94	.8844	.9367
DE, Mcal/d	6.41	6.47	6.68	.56	.6713	.8966
ME, Mcal/d	5.49	5.54	5.72	.48	.6713	.8966
ME, Mcal/(kgBW$^{\cdot 75}$.d)	.25	.25	.26	.18	.5523	.7264
S, g/d	4.2	6.6	9.2	.7	.0001	.8681
FCM yield[a], Kg/d	2.73	2.81	2.65	.20	.4671	.3581

[a]FCM yield = 4% fat-corrected milk yield.

Table 3. Composition (%) and N:S ratios of milk produced by Alpine goats during the lactation trial

Item	Sulfur, %			SE	Probability <	
	.16	.26	.36		Linear	Quadratic
5 Wk						
Protein	2.46	2.65	2.59	.10	.2041	.1600
Fat	3.85	4.21	4.25	.33	.2528	.5966
Lactose	4.52	4.56	4.61	.09	.3683	.8903
Solids-not-fat	7.66	7.88	7.86	.14	.1754	.3416
Sulfur	.023	.025	.025	.002	.4026	.5126
N:S Ratio[a]	16.4	16.9	16.2	1.7	.6640	.8321
10 Wk						
Protein	2.43	2.56	2.46	.08	.7981	.1363
Fat	3.11	3.28	3.17	.23	.7848	.5006
Lactose	4.20	4.34	4.36	.08	.0739	.4350
Solids-not-fat	7.38	7.62	7.53	.10	.1508	.0777
Sulfur	.023	.024	.024	.001	.7119	.8831
N:S Ratio[a]	16.5	16.8	16.3	1.9	.7256	.5418
15 Wk						
Protein	2.49	2.58	2.54	.09	.4749	.1581
Fat	2.92	3.04	2.90	.21	.9539	.5078
Lactose	4.20	4.27	4.26	.11	.6057	.7055
Solids-not-fat	7.45	7.60	7.55	.09	.3749	.0998
Sulfur	.022	.023	.022	.002	.8919	.7947
N:S Ratio[a]	17.4	17.6	18.0	1.7	.5121	.7655

[a]Calculated as protein/(6.38 * S).

Table 4. Ruminal volatile fatty acid concentrations (m*M*) and acetate to propionate (A/P) ratios in Alpine goats during the lactation trial

	Sulfur, %				Probability <	
Item	.16	.26	.36	SE	Linear	Quadratic
5 Wk						
Total VFA	78.7	81.7	78.5	3.8	.9600	.3840
Acetate	50.1	50.7	49.4	2.3	.7642	.6589
Propionate	18.2	18.1	18.0	1.6	.8847	.9946
Isobutyrate	.71	.77	.76	.06	.4371	.5033
Butyrate	8.1	9.4	8.9	.6	.2100	.1408
Isovalerate	.57	.78	.59	.10	.8795	.0416
Valerate	.89	.87	.84	.07	.4930	.9116
A/P Ratio	2.82	2.89	2.80	.22	.9455	.6696
10 Wk						
Total VFA	70.4	72.4	72.1	4.3	.7388	.8096
Acetate	44.7	45.0	45.0	3.4	.6064	.7893
Propionate	14.5	16.5	15.2	1.5	.6633	.2418
Isobutyrate	.71	.71	.68	.05	.6054	.6668
Butyrate	8.1	8.1	8.5	.6	.5028	.7153
Isovalerate	.95	.62	.74	.16	.2099	.1238
Valerate	.84	.73	.80	.07	.5866	.1651
A/P Ratio	3.33	2.77	3.04	.27	.3097	.1116
15 Wk						
Total VFA	70.5	72.1	66.8	4.0	.3389	.2929
Acetate	43.2	45.7	46.5	2.9	.2855	.7498
Propionate	14.7	16.5	14.3	1.4	.8066	.1408
Isobutyrate	.61	.73	.79	.06	.0118	.5763
Butyrate	7.1	7.8	8.2	.6	.0927	.7539
Isovalerate	.61	.62	.71	.05	.0631	.4330
Valerate	.70	.76	.84	.14	.3662	.9687
A/P Ratio	3.07	2.86	3.36	.23	.3498	.1497

Table 5. Ruminal pH, ammonia N (AMN), free, and nonionized ammonia N (FAMN), L-lactate, and plasma urea N concentrations in Alpine goats during the lactation trial

	Sulfur, %				Probability <	
Item	.16	.26	.36	SE	Linear	Quadratic
5 Wk						
pH	6.25	6.33	6.29	.07	.5395	.2980
AMN, mg/dL	45.2	32.7	36.6	6.3	.1923	.1497
FAMN, μg/dL	81.0	68.7	77.5	15.1	.8200	.4382
Urea N, mg/dL	10.7	10.0	11.4	.8	.3923	.1513
L-Lactate, mg/dL	7.1	7.5	6.7	.8	.6501	.4006
10 Wk						
pH	6.34	6.36	6.36	.12	.9223	.8971
AMN, mg/dL	45.5	36.7	39.2	5.8	.3023	.2844
FAMN, ug/dL	111.9	82.9	96.7	21.7	.4982	.2790
Urea N, mg/dL	12.4	9.7	11.4	.8	.2322	.0069
L-Lactate, mg/dL	6.3	7.4	7.7	.5	.0084	.4298
15 Wk						
pH	6.28	6.32	6.25	.07	.6121	.3875
AMN, mg/dL	22.1	18.0	30.4	4.4	.0838	.0465
FAMN, μg/dL	42.4	27.1	77.3	18.4	.0825	.0604
Urea N, mg/dL	12.2	9.7	11.2	1.0	.3458	.0300
L-Lactate, mg/dL	6.6	9.0	7.4	.7	.2843	.0046

Table 6. Ruminal fluid sulfur metabolite concentrations (mg/L) in Alpine goats during the lactation trial

Item	Sulfur, %			SE	Probability <	
	.16	.26	.36		Linear	Quadratic
5 Wk						
Total-S	43.5	56.6	66.4	7.0	.0041	.7878
Sulfate-S	32.0	37.7	44.7	4.2	.0071	.8745
Organic-S	11.5	18.9	21.7	3.9	.0166	.5125
Protein-S	10.1	17.8	19.4	3.5	.0141	.3343
Sulfide-S	8.4	9.9	8.8	1.3	.7825	.2972
H_2S-S	6.4	7.1	6.4	.9	.9923	.4039
10 Wk						
Total-S	39.2	47.7	64.0	8.3	.0078	.6011
Sulfate-S	30.5	33.9	41.6	5.3	.0525	.6541
Organic-S	8.8	13.8	22.3	4.3	.0053	.6506
Protein-S	6.9	13.4	18.8	3.6	.0041	.8682
Sulfide-S	8.4	9.8	9.4	1.1	.3609	.3829
H_2S-S	5.9	6.6	6.4	.7	.4703	.4367
15 Wk						
Total-S	28.8	44.3	52.6	7.3	.0049	.5901
Sulfate-S	20.7	32.7	38.7	4.8	.0068	.3667
Organic-S	8.1	12.1	13.9	4.0	.0960	.9074
Protein-S	6.0	11.7	12.3	2.9	.0499	.3524
Sulfide-S	9.7	12.1	9.9	1.1	.8788	.0307
H_2S-S	7.2	9.0	7.2	.9	.9370	.0311

Table 7. Plasma sulfur metabolite concentrations (mg/L) in Alpine goats during the lactation trial

	Sulfur, %				Probability <	
Item	.16	.26	.36	SE	Linear	Quadratic
5 Wk						
Total S	59.1	77.7	98.9	7.9	.0001	.8572
Sulfate S	32.6	43.4	71.0	9.2	.0004	.3152
Organic S	5.2	14.6	10.2	2.0	.0264	.0010
10 Wk						
Total S	36.0	52.3	79.2	10.0	.0003	.5547
Sulfate S	32.6	43.4	71.0	9.2	.0004	.3152
Organic S	3.4	8.9	8.2	1.0	.0001	.0027
15 Wk						
Total S	47.8	51.1	58.6	8.0	.1995	.7673
Sulfate S	44.0	40.5	56.0	7.3	.1310	.1634
Organic S	3.8	10.5	2.7	1.2	.3996	.0001

Table 8. Blood pH and acid-base balance in Alpine goats during lactation trial

Item[a]	Sulfur, %			SE	Probability <	
	.16	.26	.36		Linear	Quadratic
5 Wk						
pH	7.38	7.36	7.38	.02	.7515	.2161
HCO_3^-, mM	26.4	25.3	25.2	.8	.1445	.5231
pCO_2, mmHg	43.7	44.1	41.5	1.6	.2023	.3022
pO_2, mmHg	39.8	37.2	39.6	1.9	.9133	.1371
BEb, m*M*	1.59	.21	.58	.97	.3190	.3207
BEecf, m*M*	1.18	-.27	-.09	1.04	.2403	.3846
CO_2ct, m*M*	27.7	26.7	26.4	.8	.1355	.5915
SBC, m*M*	25.4	24.2	24.7	.8	.3634	.2685
sO_2c, %	72.1	67.9	72.6	3.1	.8760	.1229
10 Wk						
pH	7.40	7.40	7.39	.02	.6338	.5309
HCO_3^-, m*M*	25.4	25.9	24.8	1.1	.5583	.3857
pCO_2, mmHg	40.7	41.2	40.3	1.2	.7923	.5178
pO_2, mmHg	39.3	40.9	42.9	2.5	.1615	.9414
BEb, m*M*	1.10	1.60	.43	1.12	.5632	.4055
BEecf, m*M*	.43	.99	-.34	1.25	.5545	.4010
CO_2ct, m*M*	26.7	27.2	26.0	1.1	.5646	.3905
SBC, m*M*	25.1	25.6	24.6	.9	.6128	.3868
sO_2c, %	74.2	76.6	76.2	4.2	.6400	.7131

(to be continued)

(Table 8 cont.)

15 Wk

pH	7.40	7.39	7.39	.01	.2186	.3620
HCO_3^-, m*M*	26.6	25.9	25.1	1.0	.1738	.9200
pCO_2, mmHg	42.3	42.7	41.0	1.3	.3304	.3569
pO_2, mmHg	39.8	39.3	39.5	2.7	.9382	.8704
BEb, m*M*	2.16	1.25	.60	1.02	.1601	.8904
BEecf, m*M*	1.66	.74	-.11	1.16	.1579	.9702
CO_2ct, m*M*	27.9	27.2	26.3	1.1	.1726	.8940
SBC, m*M*	25.9	25.1	24.7	.8	.1581	.8467
sO_2c, %	73.1	71.4	72.9	3.7	.9622	.6340

[a]BEb = base excess;
BEecf = base excess in extra-cellular fluid;
CO_2CT = total CO_2 content;
SBC = standard bicarbonate; and
sO_2c = oxygen saturation at P50.

Table 9. Body weight, body weight change, intakes of dry matter, and energy in Alpine goats during the metabolism trial

	Sulfur, %				Probability <	
Item	.16	.26	.36	SE	Linear	Quadratic
BW, kg	54.6	55.0	58.0	3.2	.4576	.7370
BW change, g/d	-36.4	-20.8	-33.4	12.7	.7459	.3640
Intake						
DM, Kg/d	1.72	1.86	1.73	.16	.9562	.4815
GE, Mcal/d	7.25	8.00	7.49	.67	.8004	.4653
DE, Mcal/d	4.22	4.64	4.58	.43	.5847	.6989
ME, Mcal/d	3.62	3.96	3.93	.37	.5613	.6894
ME, Mcal/(kgBW$^{\cdot 75}$.d)	.18	.20	.19	.13	.6847	.3436

Table 10. Apparent digestibilities (%) of nutrients in Alpine goats during the metabolism trial

Item	Sulfur, %			SE	Probability <	
	.16	.26	.36		Linear	Quadratic
DM	56.6	59.0	60.3	1.1	.0417	.7035
OM	57.6	59.2	61.2	1.3	.0739	.8835
Ash	41.4	46.8	56.1	2.5	.0390	.1663
ADF	16.8	26.0	29.2	2.1	.0020	.2561
GE	57.8	58.3	60.9	1.2	.0869	.4622
CP	72.3	69.9	72.6	1.0	.8130	.0614
S	48.6	70.1	76.2	1.7	.0001	.0044

Table 11. Nitrogen metabolism in Alpine goats during the metabolism trial

Item	Sulfur, %			SE	Probability <	
	.16	.26	.36		Linear	Quadratic
Intake, g/d	38.9	40.0	39.2	3.4	.8834	.5666
Feces, % of intake	27.7	30.1	27.4	1.0	.8130	.0614
Urine, % of intake	29.1	27.0	33.7	1.7	.0880	.0637
Milk, % of intake	27.8	26.8	27.4	2.8	.9204	.8082
Retention[a], % of intake	15.4	16.1	11.6	3.9	.5037	.5882
Absorbed N retained, % of absorbed N	21.2	23.0	15.9	5.4	.4999	.5163

[a]Retention = Intake - Feces - Urine - Milk.

Table 12. Sulfur metabolism (g/d) in Alpine goats during the metabolism trial

Item	Sulfur, %			SE	Probability <	
	.16	.26	.36		Linear	Quadratic
Intake	2.78	4.79	6.30	.388	.0001	.6076
Feces	1.32	1.41	1.50	.128	.3460	.9899
Urine	1.08	1.23	2.58	.411	.0297	.2638
Milk	.66	.69	.61	.059	.6196	.6373
Retention[a]	-.28	1.46	1.60	.318	.0024	.0701

[a]See footnote in Table 11.

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CHAPTER V

SULFATE SUPPLEMENTATION OF GROWING GOATS: I. EFFECTS ON PERFORMANCE, ACID-BASE BALANCE, AND NUTRIENT DIGESTIBILITIES

K. Qi[1,2], C. D. Lu[1], and F. N. Owens[2]

Langston University[1], Langston, OK 73050 and
Oklahoma State University[2], Stillwater 74078

ABSTRACT: Goat kids (20 Alpine, 12 Angora; male castrated) were individually fed isonitrogenous and isocaloric diets containing 2.28% N and S (added as $CaSO_4$) at either .11 (basal), .20, .28 or .38% of dietary DM. Sulfate supplementation during the 10-wk growth trial quadratically increased ADG ($P < .05$) and DMI ($P < .10$), and tended to quadratically increase ($P = .19$) feed efficiency (FE, ADG/DMI). Sulfate supplementation quadratically increased blood plasma concentrations of L-lactate, HCO_3^- and total CO_2 ($P < .10$), and urinary outputs of creatinine ($P < .10$) and uric acid ($P < .05$). However, sulfate supplementation did not significantly affect ($P > .20$) plasma sulfate, plasma cystine, ruminal NH_3-N concentrations or purine N

content of isolated ruminal bacteria. Sulfur balance increased linearly ($P < .001$) and fractional N retention increased quadratically ($P < .05$) with sulfate supplementation. Calculated by regression, the optimal dietary S content for ADG was .22% S (N:S = 10.4:1), for DMI it was .24% S (N:S = 9.5:1), for FE it was .21% S (N:S = 11.1:1), for N retention it was .23% (N:S = 9.9:1) and for absorbed N retained it was .22% (N:S = 10.4:1). These results support the NRC (1981) estimate of the S requirement of goats for growth (N:S = 10:1).

Key Words: Goat, Sulfur, Growth, Metabolite, Nitrogen, Acid-base balance.

Introduction

No information has been published concerning the S requirement for growth of goats. NRC (1981) extrapolated research results from sheep to goats and suggested that the N:S ratio should be 10:1. Because goats are different from sheep, extrapolation of sheep data to goats is a crude estimate at best and needs to be verified in goats (Haenlein, 1980). Dietary S level also may alter acid-base balance (Tucker et al., 1991). Therefore, in a continuing effort focus on the S requirement of goats (Qi et al., 1992a,b,c), a trial was conducted using goat kids to 1) determine the S requirement for growth; 2) evaluate the effects of dietary S concentration on acid-base balance and blood and ruminal metabolites; 3) quantify the impact of S supplementation on DMI and digestibilities of DM, OM and

ADF; and 4) monitor S metabolism and its effect on N utilization.

Materials and Methods

Animals and Diets. Goat kids were weaned at an age of 75 d and a BW of 17 Kg. One month after weaning (at 105 d of age), 32 castrated goat kids (20 Alpine, BW = 23.70 ± .99 Kg; 12 Angora, BW = 18.13 ± .61 Kg) were selected. These goats were blocked according to breed and age, and assigned randomly to one of four dietary treatments in a randomized complete block design (Cochran and Cox, 1957). The experiment was conducted from July to October, 1991. Animals were placed in steam-cleaned stainless steel cages (2.3 X 1.0 X 1.0 m) and housed in an open barn equipped with forced air ventilation. They had ad libitum access to their test diets. The first two weeks served as an adaptation phase for goat kids to overcome stress and adjust to their diet. Daily DMI and weekly BW of each goat was recorded from wk 3 to wk 10 of the growth monitoring phase. During wk 11 to 12, goat kids were transferred to metabolic crates for total collection of feces and urine to quantify digestibilities of DM, OM, ADF and ash, and retention of N and S.

The experimental diets (Table 1) were formulated to meet ME, CP, Ca and P requirements of growing goats according to NRC (1981), and were isonitrogenous and isocaloric, containing .11% (basal), .20%, .28%, or .38% S (DM basis).

Calcium sulfate served as the source of supplemented S, and was included to achieve N:S ratios of 21.4:1, 11.8:1, 8.2:1, and 6.0:1. Calcium intake from $CaSO_4$ was balanced by adding $CaCO_3$; SiO_2 was added to equalize the nutrient density among diets. Each diet was completely mixed (Weigh-Tronix, Fairmont, MN) to minimize particle size separation and to reduce sorting. Urea N accounted for 65% of the total N in the diet. The forage to concentrate ratio of the diet was 50:50. Dietary cation-anion balance, expressed as either meq((Na + K) - Cl)/100 g of diet DM (DCAB) or meq((Na + K) - (Cl + S))/100 g of diet DM (DCAB:S) was calculated (Tucker et al., 1991). Goat kids received fresh feed once daily (1330); fresh water was available continuously.

Sample Collection and Analysis. Feed samples were collected weekly and composited for analysis. Goats were weighed before fresh feed was provided on two consecutive days each week and at the beginning and the end of the collection phase of the metabolism trial. Blood samples were procured via jugular venipuncture 4 h postprandially during the wk 8 of the growth trial. At the end of the 10-wk growth trial, ruminal samples (60 mL) were collected 4 h postprandially via stomach tube. The first 20 to 30 mL of ruminal fluid were discarded to reduce contamination by saliva. Immediately after sampling, ruminal fluid pH was determined (SA-720, Orion Research, Boston, MA). The methods for preserving subsamples and analyzing total sulfide-S have been described previously (Qi et al., 1992a). About 40 mL

of ruminal fluid were mixed with 1 mL of saturated $HgCl_2$ to preserve them for analysis. At end of metabolism trial, ruminal samples were taken 0 and 4 h postprandially and composited (280 mL) for isolating bacteria. Immediately after collection, this ruminal fluid was centrifuged (Sorvall RC-5B, Du Pont, Wilmington, DE) at 500 X g for 10 min to remove the feed particles and protozoa; the supernatant fluid subsequently was centrifuged at 20,000 X g for 20 min to sediment bacteria (Lu et al., 1983). The supernatant fluid was discarded, and the bacterial pellet was washed twice with physiological saline (.9% NaCl), and once with distilled water. The washed bacteria were examined microscopically and found to be essentially free of contaminants. These bacterial pellets were lyophilized and contents of DM, purine, S and N were determined. These bacteria should represent the unattached or free bacteria in the rumen, not necessarily the total bacterial population.

Total feces and urine were collected for 7 d and composited for chemical analysis. Dry matter, OM, ash, and N contents of feed and feces and N contents of urinary and isolated bacteria were quantified (AOAC, 1990). Urinary creatinine and uric acid were analyzed using Sigma Kit 555 and Sigma Kit 292, respectively (Sigma Diagnostics, St. Louis, MO) on fresh urine samples. Gross energy contents of feed and feces were determined using an adiabatic bomb calorimeter (Parr Instrument, Moline, IL), and ADF contents

of feed and feces were determined (Goering and Van Soest, 1970).

Energy digestibilities of experimental diets measured during the metabolism trial were used to calculate DE intake during the growth trial. The ratio of ME to DE, assumed to be .82 (Santini et al., 1992), was used to calculate ME intake of four experimental diets during the growth trial.

Total S contents of feed, feces, urine, and isolated ruminal bacteria were determined by the procedure of Mottershead (1971). Sulfate-S contents of plasma and ruminal fluids were analyzed as described by Bird and Fountain (1970) in supernatant fluids that had been deproteinized (8% perchloric acid).

Blood samples for acid-base analyses were collected anaerobically into 10-mL evacuated blood collection tubes containing sodium heparin. These tubes were placed on ice and analyzed within 2 h after collection for blood pH, bicarbonate (HCO_3^-), pCO_2, pO_2, base excess, base excess in extra-cellular fluid, total CO_2 content, and standard bicarbonate and oxygen saturation using a blood gas analyzer (System 1304, Instrumentation Laboratory, Lexington, MA).

Ruminal bacteria isolated from ruminal fluid were analyzed for purine N content using the method of Zinn and Owens (1986) as modified by Aharoni and Tagari (1991). Ruminal fluid samples were dried and also analyzed for purine N content (hereafter referred to as total purine N). The difference between the total purine N content of ruminal

fluid and the purine N content of isolated bacteria was considered to be the sum of particle associated purine N plus feed purine N not degraded in the rumen (hereafter called residual purine N).

Plasma urea N was determined using Sigma Kit 640 (Sigma Diagnostics, St. Louis, MO). Plasma glucose was determined using Sigma kit 510 (Sigma Diagnostics, St. Louis, MO). Total ruminal ammonia N (AMN) was analyzed (Broderick and Kang, 1980). Ruminal fluid L-lactate was determined using Sigma Kit 826 (Sigma Diagnostics, St. Louis, MO). In addition, ruminal free, nonionized ammonia N (FAMN) was calculated as described by Visek (1968).

Ruminal nonionized, volatile sulfide-S (H_2S-S) was calculated from total sulfide-S (Qi et al., 1992a). The H_2S-S is an estimate of the amount of sulfide-S that could volatilize and be lost via eructation.

Plasma cysteine was analyzed by a colorimetric procedure (Gaitonde, 1967). Cystine was reduced to cysteine using dithiothreitol solution (5 μmoles). Free cysteine was analyzed as above prior to reduction of cystine. An alcohol solution of phenol red (.05%) was used as an indicator to adjust the pH of the reaction solution of cysteine and of acid ninhydrin reagents to a pH of 8.4 by dropwise addition of 1 *M* NaOH. Plasma cystine, calculated as the difference between total cysteine and free cysteine, was expressed as cysteine equivalents.

Feed was analyzed for Na, K, and Ca by atomic absorption spectroscopy (Perkin-Elmer, Norwalt, CT). Chloride was analyzed using Sigma Kit 461 (Sigma Diagnostics, St. Louis, MO), and phosphorus was analyzed by a colorimetric method (AOAC, 1990) using a spectrophotometer (Gilford Response Series UV-VIS, Chicago, IL).

Statistical Analysis. Data were analyzed according to the GLM procedure of SAS (1985). The model included the effects of block, breed, diet, breed by diet interaction, block by breed by diet interaction and the residual error. The residual mean square was used to test the three-way interaction of block by breed by diet. If this three-way interaction was significant ($P < .10$), its mean square was used to test the other effects. If it was not significant ($P > .10$), the three-way interaction and the residual were pooled and used as the error term. Weaning weight and weaning age served as covariates for ADG and DMI analyses. Because the dietary S levels were not equally spaced, polynomial regressions were used to detect linear, quadratic and cubic effects of experimental diets. Significance was declared at level of $P < .10$; $P < .20$ was interpreted to indicate a trend. Exact probability values are presented for all parameters analyzed.

Results and Discussion

Growth Trial.

During the 8-wk growth study, S supplementation quadratically increased ADG ($P < .05$), DMI ($P < .10$), and

tended to quadratically increase feed efficiency (FE, P = .19) (Table 2). According to fitted quadratic regression equations, the ADG was maximum at a dietary S level of .22% with a N:S ratio of 10.4:1 whereas the DMI was maximum at a dietary S level of .24% with a N:S ratio of 9.5:1. Feed efficiency was maximum at a dietary S level of .21% with a N:S ratio of 11.1:1. These values are quite comparable to the recommendation (N:S = 10:1) of NRC (1981).

Because no breed by diet interactions were significant (P > .20) in this experiment, the S requirements for ADG, DMI and FE on the percentage of dietary DM basis were assumed to be similar for Alpine and Angora kids. However, besides growth, Angora kids grew mohair (8.97 $\pm$ 1.05 g/d clean mohair). Qi et al. (1992a) reported that mohair growth of adult Angora goats was greatest with .267% S; that percentage is 20% more S than the amount apparently needed for growth observed in this experiment. Expressed as g/d, the optimal S intake for mohair growth was 3.1 g vs 2.3 g for weight gain. Differences between Alpine and Angora goats in S metabolism and effects of S supplementation on performance and metabolite concentrations have been discussed elsewhere (Qi et al., 1992d)

Sulfur supplementation did not affect (P > .20) blood pH (Table 3). However, S supplementation tended to quadratically increase (P < .20) blood HCO_3^-, total CO_2 content, and partial pressure of CO_2 (pCO_2). Although S supplementation does not change DCAB, it decreases DCAB:S;

in this study, the decrease was approximately 8.5 meq per 100 g of dietary DM (Table 1). This was smaller than the changes achieved by added S in the studies of Fredeen et al. (1988) and Tucker et al. (1991). Indeed, instead of increasing metabolic acidity, S supplementation at the optimal level for growth tended to decrease acidity as indicated by the higher blood HCO_3^- concentration. Quantitative information about base excess, base excess in extra-cellular fluids, standard bicarbonate, and oxygen saturation in growing kids under defined dietary DCAB and(or) DCAB:S conditions also is presented in Table 3. This information should permit fuller evaluation of effects of dietary S on metabolic acidity of growing goats in the future as suggested by Fredeen et al. (1988).

Sulfur supplementation linearly increased ($P < .05$) plasma glucose, and linearly and quadratically increased ($P < .10$) plasma L-lactate (Table 4). Sulfur supplementation did not affect ($P > .20$) plasma sulfate-S. These results differed from results with adult Angora goats (Qi et al., 1992a) and lactating Alpine goats (Qi et al., 1992b). This discrepancy presumably was due to differences in DMI and physiological dissimilarities between growing kids and adult goats and performance.

Sulfur supplementation did not affect ($P > .20$) plasma concentrations of cysteine plus cystine, cysteine and cystine although values tended to be higher for the medium S

levels than the low and high S levels (Table 4). Plasma urea N tended to be lowest for goats fed .20% S diet.

Before feeding, ruminal pH exhibited a cubic response ($P < .05$) to S supplementation (Table 5). However, four h postprandially, ruminal pH was similar ($P > .20$) with all levels of S supplementation. Ruminal fluid ammonia N was not affected ($P > .20$) by added S. Free, nonionized ammonia N in the rumen showed similar trends to ruminal ammonia N.

Sulfur supplementation affected ($P < .05$) ruminal fluid L-lactate in a cubic fashion (Table 5). No such effect was detected in either adult Angora goats (Qi et al., 1992a) or lactating Alpine goats (Qi et al., 1992b). This discrepancy might be attributed to differences in physiological characteristics of growing vs adult goats.

Sulfur supplementation linearly increased ($P < .10$) ruminal fluid sulfate-S and sulfide-S concentrations (Table 5), but S supplementation did not affect ($P > .20$) contents of total purine, purine of isolated bacteria and residual purine in the rumen. Because S supplementation quadratically increased DMI, passage rate also should have increased quadratically (Owens and Goetsch, 1986). With similar concentrations of ruminal bacteria per unit of fluid, bacterial protein yield should have been greatest for goats fed the medium S diet.

Metabolism Trial.

Sulfate supplementation quadratically increased ($P < .10$) intakes of DM, OM, GE, DE, ME (Table 6), and tended to

quadratically increase ($P < .20$) ME intake per metabolic BW. These results differed from that of previous research with adult Angora goats (Qi et al., 1992a) and lactating Alpine goats (Qi et al., 1992b) in which DMI was not affected by dietary concentration of S.

Apparent digestibilities of DM, OM, ash, ADF and GE (Table 6) were numerically lowest for goats fed the .20% S diet. Presumably, these values were lower due to higher DMI of the goats fed their .20% S diet. Yet, intake of digestible DM remained greater for goats fed the .20% S diet.

Sulfate supplementation linearly ($P < .0001$) and quadratically ($P < .10$) increased S intake, and linearly increased ($P < .01$) fecal S output (Table 7). This response in fecal S output differed from results with adult goats (Qi et al., 1992a, b) in which fecal S output was not changed by S supplementation. Sulfate supplementation linearly ($P < .0001$) and quadratically ($P < .01$) increased urinary S output, and linearly increased ($P < .01$) S retention. This increase in S retention with increased S intake can be ascribed partially to greater loss of gaseous sulfide-S with the higher S diets (Qi et al., 1992a,b). These losses were not measured in this experiment; hence, they became part of S retained. Sulfur supplementation did not affect ($P > .20$) the percent of intake S retained.

Absorbed S (Y, g/d) was regressed against ingested S (X, g/d) as suggested by Biddle et al. (1975). The regression

equation was: $Y = - .2608 + .8192 X$ ($r = .9991$, $P < .01$); this can be interpreted to mean that truly absorbed S was 81.9% of ingested S and metabolic fecal S loss was .261 g/d or 24.5 mg/(BWkg$^{\cdot 75}$.d).

Biological value of the ingested S and endogenous urinary S were estimated by regressing total urinary S output (Y, g/d) against truly absorbed S (X, g/d) as proposed by Biddle et al. (1975). The equation for this relationship was: $Y = - .1892 + .6720 X$ ($r = .9928$, $P < .01$) that can be interpreted to mean that the biological value of supplemental S was 32.8% (100% - 67.2%) and endogenous urinary S totaled .189 g/d or 17.8 mg/(BWkg$^{\cdot 75}$.d).

From these values for metabolic fecal S and endogenous urinary S, the amount of absorbed S needed for replacement of fecal and urinary loss (ignoring scurf and mohair needs), the amount required for maintenance of growing goat kids can be calculated. It was 450 mg/d or 42.3 mg/(BWkg$^{\cdot 75}$.d). On a basis of S intake S assuming a digestibility of 81.9%, the S requirement for maintenance was 549 mg/d or 51.6 mg/(BWkg$^{\cdot 75}$.d). This estimate was similar to that (540 mg/d) estimated by Joyce and Rettray (1970) for growing sheep of 20 to 30 kg BW but lower than the estimated need for growing sheep (1.4 g/d or 113.2 mg/BWkg$^{\cdot 75}$) proposed by Johnson et al. (1971) using radioactive S from sodium sulfate.

Sulfur supplementation increased (linearly, $P < .0001$; quadratically, $P < .05$) digestibility of dietary S.

Digestibility of dietary S was linearly partitioned into digestibility of S in the basal diet vs added S. Digestibility of S in the basal diet was 50.3 vs 79.4% for added S. The value for S added as $CaSO_4$ was very similar to that by adult Angora goats (78.1%; Qi et al., 1992a), but lower than by lactating Alpine goats (95.8%; Qi et al., 1992b).

Nitrogen intake and fecal N output increased quadratically ($P < .05$) with S supplementation as a result of changes in DMI (Table 8). Although N digestibility and urinary N output (g/d) were not affected by added S, N retention increased quadratically ($P < .05$) with S supplementation. Expressed as a percentage of N intake, fecal N was not affected ($P > .20$), but urinary N decreased quadratically ($P < .10$) with S supplementation. The percentage of absorbed N retained increased quadratically ($P < .05$) as S was supplemented. Based on fitted quadratic regression equations of N retention, percent of intake N retained, and percent of absorbed N retained against dietary S level, N retention was maximum at a dietary S level of .23% with a N:S ratio of 9.9:1, percent of intake N retained was maximum at a dietary S level of .21% with a N:S ratio of 11.1:1, and percent of absorbed N retained was maximum at a dietary S level of .22% with a N:S ratio of 10.4:1. These values were similar to the values calculated from ADG, DMI and FE. Qi et al. (1992a,b) also observed that efficiency of N utilization increased when S was added to a .16% S diet

for adult Angora goats and to a .16% S diet for lactating Alpine goats.

Urinary creatinine output was measured in the metabolism trial to evaluate lean tissue growth and metabolism in goat kids. Muscle tissue contains phosphocreatine that cyclizes spontaneously with loss of inorganic phosphate to form creatinine. Conversion of creatine to creatinine is a nonenzymatic, irreversible process that occurs at a rate of 1.6 to 2% of the total body content of creatine daily; turnover rate varies with dietary creatine intake, rate of synthesis of creatine, and muscle mass (Finco, 1989). Schroeder et al. (1988) found that urinary creatinine excretion was highly correlated to lean body mass ($r = .92$), empty body protein ($r = .90$) and skeletal muscle protein ($r = .87$) in beef steers.

Urinary creatinine concentration tended to increase quadratically ($P = .15$), and urinary creatinine output, expresed either in absolute units or per unit of body weight or metabolic body size, increased quadratically ($P < .10$) with S supplementation (Table 9). Creatinine output of our growing goat kids was much lower than that of adult West African Dwarf goats (Verstegen et al., 1991), but similar to Swedish Landrace goat kids (Lindberg, 1989). The quadratic increase in creatinine output could be interpreted to suggest that lean tissue mass was greater as a fraction of BW or metabolic size in goats fed optimal S diets.

Purine derivatives in the urine (uric acid, allantoin, xanthine and hypoxanthine) have been related quantitatively to the postruminal microbial protein supply in sheep (Chen et al., 1990b). According to Chen et al. (1990b, 1992), microbial purine was 83% digested and 84% of absorbed microbial purine was recovered in the urine; microbial N supply (g/d) was equal to .727 times the amount of microbial purine absorbed (mmole/d). We used urinary uric acid as an indirect index of microbial protein supply. Sulfate supplementation quadratically increased ($P < .10$) urinary uric acid concentration and uric acid output expressed as amount per day, per kg of BW or per kg of metabolic BW (Table 9).

The amount of microbial protein synthesized in the rumen generally is proportional to DMI of ruminants (Owens and Goetsch, 1986; Chen et al., 1992). Urinary uric acid output was highly correlated ($r = .55$) with DMI in this experiment. Chen et al. (1990a) found that the profile of purine derivatives excreted differed between sheep and cattle. The profile of urinary purine derivative excretion in goats has not been determined.

Implications

The optimal dietary sulfur level for maximum daily gain of goat kids was approximately .22% of dietary dry matter with a N:S ratio of 10:1. Sulfate supplementation tended to decrease metabolic acidity of growing kids. The improved

performance presumably was due to enhanced bacterial protein synthesis in the rumen and increased nitrogen utilization.

Table 1. Composition of experimental diets[a]

Item	Diet 1	2	3	4
Ingredient				
Ground peanut hulls	50.00	50.00	50.00	50.00
Corn starch[b]	37.40	37.40	37.40	37.40
Soybean meal	6.10	6.10	6.10	6.10
Urea	1.50	1.50	1.50	1.50
Na_2HPO_4	1.35	1.35	1.35	1.35
$CaCO_3$	.85	.53	.25	-
$CaSO_4$	-	.40	.80	1.15
Trace mineralized salt[c]	1.50	1.50	1.50	1.50
Vitamin A,D,E[d]	1.00	1.00	1.00	1.00
SiO_2	.30	.22	.10	-
Chemical Composition[e]				
GE, Mcal/kg	4.20	4.18	4.20	4.17
ME, Mcal/kg	1.80	1.67	1.72	1.70
N, %	2.28	2.28	2.27	2.29
S, %	.11	.20	.28	.38
N:S Ratio	21.27	11.69	8.20	5.99
ADF, %	29.77	29.62	31.98	30.41
Ash, %	6.65	6.66	6.69	6.93
Ca, %	.60	.62	.61	.62
P, %	.50	.49	.52	.51
Na, %	.97	.96	.98	.99
K, %	.57	.55	.58	.56
Cl, %	.75	.77	.76	.74

DCAB[f], meq/100 g	35.62	34.11	36.03	36.52
S, meq/100 g	3.35	6.08	8.68	11.91
DCAB:S[g], meq/100 g	32.27	28.03	27.35	24.61

[a]DM basis.

[b]Dyets, Bethlehem, PA.

[c]Containing (percentage): NaCl, 95.5 - 98.5; Mn, > .24; Fe, > .24; Mg, > .05; Cu, > .032; Co, > .011; I, > .007; Zn, > .005.

[d]Contained 2,200 IU of vitamin A; 1,200 IU of Vitamin D_3; 2.2 IU of vitamin E per gram.

[e]All values except ME were measured. Feed and fecal energies were measured; ME was calculated as DE X .82 (Santini et al., 1992).

[f]Dietary cation-anion balance was calculated as meq((Na + K) - Cl)/100 g of diet DM.

[g]Dietary cation-anion balance was calculated as meq((Na + K) - (Cl + S))/100 g of diet DM.

Table 2. Least squares means of average daily gain (ADG), dry matter intake (DMI), and feed efficiency (FE)

	Sulfur, %					Probability <		
Item	.11	.20	.28	.38	SE	Linear	Quadratic	Cubic
ADG[a], g/d	82.4	107.1	70.1	69.3	9.69	.1721	.0395	.1792
DMI[b], g/d	914.2	1050.5	901.7	907.5	51.87	.8490	.0671	.2915
FE[c], g ADG/Kg DMI	89.8	102.7	82.0	78.1	8.67	.1998	.1948	.4873

[a]ADG = 40.36 + 549.27 X - 1248.43 X^2, where X = dietary S level (% of DM);
[b]DMI = 666.48 + 3285.85 X - 6789.03 X^2, where X = dietary S level (% of DM);
[c]FE = 67.19 + 281.15 X - 681.35 X^2, where X = dietary S level (% of DM).

Table 3. Least squares means of blood pH and acid-base balance

Item[a]	Sulfur, %					Probability <		
	.11	.20	.28	.38	SE	Linear	Quadratic	Cubic
pH	7.38	7.38	7.39	7.39	.01	.3593	.9724	.8969
HCO_3^-, m*M*	23.54	22.86	25.18	23.79	.68	.5092	.1158	.1760
CO_2ct, m*M*	24.75	24.02	26.45	24.98	.70	.5198	.1034	.1690
pCO_2, mmHg	39.48	37.99	41.01	39.05	1.14	.9766	.1033	.2683
pO_2, mmHg	43.25	41.40	40.03	40.80	2.02	.4300	.4349	.7583
BEb, m*M*	-.84	-1.25	.79	-.39	.69	.4203	.2161	.2593
BEecf, m*M*	-1.79	-2.40	.08	-1.37	.78	.4539	.1731	.2195
SBC, m*M*	23.66	23.26	24.84	23.93	.55	.4855	.2806	.2387
sO_2c, %	76.72	75.03	73.94	74.09	2.78	.5609	.4561	.7103

[a]BEb = base excess;
BEecf = base excess in extra-cellular fluid;
CO_2ct = total CO_2 content;
SBC = standard bicarbonate; and
sO_2c = oxygen saturation at p50.

Table 4. Least squares means of plasma metabolites

Item	Sulfur, %				SE	Probability <		
	.11	.20	.28	.38		Linear	Quadratic	Cubic
Glucose, mg/dL	54.34	58.55	66.25	64.79	3.14	.0147	.1983	.9703
L-lactate, mg/dL	28.77	36.75	29.35	20.64	3.73	.0634	.0594	.3862
Sulfate-S, mg/L	138.60	131.98	134.90	132.32	5.25	.7026	.6864	.3379
Cysteine plus cystine[a], μM	14.44	15.58	16.49	15.17	1.07	.5861	.2910	.7634
Cysteine, μM	4.27	4.18	4.28	4.22	.24	.7639	.5911	.7354
Cystine[a], μM	10.18	11.39	12.21	10.96	1.04	.5288	.2274	.8156
Urea N, mg/dL	29.39	23.24	27.07	26.64	1.12	.1194	.1637	.1220

[a]Expressed as cysteine equivalents.

Table 5. Least squares means of ruminal metabolites

Item	Sulfur, %				SE	Probability <		
	.11	.20	.28	.38		Linear	Quadratic	Cubic
Ruminal pH								
0 h postprandially	6.97	6.60	7.04	6.63	.15	.2745	.7719	.0050
4 h postprandially	5.78	5.67	5.87	5.79	.14	.8204	.9693	.2016
L-lactate, mg/dL	32.33	25.31	34.60	33.12	4.27	.3706	.2347	.0376
Sulfate-S, mg/L	109.61	121.55	167.34	167.33	16.75	.0032	.6260	.3018
Sulfide-S, mg/L								
Total	1.95	3.51	3.53	3.86	.33	.0011	.0817	.0672
H_2S-S	1.67	3.18	2.93	3.28	.28	.0015	.0647	.0121
Ammonia N								
Total, mg/dL	34.14	27.74	30.71	34.00	4.63	.9036	.7056	.2946
NH_3-N, μg/dL	35.63	15.46	41.24	41.80	19.73	.6998	.9255	.2405

(to be continued)

(Table 5 cont.)

Purine N content, % of ruminal fluid (wt/wt)								
Total	.84	.81	.86	.78	.10	.9526	.8320	.5719
In isolated bacteria	.80	.64	.71	.74	.13	.9998	.5271	.4457
Residual	.05	.17	.15	.04	.06	.9274	.1269	.4371
Bacterial S, % of dry mass	.43	.43	.40	.48	.03	.4035	.1561	.7945
Bacterial N, % of dry mass	7.86	8.14	8.30	7.52	.49	.8783	.3866	.8422
Bacterial N:S ratio	18.83	19.41	21.11	16.12	1.61	.4866	.1808	.7340

Table 6. Least squares means of intakes and digestibilities during the metabolism trial

	Sulfur, %					Probability <		
Item	.11	.20	.28	.38	SE	Linear	Quadratic	Cubic
Intake								
DM, g/d	746.5	874.0	859.0	756.1	60.5	.8522	.0214	.8090
OM, g/d	692.4	810.7	796.4	699.0	56.0	.8757	.0204	.8103
Digestible OMI, g/d	358.2	393.9	398.8	347.9	34.7	.9176	.0783	.6501
GE, Mcal/d	3.40	3.96	3.91	3.42	.75	.9019	.0205	.8561
DE, Mcal/d	1.78	1.95	1.98	1.71	.17	.9255	.0606	.7629
ME, Mcal/d	1.46	1.60	1.63	1.40	.14	.9255	.0606	.7629
ME, Mcal/(kgBW$^{.75}$.d)	.14	.15	.15	.13	.013	.8939	.1432	.6128
Digestibility, %								
DM	52.05	47.79	49.58	49.45	1.54	.4364	.5663	.1659
OM	51.93	47.83	49.41	49.46	1.60	.4593	.5681	.2074
ADF	11.85	9.24	10.21	10.11	2.78	.9527	.5710	.7017
Ash	53.48	47.21	51.76	49.30	2.03	.4753	.7998	.0672
GE	52.57	48.61	50.06	49.75	1.51	.3445	.6581	.1745

Table 7. Least squares means of sulfur metabolism during the metabolism trial

	Sulfur, %					Probability <		
Item	.11	.20	.28	.38	SE	Linear	Quadratic	Cubic
Intake, g/d	.80	1.71	2.39	2.89	.16	.0001	.0772	.9326
Fecal output, g/d	.38	.59	.72	.75	.07	.0021	.1390	.8837
Digestibility, %	50.27	65.09	67.89	74.32	1.91	.0001	.0204	.0996
Urinary output, g/d	.21	.66	1.13	1.44	.05	.0001	.0023	.1548
Retention, g/d	.20	.45	.54	.69	.09	.0006	.9158	.5736
Intake S retained, %	25.52	27.55	23.43	23.32	3.44	.5048	.6275	.5122
Absorbed S retained %	52.23	42.68	35.57	32.10	5.24	.0235	.2460	.8558

Table 8. Least squares means of nitrogen metabolism during the metabolism trial

Item	Sulfur, %				SE	Probability <		
	.11	.20	.28	.38		Linear	Quadratic	Cubic
Intake, g/d	17.14	20.04	19.70	17.34	1.387	.8612	.0218	.8126
Fecal output, g/d	5.67	6.57	6.62	5.79	.518	.8512	.0431	.9689
Digestibility, %	67.37	67.16	66.57	66.58	1.086	.6642	.9851	.7749
Urinary output, g/d	7.82	8.79	7.69	8.85	.929	.2828	.8512	.2299
Retention[a], g/d	3.64	4.69	5.39	2.70	.909	.3457	.0120	.3683
Percentage of intake								
Fecal output	32.63	32.84	33.43	33.42	1.089	.6642	.9851	.7749
Urinary output	44.66	43.87	37.69	49.84	3.67	.2057	.0300	.1338
Retention[b]	22.71	23.30	28.88	16.74	3.73	.1729	.0332	.1628
Absorbed N retained[c], %	33.37	34.63	43.41	25.23	5.492	.1921	.0284	.1527

[a]N retention (g/d) = 1.76 + 62.25 X - 137.15 X^2, where X = dietary S level (% of DM);
[b]N retention (% of N intake) = 4.99 + 190.58 X - 445.74 X^2, where X = dietary S level (% of DM);
[c]Absorbed N retained (%) = 6.22 + 293.14 X - 678.76 X^2, where X = dietary S level (% of DM).

Table 9. Least squares means of urinary creatinine and uric acid output during the metabolism trial

Item	Sulfur, %				SE	Probability <		
	.11	.20	.28	.38		Linear	Quadratic	Cubic
Creatinine concentration, mg/dL	2.93	8.63	5.02	2.99	2.33	.8416	.1489	.4041
Creatinine output, mg/d	15.38	36.30	32.38	17.50	16.56	.8542	.0986	.9749
Creatinine output, mg/BWKg	.65	1.50	1.33	.73	.63	.8433	.1028	.9894
Creatinine output, mg/BWKg$^{.75}$	1.42	3.32	2.95	1.62	1.43	.8447	.1017	.9964
Uric acid concentration, mg/dL	8.18	17.92	9.98	8.98	2.04	.7802	.0813	.0673
Uric acid output, mg/d	47.36	108.76	67.16	61.51	11.44	.5331	.0016	.0218
Uric acid output, mg/BWKg	1.98	4.48	2.73	2.55	.47	.5725	.0039	.0328
Uric acid output, mg/BWKg$^{.75}$	4.37	9.92	6.07	5.64	1.05	.5590	.0031	.0297

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CHAPTER VI

SULFATE SUPPLEMENTATION OF GROWING GOATS: II. EFFECTS ON PERFORMANCE, ACID-BASE BALANCE, RUMINAL MICROBES, AND NUTRIENT METABOLISM IN ANGORA AND ALPINE KIDS

K. Qi[1,2], C. D. Lu[1], and F. N. Owens[2]

Langston University[1], Langston, OK 73050 and
Oklahoma State University[2], Stillwater 74078

ABSTRACT: Twelve Angora goat kids (BW ± SE = 18.1 ± 0.6 Kg; castrated males) and 20 Alpine goat kids (23.7 ± 1.0 kg) were individually fed isonitrogenous and isocaloric diets containing 2.28% N and either .11 (basal), .20, .28 or .38% S (added as $CaSO_4$). Sulfate supplementation of the basal diet to .20% S numerically increased ADG, DMI, and feed efficiency (gain/feed, g/kg) of Angora kids during 10-wk growth trial. Clean mohair production was not affected ($P > .20$) by added S, but mohair staple length tended to increase quadratically ($P < .20$) with sulfate supplementation. Average daily gain ($P < .05$) and DMI ($P < .0001$) were lower for Angora than for Alpine kids (69.7 g/d and 94.7 g/d,

respectively), but FE did not differ ($P > .20$) between breeds. Blood pH values did not differ between breeds. Blood HCO_3^-, total CO_2 content, pCO_2, base excess, base excess in extra-cellular fluids, and standard bicarbonate were lower ($P < .05$) for Angora than for Alpine kids, but blood partial pressure of O_2 and oxygen saturation were higher ($P < .05$) for Angora than for Alpine kids). Plasma glucose was lower, and plasma free cysteine concentration was higher ($P < .01$) for Angora than for Alpine kids. Ruminal L-lactate concentration ($P < .001$) and purine N content in isolated bacteria ($P < .01$) were lower, but ruminal NH_3-N ($P < .10$) and sulfide-S contents tended to be higher ($P < .20$) for Angora than for Alpine kids. Angora kids were faunated whereas Alpine kids were defaunated in this experiment. Sulfate supplementation did not affect ($P > .20$) the ruminal concentration of protozoa in Angora kids. The N:S ratio in isolated ruminal bacteria was lower ($P < .10$) for Angora than for Alpine kids. Calculated by regression, ADG was maximum with .22% S (N:S = 10.4:1) for Angora kids, and with .21% (N:S = 10.9:1) for Alpine kids. These results substantiate the S requirement for growth of goats (N:S = 10) recommended by NRC (1981).

Introduction

Sulfur metabolism and requirements of adult Angora goats and lactating Alpine goats were evaluated previously (Qi et al., 1992a,b). Differences between Angora goats and Alpine goats were detected in S metabolism and requirements and in

plasma and ruminal metabolite responses to added S in those trial. However, because experimental diet and management were confounded with time and the effects of sulfate supplementation, results could not be compared directly. Therefore, we conducted an additional trial using 12 Angora kids and 20 Alpine kids simultaneously to 1) determine and compare the S requirement for growth between Alpine and Angora kids; 2) evaluate the effects of dietary S levels on acid-base balance, blood and ruminal metabolites in these two breeds of goat kids; 3) quantify the impact of S supplementation on DMI and digestibilities of DM, OM and ADF in these two breeds of goat kids; and 4) compare the metabolic responses between Alpine and Angora goat kids to S supplementation. The methods for determination of the S requirement and evaluation of the plasma and ruminal metabolites were presented previously (Qi et al., 1992c). This paper will focus on the effects of sulfate supplementation in Angora kids and the differences in response between Angora and Alpine kids to sulfate supplementation.

Materials and Methods

Animals and Diets. Goat kids were castrated three weeks after birth and weaned at the age of 75 d and 17 Kg of BW. One month after weaning, 12 Angora kids (18.1 $\pm$ .6 Kg) and 20 Alpine kids (23.7 $\pm$ 1.0 Kg) were selected. These goats kids were blocked according to breed and age, and randomly assigned to one of four diets in a randomized complete block

(2 blocks) design (Cochran and Cox, 1957) with three Angora and five Alpine goats fed each diet in each block.

Compositions of the diets, the management procedures, and the method for collection and analysis of feces and urine were presented previously (Qi et al., 1992c).

The methods for collection and analyses of feed, blood and ruminal samples also were presented previously (Qi et al., 1992c). For fixing, staining and counting protozoa, two mL of fresh ruminal fluid from ruminal fluid sample of each goat were transferred to bottles (1 mL per bottle) containing 24 mL of methylgreen-formalin-saline solution (Ogimoto and Imai, 1981); protozoa were counted using an Olympus microscope (BHA model, Olympus, Lake Success, NY) and a Petroff-Hausser bacteria counter (Hausser Scientific, Blue Bell, PA). Microscopic examination of ruminal samples revealed that the Angora kids were faunated but that the Alpine kids were fauna-free.

Angora kids were totally sheared with an animal clipper (Model EW610, Sunbeam, Milwaukee, WI) before and after the growth phase (8 wks). Mohair was weighed and evaluated for grease fleece weight, laboratory scoured yield (ASTM, 1990a), clean fleece weight and staple length (ASTM, 1990b).

Statistical Analysis. Data were analyzed according to GLM procedure of SAS (1985). The analysis for Angora kids was conducted with the effects of block, diet, and the block by diet interaction in the model. The residual mean square was used to test the interaction of block by diet. If this two-

two-way interaction was significant ($P < .10$), its mean square was used to test the other effects. If the interaction was not significant ($P > .10$), the two-way interaction and residual were pooled and used as the error term. Weaning weight served as a covariate for ADG and DMI analyses. Because the dietary S levels were not equally spaced, polynomial regressions were used to detect linear, quadratic and cubic effects of S concentration in the diet. The comparison of breed effect was conducted using the overall model of analysis (Qi et al., 1992c). Difference was declared when $P < .10$, whereas $P < .20$ was interpreted to indicated a trend.

Results and Discussion

Growth Trial.

During the 8-wk growth phase, ADG, DMI, and feed efficiency (gain/feed, g/kg) (Table 1) were numerically highest for the Angora kids fed .20% S diet. According to the fitted quadratic regression equation, ADG was maximum at a dietary S level of .22% which is equivalent to a N:S ratio of 10.4:1; DMI was maximum at a dietary S level of .16% or a N:S ratio of 14.3:1; feed efficiency was maximum at a dietary S level of .24% or a N:S ratio of 9.5:1. When averaged, these values equal .21% S of dietary DM or a N:S ratio of 10.9:1. This estimate is quite similar to the recommendation (N:S = 10:1) of NRC (1981). Clean mohair production was numerically higher for Angora kids fed the .28% S diet. Mohair staple length tended to increase

quadratically ($P < .20$) (Table 1) with sulfate supplementation. These responses by Angora kids differed from those by adult Angora goats (Qi et al., 1992a); in adults, sulfate supplementation did not affect BW gain and DMI, but quadratically increased mohair production. The S requirement for mohair growth of the adult Angora goats was estimated at .267% of dietary DM. This difference presumably is due to differences in the priority of partitioning nutrients to BW gain versus mohair growth. The BW of the Angora kids used in this trial averaged less than half that of the BW of adult Angora goats (Qi et al., 1992a) even though mohair production by the Angora kids was 80% that by the adult Angora goats. The S intake for maximum mohair growth was 3.1 g/d in the adult Angora goats versus 1.7 g/d for maximum BW gain in the Angora kids.

Sulfate supplementation did not affect ($P > .20$) blood pH (Table 2). However, S supplementation tended to cubically increase ($P < .20$) blood HCO_3^-; added S cubically increased ($P < .10$) total CO_2 content and partial pressure of CO_2. These cubic trends also were found in blood base excess, base excess in extra-cellular fluids, standard bicarbonate, and oxygen saturation. In all cases, numerical values were lowest for Angora kids fed the .20% S diet.

Sulfate supplementation tended to linearly increase ($P < .20$) plasma glucose concentration (Table 3). Sulfate supplementation linearly increased ($P < .10$) plasma sulfate-S, and quadratically increased ($P < .10$) plasma L-lactate

concentrations. Sulfate supplementation tended to quadratically increase ($P < .20$) plasma total cysteine and cystine concentrations, but sulfate supplementation did not affect ($P > .20$) free cysteine concentration of blood plasma. Plasma urea N responded cubically ($P < .10$) to sulfate supplementation.

Sulfate supplementation did not affect ruminal pH, but ruminal pH was higher ($P < .05$) before feeding than 4 h postprandially (Table 4). Before feeding, ruminal concentration of protozoa was numerically lower for goats fed the .20% S diet; however, four h postprandially, ruminal concentration of protozoa was numerically higher for goats fed this diet. Patton et al. (1970) found that sheep wethers fed a concentrate diet had more ruminal protozoa when they received methionine hydroxy analog (MHA, another S source) supplemented at 11 g/kg of dietary DM.

Sulfate supplementation did not affect ($P > .20$) ruminal fluid L-lactate concentration (Table 5), but it tended to linearly increase ($P < .20$) ruminal fluid sulfide-S concentration. Sulfate supplementation linearly increased ($P < .01$) the ruminal sulfide-S and free, non-ionized (H_2S) sulfide-S concentration.

Ruminal fluid ammonia N tended to decrease quadratically ($P < .20$) with sulfate supplementation (Table 5). Because both total ammonia N and pH tended to be lower, the free, nonionized (NH_3) ammonia N in the rumen was numerically lowest for goat kids fed .20% S diet.

Sulfate supplementation did not affect (P > .20) ruminal total purine N, purine N content of isolated bacteria or residual purine N content (Table 5). Sulfate supplementation did not affect (P > .20) S content of isolated bacteria, but linearly decreased (P < .05) their N content. As a result, the bacterial N:S ratio tended to decrease linearly (P < .20) with sulfate supplementation.

Metabolism Trial.

During the metabolism trial (wk 11 to wk 12 following the growth trial), sulfate supplementation did not significantly affect (P > .20) intakes of DM, OM, digestible OM, GE, DE, ME and ME per metabolic BW (Table 6), although values again tended to be highest for Angora kids fed the .20% S diet.

Apparent digestibilities of DM, OM, GE, and ash tended to decrease quadratically (P < .20) with sulfate supplementation (Table 6). Presumably, these decreases were due to higher DMI of the goats fed the diets supplemented with an optimal amount of S. Sulfate supplementation did not significantly affect (P > .20) ADF digestibility, but it was low for all diets, probably due to the low ruminal pH (Table 4).

Sulfate supplementation linearly increased S intake (P < .01), and fecal S output (P < .05) (Table 7). This response in fecal S output differed from results with adult Angora goats (Qi et al., 1992a), in which fecal S output was not affected by added S.

Sulfate supplementation linearly increased ($P < .01$) apparent digestibility of dietary S (Table 7). Partitioned by linear regression into S from the basal diet versus added S, digestibility of S was 45% for the basal dietary S versus 70% for S added as calcium sulfate. This value for added S was slightly lower than we observed for adult Angora goats (78.1%; Qi et al., 1992a).

Sulfate supplementation linearly increased urinary S output ($P < .0001$), S retention ($P < .01$), and absorbed S retained ($P < .001$) (Table 7). Mohair S yield was not significantly affected by sulfate supplementation.

Nitrogen intake was numerically highest for Angora kids fed .20% S diet (Table 8) because feed intake tended to be highest with this diet. Fecal N output tended to increase linearly ($P < .20$) with sulfate supplementation. Nitrogen digestibility, urinary N output, N retention and mohair N yield were not affected ($P > .20$) by sulfate supplementation. Expressed as a percentage of N intake, N metabolism was not significantly affected ($P > .20$) by sulfate supplementation.

Urinary creatinine concentration and output, expressed as absolute units or per unit body weight or metabolic size tended to increase quadratically ($P < .20$) with S supplementation (Table 9). The quadratic trend in creatinine output might be interpreted to indicate that lean tissue mass was greater in Angora kids fed optimal amount of S.

Sulfate supplementation quadratically increased ($P < .05$) urinary uric acid concentration, and tended to quadratically increase ($P < .20$) uric acid output expressed either as amount per kg of BW or per kg of metabolic BW (Table 9).

Comparisons of Angora Kids with Alpine Kids.

No diet by breed interactions were detected ($P > .10$). Thus, means of the two breeds were compared. Average daily gain (ADG) and DMI were lower ($P < .01$) for Angora than Alpine kids (Table 10). However, feed efficiency was similar ($P > .20$) between two breeds. Because Angora kids deposited 8.97 $\pm$ 1.05 g/d of clean mohair, total efficiency of energy utilization would tend to be higher for Angora than Alpine kids.

Blood pH did not differ ($P > .20$) between two breeds (Table 10). However, the other criteria for blood acid-base balance were different ($P < .05$) between two breeds. Blood HCO_3^-, total CO_2 content, partial pressure of CO_2, base excess, base excess in extra-cellular fluids, and standard bicarbonate were lower ($P < .05$) for Angora than for Alpine kids, but blood partial pressure of O_2 and oxygen saturation were higher ($P < .01$) for Angora than for Alpine kids. Perhaps the greater hair cover in Angora goats reduce surface heat loss so that Angora goats develop respiration system to dispatch the metabolic heat and result in lower base excess of blood.

Blood plasma glucose concentration was lower ($P < .001$) for Angora than for Alpine kids (Table 11), possibly reflecting lower DMI. Blood plasma cysteine was higher ($P < .01$) for Angora than for Alpine kids. Plasma L-lactate, sulfate-S, cysteine plus cystine, cystine and urea N were not significantly different ($P > .20$) between two breeds.

Ruminal pH values at both sampling times were higher ($P < .05$) for Angora than for Alpine kids (Table 12), but ruminal fluid L-lactate concentration was lower ($P < .0001$) for Angora than for Alpine kids (Table 13). These differences can be ascribed to lower feed intake by the Angora kids or differences in ruminal protozoa number. Angora kids were faunated whereas the Alpine kids were fauna-free in this experiment, possibly due to isolation of the Alpine kids from adult goats. Protozoa, by engulfing starch particles to reduce starch fermentation rate, can stabilize pH and decrease the ruminal L-lactate concentration (Veira, 1986). The concentrations of ruminal ammonia N ($P < .10$) and sulfide-S ($P < .20$) tended to be higher in Angora than in Alpine kids. These increases presumably were due to presence of protozoa in the rumen of Angora kids. Ivan (1988) reported that when ruminal protozoa were present, both ruminal ammonia N and sulfide-S concentrations were increased, presumably due to greater proteolytic activity of the ruminal microflora.

Ruminal total purine N content and purine N content of isolated bacteria were not significantly different ($P > .20$)

between two breeds (Table 13). However, residual purine N content in the rumen was lower ($P < .001$) for Angora than for Alpine kids. Again, this difference in ruminal residual purine N content can be ascribed to presence of protozoa in the rumen of Angora kids. Protozoa attach to particles in the rumen and would be removed from ruminal fluid by centrifugation during isolation of bacteria. On this basis, 8% ruminal purine could have been present as protozoa and only 9% as firmly attached bacteria. Ruminal bacterial N content was not different ($P > .20$) between two breeds, but ruminal S content of the isolated bacteria was higher for Angora than for Alpine kids. As a result, the N:S ratio of isolated bacteria tended to be lower ($P < .20$) for Angora than for Alpine kids.

During the metabolism trial, intakes of DM, OM, GE, DE, ME and ME per metabolic BW again were lower ($P < .10$) for Angora than for Alpine kids (Table 14). However, digestibilities of GE, DM, OM, and ADF were not different ($P > .20$) between two breeds. Ash digestibility tended to be lower ($P < .20$) for Angora than for Alpine kids.

Sulfur intake and urinary S output were lower ($P < .0001$) for Angora than for Alpine kids (Table 15) because DMI was less. Apparent S digestibility was lower ($P < .0001$) for Angora than for Alpine kids because the proportion of metabolic fecal S in total facal S was higher for Angora than for Alpine kids (data not shown). However, S retention was identical for the two breeds. Efficiency of

S retention was higher ($P < .05$) for Angora than for Alpine kids. Because Angora kids also grew a mean of 8.97 g/d clean mohair, and mohair contains about 3.12% S, approximately 50% of retained S was deposited in mohair by Angora kids.

Because DMI was lower, nitrogen intake and urinary N output were lower ($P < .0001$) for Angora than for Alpine kids (Table 15). However, unlike S digestibility, N digestibility was not affected ($P > .20$) by breeds. Lower urinary N output by Angora kids resulted in higher ($P < .10$) N retention by Angora than by Alpine kids, largely ascribable to retention of N in mohair. As a percentage of N intake, fecal N output was similar, but urinary N output was lower for Angora than for Alpine kids. The percentage of absorbed N retained was more than twice as great ($P < .0001$) for Angora than for Alpine kids.

Urinary creatinine concentration was numerically higher for Angora than for Alpine kids, but urinary creatinine output was numerically lower for Angora than for Alpine kids (Table 16). Urinary uric acid concentration and output were lower ($P < .05$) for Angora than for Alpine kids (Table 16).

The Alpine kids were fauna-free due to their isolation. Angora kids were allowed to nurse from birth to weaning at 75 days of age whereas Alpine kids were moved to their cages (steam-cleaned, stainless steel cage) and fed pasteurized milk to 75 days of age. One week postweaning (at 82 days of age), they were moved to a fenced pasture for 3 wks until

they were returned to steam-cleaned stainless steel cages for this experiment. These Alpine kids were never mixed with adult goats and remained fauna-free until the end of the growth monitoring phase. Two of the 20 Alpine kids (no. 24 and no. 31) had protozoa present, presumably due to accidental contact with adult goats.

The metabolic differences between Angora kids and Alpine kids were surprisingly large. However, differences cannot be fully ascribed to physiological dissimilarities because Alpine kids were largely fauna-free. Presence of protozoa in the rumen of Angora kids can explain their higher ruminal ammonia N and sulfide S concentration (Table 12). Angora kids also proved more difficult to adapt to their experimental diets than did Alpine kids. Eight of the original 20 Angora kids refused to eat their diets and were removed from the experiment compared with only 1 Alpine kid. This Alpine kid finally became adapted to its diet and finished the experiment.

Implications

The optimal dietary sulfur level for maximum daily gain of Angora kids was approximately .21% of dietary dry matter for a N:S ratio of 10.9:1, similar to that of Alpine kids (.22% S) in the percentage of dietary DM basis. The performance of Angora kids tended to increase quadratically with sulfate supplementation due to enhanced bacterial protein synthesis in the rumen. The performance and nutrient metabolism of Angora and Alpine kids were differed

substantially partially because of inherent physiological dissimilarities and partially due to environmental effects (fauna-free vs faunated). Some of the specific and breed difference reported in the literature may be due to presence or absence of specific types of ruminal microbes.

Table 1. Least squares means of average daily gain (ADG), dry matter intake (DMI), and feed efficiency (Gain/Feed) in Angora kids

Item	Sulfur, %					Probability		
	.11	.20	.28	.38	SE	Linear	Quadratic	Cubic
ADG[a], g/d	66.96	89.29	59.23	59.53	14.74	.5314	.3700	.4150
DMI[b], g/d	757.59	849.56	733.56	689.23	57.34	.2090	.5830	.1616
Gain/Feed[c], g/Kg	88.00	105.53	83.30	86.44	18.91	.8935	.4524	.8321
Grease mohair production g/d	16.81	17.12	16.96	15.30	4.19	.4938	.8965	.7782
Mohair yield[d], %	55.72	55.41	56.76	56.28	.03	.8759	.8003	.9330
Clean mohair production g/d	9.28	9.53	9.67	8.50	1.05	.5039	.9062	.7107
Mohair staple length, mm/d	.879	.986	1.001	.860	.006	.6753	.1904	.5907

[a]ADG = 39.13 + 363.57 X - 821.62 X^2, where X is the dietary S level (% of dietary DM);
[b]DMI = 723.96 + 643.94 X - 1991.57 X^2, where X is the dietary S level (% of dietary DM);
[c]Gain/Feed = 53.64 + 419.33 X - 876.30 X^2, where X is the dietary S level (% of dietary DM);
[d]Standard moisture regain used is 13.87%.

Table 2. Least squares means of blood pH and acid-base balance in Angora goats

Item[a]	Sulfur, %				SE	Probability		
	.11	.20	.28	.38		Linear	Quadratic	Cubic
pH	7.38	7.39	7.39	7.39	.01	.4683	.8668	.7656
HCO_3^-, m*M*	22.50	20.25	24.05	22.43	1.00	.7344	.9887	.1007
CO_2, m*M*	23.68	21.25	25.27	23.53	1.04	.7603	.9924	.0942
pCO_2, mmHg	37.78	33.20	39.51	36.55	1.43	.9601	.9385	.0491
pO_2, mmHg	47.00	45.50	40.50	43.50	3.46	.5115	.8149	.8684
BEb, m*M*	-1.65	-3.20	.17	-1.43	.92	.6376	.9404	.1602
BEecf, m*M*	-2.80	-4.95	-1.12	-2.70	1.09	.6860	.9815	.1332
SBC, m*M*	23.15	21.90	24.12	23.20	.69	.7092	.9544	.1529
sO_2c, %	80.85	81.30	75.52	77.30	3.63	.4998	.9871	.7418

[a] CO_2 = total CO_2 content;
pCO_2 = partial pressure of carbon dioxide;
pO_2 = partial pressure of oxygen;
BEb = base excess;
BEecf = base excess in extra-cellular fluid;
SBC = standard bicarbonate; and
sO_2c = oxygen saturation at p50.

Table 3. Least squares means of blood plasma metabolites in Angora kids

Item	Sulfur, %				SE	Probability		
	.11	.20	.28	.38		Linear	Quadratic	Cubic
Glucose, mg/dL	45.68	49.65	63.44	58.40	6.90	.1109	.4814	.4388
L-lactate, mg/dL	24.83	38.65	26.95	19.55	3.91	.1475	.0303	.1434
Sulfate-S, mg/L	124.08	123.08	130.05	145.48	8.23	.0578	.4837	.7381
Cysteine plus cystine[a], *μM*	13.00	16.09	17.08	15.03	1.56	.2242	.1087	.8046
Cysteine, *μM*	4.27	4.57	5.10	4.81	.38	.2259	.6033	.8307
Cystine[a], *μM*	8.73	11.53	11.98	10.49	1.52	.3330	.1231	.8402
Urea N, mg/dL	29.18	19.14	29.44	27.52	2.08	.9104	.2074	.0063

[a]Expressed as cysteine equivalent.

Table 4. Least squares means of ruminal pH and protozoa density in Angora kids

Item	Sulfur, %				SE	Probability		
	.11	.20	.28	.38		Linear	Quadratic	Cubic
Ruminal pH								
0 h postprandially	7.14	7.08	7.89	7.19	.30	.2338	.5150	.8073
4 h postprandially	6.07	5.90	6.20	6.00	.23	.9349	.5158	.9130
Ruminal Protozoa, thousand/mL								
0 h postprandially	55.1	33.8	52.7	78.2	41.7	.6968	.9114	.5857
4 h postprandially	83.1	102.5	38.9	48.0	38.6	.3528	.6983	.6127

Table 5. Least squares means of ruminal metabolites in Angora kids

Item	Sulfur, %					Probability		
	.11	.20	.28	.38	SE	Linear	Quadratic	Cubic
L-lactate, mg/dL	14.20	16.10	13.28	21.91	4.05	.2485	.9423	.9573
Sulfate-S, mg/L	110.75	122.85	172.57	138.21	18.79	.1490	.3851	.3935
Sulfide-S, mg/L								
Total	2.23	3.38	4.46	4.38	.45	.0043	.3230	.9070
H_2S-S	1.75	2.92	3.48	3.55	.41	.0079	.1805	.9778
Ammonia N								
Total, mg/dL	39.25	30.83	31.45	43.13	4.89	.6727	.1140	.7587
NH_3-N, μg/dL	60.96	22.40	60.69	64.62	34.00	.7725	.2520	.9523

(to be continued)

(Table 5 cont.)

Purine N, % of ruminal fluid (wt/wt)								
Total	.89	.85	.77	.66	.14	.2187	.7258	.9323
In isolated bacteria	.85	.73	.61	.66	.20	.4068	.8176	.9804
Residual	.04	.12	.16	.01	.07	.8017	.2161	.9204
Bacterial S, % of dry mass	.46	.45	.44	.51	.04	.4958	.2647	.4668
Bacterial N, % of day mass	8.08	8.16	7.91	7.19	.28	.0405	.4017	.7028
Bacterial N:S ratio	18.44	18.11	18.79	14.29	1.99	.1574	.2250	.4164

Table 6. Least squares means of nutrient intakes in Angora kids during the metabolism trial

Item	Sulfur, %				SE	Probability		
	.11	.20	.28	.38		Linear	Quadratic	Cubic
Intake								
DM, g/d	544.12	780.62	655.36	704.58	106.52	.3339	.3330	.4233
OM, g/d	504.73	724.12	607.69	651.45	98.63	.3404	.3284	.4235
Digestible OM Intake, g/d	269.48	347.77	278.45	323.24	60.01	.6145	.6438	.5299
GE, Mcal/d	2.48	3.54	2.98	3.18	.48	.3483	.3301	.4356
DE, Mcal/d	1.34	1.73	1.39	1.59	.30	.6425	.6220	.5336
ME, Mcal/d	1.01	1.42	1.14	1.31	.24	.6425	.6220	.5336
ME, Mcal/(kgBW$^{\cdot 75}$.d)	.12	.15	.12	.14	.024	.6287	.5405	.4724
Digestibility, %								
DM	54.38	46.55	46.01	49.18	2.50	.1816	.1307	.6088
OM	53.33	46.70	45.78	49.43	2.62	.2181	.1424	.6754
GE	54.08	47.72	46.61	49.74	2.51	.1649	.1528	.6941
Ash	53.99	44.81	48.81	46.08	3.25	.2213	.1917	.2789
ADF	11.84	9.22	10.24	10.23	3.29	.3076	.2335	.2817

Table 7. Least square means of sulfur metabolism in Angora kids during the metabolism trial

Item	Sulfur, %					Probability		
	.11	.20	.28	.38	SE	Linear	Quadratic	Cubic
Intake, g/d	.58	1.52	1.83	2.68	.34	.0015	.6805	.6571
Fecal output, g/d	.32	.59	.73	.93	.17	.0226	.6484	.9982
Digestibility, %	44.9	61.6	60.5	66.7	3.9	.0028	.2698	.1820
Urinary output, g/d	.08	.45	.62	1.04	.09	.0001	.9676	.4833
Retention, g/d	.18	.48	.48	.71	.08	.0016	.5006	.3289
Mohair S, g/d	.25	.26	.27	.23	.02	.5039	.9062	.7107
Absorbed S retained, %	68.74	52.48	41.31	40.67	4.25	.0008	.1396	.9809

Table 8. Least square means of nitrogen metabolism in Angora kids during the metabolism trial

Item	Sulfur, %				SE	Probability		
	.11	.20	.28	.38		Linear	Quadratic	Cubic
Intake, g/d	12.49	17.90	15.03	16.16	2.44	.3362	.3342	.4240
Fecal output, g/d	3.78	5.86	5.15	5.47	.85	.1874	.2532	.5021
Digestibility, %	69.43	66.83	66.66	66.31	1.95	.2479	.4350	.9648
Urinary output, g/d	4.89	6.40	4.75	5.10	.74	.9967	.7258	.1256
Total retention, g/d	3.82	5.64	5.13	5.59	1.14	.3002	.3271	.8798
Mohair N, g/d	1.30	1.34	1.36	1.20	.12	.5039	.9062	.7107
On % of intake basis								
Fecal output	30.57	33.17	33.34	33.69	1.95	.2479	.4350	.9648
Urinary output	38.93	36.27	32.82	32.44	3.80	.2130	.2928	.3686
Retention	30.49	30.56	33.84	33.87	3.64	.4751	.4813	.3385
Absorbed N retained, %	43.92	45.54	51.07	51.18	5.29	.2993	.3690	.3114

Table 9. Least squares means of urinary creatinine and uric acid outputs in Angora kids during the metabolism trial

Item	Sulfur, %				SE	Probability		
	.11	.20	.28	.38		Linear	Quadratic	Cubic
Creatinine concentration, mg/dL	3.91	11.49	8.38	3.20	2.74	.8846	.1634	.2105
Creatinine output, mg/d	12.12	29.16	17.59	12.56	4.16	.9631	.1462	.1342
Creatinine output, mg/BWKg	.61	1.47	.90	.59	.36	.8708	.1459	.1457
Creatinine output, mg/BWKg$^{.75}$	1.29	3.10	1.89	1.27	.46	.8916	.1446	.1121
Uric acid concentration, mg/dL	10.33	25.95	13.86	10.38	2.69	.6860	.0129	.0232
Uric acid output, mg/d	31.13	97.43	28.09	45.12	21.12	.9317	.2231	.1006
Uric acid output, mg/BWKg	1.57	4.59	1.45	2.12	.91	.9777	.1849	.1085
Uric acid output, mg/BWKg$^{.75}$	3.309	9.85	3.04	4.56	1.99	.9652	.1944	.2916

Table 10. Comparisons of performance and blood acid-base balance between Angora and Alpine kids

Item[a]	Alpine	Angora	SE	Probability
Performance				
ADG, g/d	94.7	69.7	6.80	.0060
DMI, g/d	1.12	.76	.02	.0001
Gain/feed, g/Kg	84.0	92.3	6.09	.5684
Clean mohair, g/d	-	8.97	1.05	-
Blood acid-base balance				
Blood pH	7.38	7.39	.01	.7046
HCO_3^-, m*M*	25.32	22.36	.48	.0003
TCO_2, m*M*	26.62	23.48	.49	.0002
pCO_2, mmHg	42.08	36.69	.80	.0002
pO_2, mmHg	38.35	44.39	1.42	.0054
BEb, m*M*	.69	-1.53	.49	.0045
BEect, m*M*	.07	-2.81	.55	.0016
SBC, m*M*	24.68	23.17	.39	.0131
SO_2C, %	70.88	79.01	1.95	.0088

[a]See Table 2 footnote.

Table 11. Comparisons of blood plasma metabolites between Angora and Alpine kids

Item	Alpine	Angora	SE	Probability
Glucose, mg/dL	67.52	54.45	2.20	.0002
L-lactate, mg/dL	30.06	27.68	2.62	.2744
Sulfate, mg/dL	138.0	131.3	3.69	.3615
Cysteine plus cystine[a], μM	15.45	15.40	.75	.6589
Cysteine, μM	3.86	4.62	.17	.0066
Cystine[a], μM	11.59	10.78	.73	.2634
Urea N, mg/dL	26.81	26.36	.79	.8614

[a]Expressed as cysteine equivalents.

Table 12. Comparisons of ruminal pH and protozoa between Angora and Alpine kids

Item	Alpine	Angora	SE	Probability
Ruminal pH				
0 h postprandially	6.55	7.07	.10	.0026
4 h postprandially	5.60	6.00	.09	.0040
Ruminal protozoa, thousand/mL				
0 h postprandially	-	59.4	41.7	-
4 h postprandially	-	70.7	38.6	-

Table 13. Comparisons of ruminal metabolites between Angora and Alpine kids

Item	Alpine	Angora	SE	Probability
Ruminal L-lactate, mg/dL	46.38	16.29	2.96	.0001
Ruminal ammonia N				
Total, mg/dL	27.92	35.37	3.20	.0729
NH_3-N, μg/dL	20.08	46.99	9.04	.1004
Ruminal sulfate-S, mg/dL	149.0	134.0	11.59	.2978
Sulfide-S, mg/dL				
Total	2.89	3.54	.23	.1569
H_2S-S	2.62	2.91	.19	.6457
Ruminal purine N, % of ruminal fluid (wt/wt)				
Total	.85	.80	.07	.5188
In isolated bacteria	.72	.72	.09	.8416
Residual	.13	.07	.04	.0010
Bacterial N, % of dry mass	8.06	7.86	.34	.6560
Bacterial S, % of dry mass	.41	.46	.02	.0701
Bacterial N:S ratio	19.94	17.80	1.12.	.1572

Table 14. Comparisons of nutrient intakes and digestibilities between Angora and Alpine kids

Item	Alpine	Angora	SE	Probability
Intakes				
DM, g/d	941.0	676.7	41.84	.0001
OM, g/d	872.2	627.1	38.77	.0001
Digestible OM, g/d	440.9	308.6	24.00	.0004
GE, Mcal/d	4.27	3.07	.19	.0001
DE, Mcal/d	2.18	1.53	.12	.0008
ME, Mcal/d	1.79	1.26	.10	.0008
ME, Mcal/BWKg$^{.75}$	.15	.13	.01	.0817
Digestibility, %				
GE	50.81	49.70	1.04	.8370
DM	50.48	48.95	1.07	.6534
OM	50.32	49.00	1.11	.7595
ADF	11.27	10.44	1.93	.9583
Ash	52.57	48.31	1.41	.1194

Table 15. Comparisons of sulfur and nitrogen metabolism between Angora and Alpine kids

Item	Alpine	Angora	SE	Probability
S Metabolism				
Intake, g/d	2.22	1.67	.11	.0007
Apparent digestibility, %	70.52	58.27	1.32	.0001
Urinary output, g/d	1.17	.55	.04	.0001
Total retention, g/d	.47	.47	.07	.7218
Mohair S, g/d	-	.25	.02	-
Intake S retained, %	20.61	29.30	2.38	.0240
N Metabolism				
Intake, g/d	21.58	15.52	.96	.0001
Apparent digestibility, %	66.61	67.23	.75	.4092
Urinary output, g/d	11.24	5.34	.64	.0001
Total retention, g/d	3.13	5.07	.63	.0800
Mohair N, g/d	-	1.26	.12	-
Fecal output, % of intake	33.39	32.77	.75	.4092
Urinary output, % of intake	53.11	34.92	2.54	.0001
Retention, % of intake	13.50	32.32	2.58	.0001
Absorbed N retained, %	20.18	48.14	3.80	.0001

Table 16. Comparisons of urinary creatinine and uric acid outputs between Angora and Alpine kids

Item	Alpine	Angora	SE	Probability
Creatinine, mg/dL	3.61	6.18	1.61	.4250
Creatinine output, mg/d	35.02	15.76	11.46	.2588
Creatinine output, mg/BWKg	1.30	.80	.44	.4173
Creatinine output, $mg/BWKg^{.75}$	2.97	1.69	.99	.3689
Uric acid, mg/dL	7.70	14.83	1.36	.0079
Uric acid output, mg/d	91.91	50.48	7.92	.0009
Uric acid output, mg/BWKg	3.43	2.44	.33	.0242
Uric acid output, $mg/BWKg^{.75}$	7.81	5.20	.72	.0109

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CHAPTER VII

SULFATE SUPPLEMENTATION OF ANGORA GOATS: SULFUR METABOLISM AND INTERACTIONS WITH ZINC, COPPER AND MOLYBDENUM

K. Qi[1,2], C. D. Lu[1], and F. N. Owens[2]
Langston University[1], Langston, OK 73050 and
Oklahoma State University[2], Stillwater 74078

ABSTRACT: We evaluated the effects of sulfur intake on zinc, copper, and molybdenum metabolism in Angora goats fed isocaloric and isonitrogenous diets with S at .16%, .23%, .29% or .34% of DM. Dietary Zn, Cu and Mo were held constant at 29.2, 8.8 and 1.0 ppm respectively. Metabolic fecal S, endogenous urinary S, and biological value of supplemented S were calculated to be .55 g/d (32.2 mg/BWkg$^{\cdot 75}$), .48 g/ d (27.8 mg/BWkg$^{\cdot 75}$) and 37.7% respectively. The absorbed S requirement for maintenance was calculated to be 1.03 g/d (59.92 mg/BWkg$^{\cdot 75}$) or 457 mg/d (26.61 mg/BWkg$^{\cdot 75}$) of retainable S. Serum Cu and Zn concentrations were not affected by S supplementation. Concentration of protein-S in the rumen and apparent absorption of Zn increased quadratically ($P < .05$) with S supplementation. Urinary Zn excretion was increased ($P <$

.05) when diets containing higher amounts of S were fed. Zinc retention was increased quadratically ($P < .05$) by added S. Presumably, this was due to the combination of enhanced absorption of Zn by S-amino acids with the lower level of added S, but decreased absorption due to ZnS precipitation with higher amounts of added S. Urinary Cu output decreased quadratically ($P < .01$) with S supplementation. Metabolism of Mo was not altered ($P > .10$) by dietary S level. The models for S-Cu, S-Mo and S-Mo-Cu interactions proposed by Huisingh et al. (1973) were updated in view of these findings.

Key Words: Goat, Sulfur, Zinc, Copper, Molybdenum, Mineral interaction.

Introduction

In a previous report (Qi et al., 1992a), we observed that: 1) sulfur supplementation quadratically increased mohair production and quality in Angora goats, 2) ruminal and plasma metabolites responded to added S and 3) the dietary S requirement for maximum mohair growth of Angora goats was .267% of dietary DM. Sulfur intake has been reported to substantially affect metabolism of Zn, Cu, and Mo (Suttle, 1974a; NRC, 1980; Gawthorne et al., 1985). Huisingh et al. (1973) summarized findings of the S-Mo-Cu interactions and proposed several models to explain the mechanisms of these interactions. In recent years, considerable progress has been made in unravelling the S-Zn, S-Cu, S-Mo, and S-Mo-Cu interactions in ruminants (Suttle,

1980, 1991). Effects of S supplementation on Zn, Cu and Mo metabolism were examined to evaluate whether the proposed interactions of S-Zn, S-Cu, S-Mo, and S-Mo-Cu could explain the findings from our experiment with goats.

Materials and Methods

The animals, design, diets, methods of sample collection and analysis and statistical analysis were reported previously (Qi et al., 1992).

The diets contained Zn, Cu, and Mo at 29.22, 8.77, and .99 ppm respectively. Blood samples were procured via jugular venipuncture at 0, 2, 4 and 6 h postprandially during the wk 4 of each period into evacuated tubes (Becton Dickinson Vacutainer, Rutherford, NJ); serum was harvested 24 h after blood collected for trace mineral analysis. Feed, feces, urine and blood serum were analyzed for Zn, Cu and Mo using a Plasma Emission Spectrospan V (Beckman Instruments, Irvine, CA). Plasma Mo content was lower than the detection limit (< .08 ppm).

Results and Discussions

Sulfur Metabolism

Effects of added S on S metabolism were discussed previously (Qi et al., 1992a).

In addition, we regressed apparently absorbed S (Y, g/d) against ingested S (X, g/d) as suggested by Biddle et al. (1975). The regression equation was: $Y = - .5525 + .9411 X$ ($r = .9989$, $P < .01$) in which truly absorbed S was 94.11% of ingested S and metabolic fecal S totaled .5525 g/d or,

because these animals had a metabolic body weight of 17.2 $kg^{\cdot 75}$, metabolic fecal S was 32.15 $mg/BWkg^{\cdot 75}$.

We estimated biological value of the supplemental S and endogenous urinary S by regressing total urinary S output (Y, g/d) against truly absorbed S (X, g/d) as suggested by Biddle et al. (1975). The regression equation was: Y = -.4773 + .6273 X ($r = .9963$, $P < .01$) in which biological value was 37.72% (100 - 62.73%) and endogenous urinary S totaled .4773 g/d or 27.77 $mg/BWKg^{\cdot 75}$.

For maintenance, S is required to replace metabolic fecal S and endogenous urinary S. This ignores the S used for hair production and replacement of scurf losses. The amount of absorbed S needed for maintenance of adult Angora goats was calculated to be 1.03 g/d (27.77 + 32.15 = 59.92 $mg/BWkg^{\cdot 75}$). Assuming that 44.4% of absorbed S can be retained, this equals 457 mg/d (26.61 $mg/BWkg^{\cdot 75}$) of retainable S. This value of retainable S requirement was similar to a previous estimate for growing sheep (24.26 $mg/BWkg^{\cdot 75}$) estimated by Johnson et al. (1971) using radioactive S from sodium sulfate. This maintenance need for S, based on S intake assuming a true digestibility of 94.11%, the amount of S needed for maintenance was 1.1 g/d (63.68 $mg/kg^{\cdot 75}.d$). This is 32% higher than a previous estimate (540 mg/d or 48.3 $mg/kg^{\cdot 75}.d$) proposed by Joyce and Rettray (1970) for growing sheep of 20 to 30 kg BW.

Zinc Metabolism

Zinc is required at every stage of the life cycle, but requirements for goats and other ruminants are poorly defined (NRC, 1980, 1981). The inconsistent responses to Zn supplementation in ruminants suggests that zinc requirements are affected by dietary or physiological factors (Spears, 1991).

Sulfur supplementation quadratically decreased ($P < .01$) fecal Zn concentration, but did not affect urinary Zn concentration (Table 1). Due to slightly higher feed intake and variation in feed Zn contents, Zn intake tended to increase linearly and quadratically ($P < .10$) with S supplementation. Hence, we used Zn intake as a covariate in testing other Zn metabolic criteria. Based on such analysis, we found that the added dietary S quadratically decreased ($P < .01$) fecal Zn output, but quadratically increased ($P < .01$) net Zn retention. Urinary Zn output tended to be lowest with the .23% S diet. All experimental animals were in negative Zn balance; this fact indicated the experimental diets needed to be supplemented with more Zn than was provided in the diet (29 ppm). This finding did not support the Zn requirement of 10 ppm for goats recommended by NRC (1981). The Zn requirements for sheep and beef cattle are reported to be 20-33 and 20-40, respectively (NRC, 1984, 1985); both are higher than the recommendation for goats (NRC, 1981).

Copper Metabolism

No research concerning Cu requirements of goats is available (NRC, 1981). To establish the Cu requirement of goats, we must consider the availability of Cu and the interfering substances in various feeds.

Our diet contained 8.8 ppm Cu. This Cu level was close to the estimated requirement for Cu by sheep (7-11 ppm; NRC, 1985). No requirement for Cu by goats indicated in NRC (1981). Sulfur supplementation affected fecal Cu concentration in a cubic fashion ($P < .05$), but it decreased urinary Cu concentration quadratically (Table 2). Added S did not affect ($P > .10$) Cu intake or fecal Cu output; however, it quadratically decreased ($P < .01$) urinary Cu output. Apparent Cu absorption was highest with .29% S diet and net Cu retention tended to increase (linear, $P < .10$) with higher S intake. The positive Cu retention regardless of S level in our experiment suggested that the dietary Cu level (8.8 ppm) was adequate for adult Angora goats.

Molybdenum Metabolism

Anke et al. (1985) summarized the established functions of Mo in 8 enzymatic systems of animals and plants. They also determined the Mo requirement of goats (.1 ppm, DM basis). In practice, toxicity rather than deficiency is the major problem for molybdenum. Spears et al. (1977), using an in vitro incubation technique, found that Mo supplementation to 8 ppm of dietary DM increased both sulfate and sulfide requirement for maximum cellulose

digestion. In our experiment with goats, we found that S supplementation did not affect ($P > .10$) concentrations of Mo in feces and urine, fecal and urinary Mo outputs, apparent Mo absorption, or net Mo retention (Table 3).

Serum Cu and Zn Concentrations

Sulfate supplementation up to .34% of dietary DM did not affect serum Cu and Zn concentrations (Table 4) in our experiment. These results differ from those of Suttle and Peter (1985) in which a plasma repletion method was used (Suttle, 1974b) to study the effects of Na_2SO_4 supplementation with dietary S at .30% of dietary DM on the dietary Cu availability of sheep; they concluded that ruminal sulfide was a major determinant of Cu availability -- the higher the sulfide, the lower the Cu availability. Goats may have greater potential for mobilization of Cu and Zn from body stores than sheep. When ruminants are fed diets deficient in Cu and Zn, Cu and Zn stores can be mobilized (NRC, 1980) and these minerals can be recycled (Purser et al., 1984; Cousins, 1985). Suttle (1974b) suggested that hypocupraemic animals would be more sensitive to S supplementation. Furthermore, we should have measured TCA soluble Cu of serum, not simply total serum Cu (Kincaid and White, 1988) to avoid effects of thiomolybdate on Cu. The cupric thiomolybdate complex formed in the blood can render Cu unavailable for metabolism. Further, for more accurate evaluation of the effect of S supplementation on Zn metabolism, we should have fed a higher amount of Zn in

order to meet the goat's needs (Hallmans et al., 1985). Methods using Zn stable isotope also could enhance our understanding of Zn-S interactions (Hambidge et al., 1985).

Puls (1990) suggested that serum Cu concentration between .80 to 1.20 was adequate. Our values for each diet and sampling time (Table 4 and Table 5) were close to the upper range. Puls (1990) also indicated that serum Zn concentration between .36 to .85 was deficient (adequate serum Zn ranged from .65 to 2.70 ppm), our values for each diet and sampling time (Table 4 and Table 5) fell in this range. This result further supported the suggestion that diet containing 29 ppm Zn was inadequate and the recommendation of Zn requirement for goats by NRC (1981) was too low.

When evaluating the effect of S intake on the availability of Cu in sheep, Bird (1970) found that soluble Cu output from rumen to omasum was inversely related to ruminal sulfide concentration, but when ruminal sulfide concentration exceeded 3 mg/L, there was no further reduction in soluble Cu output from the rumen. No explanation for this plateau was offered. The ruminal sulfide concentrations of all our animals exceed 5 mg/L (Qi et al., 1992a). This might explain why S supplementation did not alter Cu concentration of serum.

Effects of postprandial sampling time on serum Cu and Zn concentrations were detected ($P < .01$) (Table 5). Considering the reasonable constant flux of nutrients to the

intestines, this effect was surprising and no explanation is available.

Interaction of S and Zn

Zinc is absorbed by facilitated diffusion in the duodenum and upper jejunum (NRC, 1980). Facilitating agents have been reported to include amino acids, particularly histidine (Nielsen et al., 1967) and cysteine (NRC, 1980; Ruth and Kirchgessner, 1985). However, an excess amount of sulfide can reduce Zn uptake. Sulfide produced in the rumen reacts with Zn to form zinc sulfide (ZnS) which is largely unabsorbed due to its low solubility (Underwood, 1971).

In our study, the lowest S level may have been inadequate for stimulated synthesis of S-containing amino acids as indicated by quadratic increase in ruminal protein-S and plasma organic S concentrations to added dietary S (Qi et al., 1992a). This increase in S-containing amino acids could explain the enhanced Zn absorption from S supplementation at a low level. However, ruminal sulfide concentration increased linearly with increased S intake (Qi et al., 1992a). When the level of sulfate supplementation was higher than the optimum, ZnS precipitation should be dominant that would reduce Zn absorption. The combination of these two effects might explain why S supplementation quadratically decreased fecal Zn excretion and quadratically increased Zn retention.

Hemple et al. (1991) found that a low molecular weight protein (cysteine-rich intestinal protein, CRIP) functions

as an intracellular Zn carrier and binds Zn during transmucosal Zn transport. Perhaps, this CRIP and its synthesis in response to the available S-amino acids in the intestinal digesta forms the basis for these responses in Zn absorption and retention.

One can formulate a S-Zn interaction model to highlight several points (Figure 1). Firstly, sulfate is reduced to sulfide by ruminal bacteria. The higher the sulfate, the higher the amount of sulfide produced (Qi et al., 1992a). Protozoa in the rumen, via increased degradation of dietary or bacterial protein, can further increase the sulfide concentration (Ivan, 1988; Qi et al., 1992b). Secondly, sulfide, reacting with Zn, will produce zinc sulfide. Zinc sulfide precipitation in the rumen reduces the Zn absorption (Underwood, 1971). Thirdly, a deficiency of S in the diet can reduce bacterial protein synthesis (Qi et al., 1992a) and decrease S-amino acid content of bacterial protein (Weston et al., 1988). These S-containing amino acids are involved with Zn absorption (NRC, 1980; Ruth and Kirchgessner, 1985). Fourthly, with higher S diets, sulfide production and absorption may be so rapid that the capacity of liver oxidation of sulfide to sulfate is surpassed (Kandylis, 1984); this sulfide can accumulate in the tissue causing precipitation of ZnS at the tissue level.

Interaction of S and Cu

Sulfur affects Cu availability via formation of cupric sulfide (CuS). Hence, the S-Cu interaction model proposed

by Huisingh et al. (1973) was updated (Figure 2). This model emphasizes several points. Firstly, sulfate is reduced to sulfide by ruminal bacteria (Moir, 1979). Secondly, protozoa in the rumen degrade bacterial and feed protein and thereby increase the ruminal sulfide concentration (Ivan, 1988; Qi et al., 1992b). Thirdly, copper sulfide precipitation in the rumen reduces Cu absorption (Huisingn et al., 1973). However, why CuS formation reaches a maximum when sulfide reaches 3 mg/L is not clear (Bird, 1970). Fourthly, tissue sulfide accumulation can lead to a precipitation of CuS in tissue (Smith and Wright, 1975).

Interaction of S and Mo

Molybdate may either aggravate or alleviate the Cu deficiency symptoms observed in ruminants, depending on both sulfate intake and the Cu status of the animals. Several mechanisms are possible. Firstly, molybdate and sulfate are antagonistic due to their similarity in chemical characteristics (Huisingh et al., 1973). Sulfate competes with molybdate for carrier sites in the intestinal mucosa and distal tubules of the kidney (Mason and Cardin, 1977). Therefore, sulfate limits Mo retention both by reducing intestinal absorption and by increasing urinary excretion (Grace and Suttle, 1979). Secondly, molybdate inhibits formation of sulfide from sulfate reduction and S-amino acid desulfuration (Huisingh et al., 1973). Thirdly, molybdate inhibits sulfide absorption from the rumen and sulfide

oxidation in tissues (Gawthorne et al., 1985). Fourthly, molybdate in the tissue of animals blocks the formation of adenosine-5'-phosphosulfate, the activated form of sulfate (Huisingh et al., 1973). Finally, in the rumen, molybdate can react with sulfide to form thiomolybdate. Thiomolybdates, being poorly dissociated, excrete in feces or accumulate in the tissues. Based on these findings, we updated the S-Mo interaction model of Huisingh et al. (1973) (Figure 3).

Three-way Interactions of S, Cu and Mo

Sulfate can either enhance or relieve Cu deficiency depending on both the Cu status of the animal and the level of dietary molybdate. Several points need to be mentioned in our updated model of S-Mo-Cu interactions (Figure 4). Firstly, formation of thiomolybdates in the rumen forms the basis of the interaction of Cu, Mo and S (Dick et al., 1975); this hypothesis is supported by recent research (Mason, 1986; Kincaid and White, 1988; Gooneratne et al., 1989). Secondly, Cu can react with tetrathiomolybdate in the rumen to form a complex that is poorly available to animals (Kincaid and White, 1988). Thirdly, dithiomolybdate and, to a lesser degree, trithiomolybdate can be absorbed and bind with endogenous Cu thereby affect systemic metabolism of Cu (Suttle, 1991). Fourthly, tri- and tetrathiomolybdates are primarily responsible for reducing Cu absorption (Price et al., 1987). Fifthly, certain Cu dependent enzymes appear to be inhibited directly by

thiomolybdate (Mason, 1986). Finally, we included CuS formation, sulfate and molybdate competition for carrier sites for absorption and excretion, cupric molybdate formation (Bremner and Young, 1978; Moshtaghi-Nia et al., 1989) in this model.

Implications

Sulfur homeostasis of goats appears to be regulated primarily by the kidney. However, S supplementation affected Zn, Cu and Mo metabolism and utilization in a complex fashion. An optimum concentration of dietary S stimulated ruminal bacterial protein synthesis to increase the supply of S-amino acids. These S-amino acids presumably facilitated Zn absorption. In contrast, an excess of S reduced Zn availability through ZnS precipitation. The interactions of S-Cu, S-Mo and S-Mo-Cu appear quite complex; specific models of interactions need to be tested to enhance our understanding of the adverse effects of excess S.

Table 1. Fecal, and urinary zinc contents, and zinc balance at different dietary sulfur levels

	Sulfur, %					Probability <		
	.16	.23	.29	.34	SE	Linear	Quadratic	Cubic
Feces concentration, DM basis, ppm	73.11	63.12	58.07	72.33	4.190	.6983	.0097	.4533
Urine concentration, ppm	4.02	2.61	4.69	6.89	1.677	.0814	.1814	.5687
Balance								
Intake, mg/d	28.51	34.57	36.83	34.28	2.326	.0760	.0805	.9235
Fecal output, mg/d	51.05	40.40	37.24	41.91	2.425	.0195	.0101	.9749
Apparent absorption, %	-55.70	-34.20	-15.71	-33.25	8.705	.0600	.0556	.4082
Urinary output, mg/d	2.95	1.78	4.05	5.53	1.212	.1092	.3308	.4487
Net retention, mg/d	-20.46	-8.64	-7.74	-13.90	2.557	.1187	.0050	.7399

Table 2. Fecal, and urinary copper contents, and copper balance at different sulfur levels

	Sulfur, %					Probability <		
	.16	.23	.29	.34	SE	Linear	Quadratic	Cubic
Feces concentration, DM basis, ppm	9.67	10.45	8.85	9.12	.370	.0640	.4955	.0193
Urine concentration, ppm	.010	.005	.005	.028	.005	.0213	.0073	.4115
Balance								
Intake, mg/d	9.71	9.91	10.51	9.83	.537	.6985	.4203	.4893
Fecal excretion mg/d	6.25	6.65	6.40	5.70	.449	.3546	.2356	.9153
Apparent absorption, %	36.86	30.99	41.38	40.75	3.387	.1626	.4502	.0884
Urinary excretion, mg/d	.008	.004	.006	.023	.004	.0113	.0103	.4842
Net retention, mg/d	3.45	3.25	4.11	4.10	.417	.1503	.8180	.3169

Table 3. Fecal, and urinary molybdenum contents, and molybdenum balance at different sulfur levels

	Sulfur, %					Probability <		
	.16	.23	.29	.34	SE	Linear	Quadratic	Cubic
Feces concentration, DM basis, ppm	.90	.90	.91	.90	.082	.8636	.4412	.3615
Urine concentration, ppm	.24	.35	.21	.28	.073	.9834	.8048	.1891
Balance								
Intake, mg/d	1.11	1.13	1.21	1.12	.056	.6568	.2903	.3666
Fecal output, mg/d	.57	.58	.63	.57	.037	.8626	.3112	.3618
Apparent absorption, %	48.39	48.37	48.17	49.06	.819	.6253	.5875	.7351
Urinary output, mg/d	.24	.28	.20	.24	.051	.7095	.9745	.3216
Net retention, mg/d	.29	.27	.38	.31	.052	.4709	.6847	.1963

Table 4. Means of serum copper, zinc, and molybdenum concentrations at different dietary sulfur levels

	Sulfur, %					Probability <		
	.16	.23	.29	.34	SE	Linear	Quadratic	Cubic
Copper, ppm	1.23	1.27	1.15	1.22	.101	.5427	.8229	.2358
Zinc, ppm	.62	.72	.57	.53	.128	.1679	.3542	.2621
Molybdenum, ppm	<.08	<.08	<.08	<.08				

Table 5. Effects of sampling time on serum copper, zinc, and molybdenum concentrations at different sampling times

	Sampling Time, h postprandial					Probability	
	0	2	4	6	SE	Linear	Quadratic	Cubic
Copper, ppm	1.25	1.20	1.18	1.23	.018	.3796	.0105	.6955
Zinc, ppm	.74	.55	.48	.67	.050	.2784	.0010	.5366
Molybdenum, ppm	<.08	<.08	<.08	<.08				

Figure 1. The proposed zinc-sulfur interaction model. In this figure, SO_4^{2-} is sulfate ion, S^{2-} is sulfide ion, Zn^{2+} is zinc ion, and ZnS is zinc sulfide. The symbol "+" means stimulation; "-" means depression. Symbol "O" attached to the intestinal lumen represents cysteine-rich intestinal protein carrier.

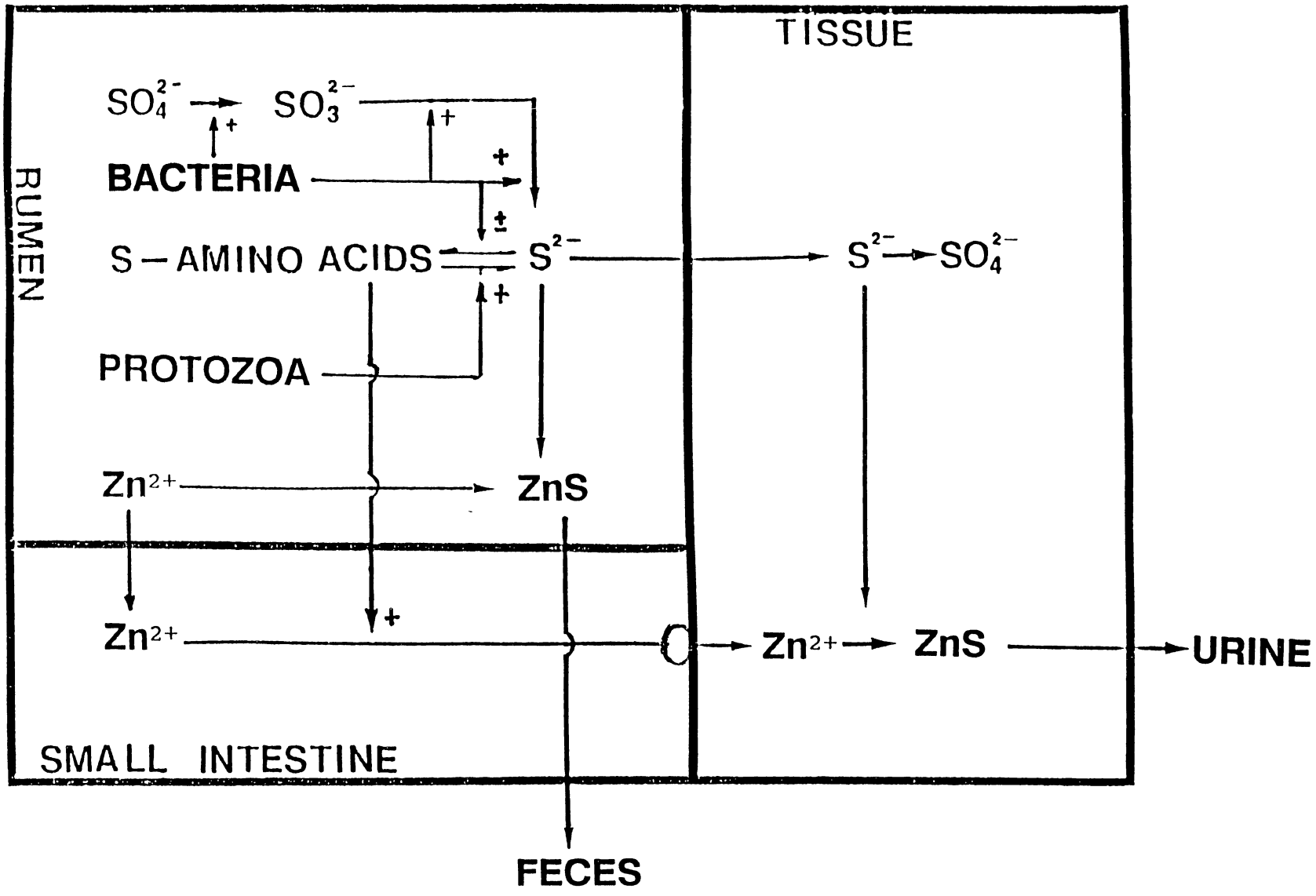

TISSUE
RUMEN
SO_4^{2-}
SO_3^{2-}
BACTERIA
S – AMINO ACIDS
S^{2-}
$S^{2-} \rightarrow SO_4^{2-}$
PROTOZOA
Zn^{2+}
ZnS
Zn^{2+}
Zn^{2+} → ZnS → URINE
SMALL INTESTINE
FECES

Figure 2. The updated copper-sulfur interaction model. In this figure, Cu^{2-} is copper ion (cupric), and CuS is cupric sulfide. Other symbols are the same as Figure 1.

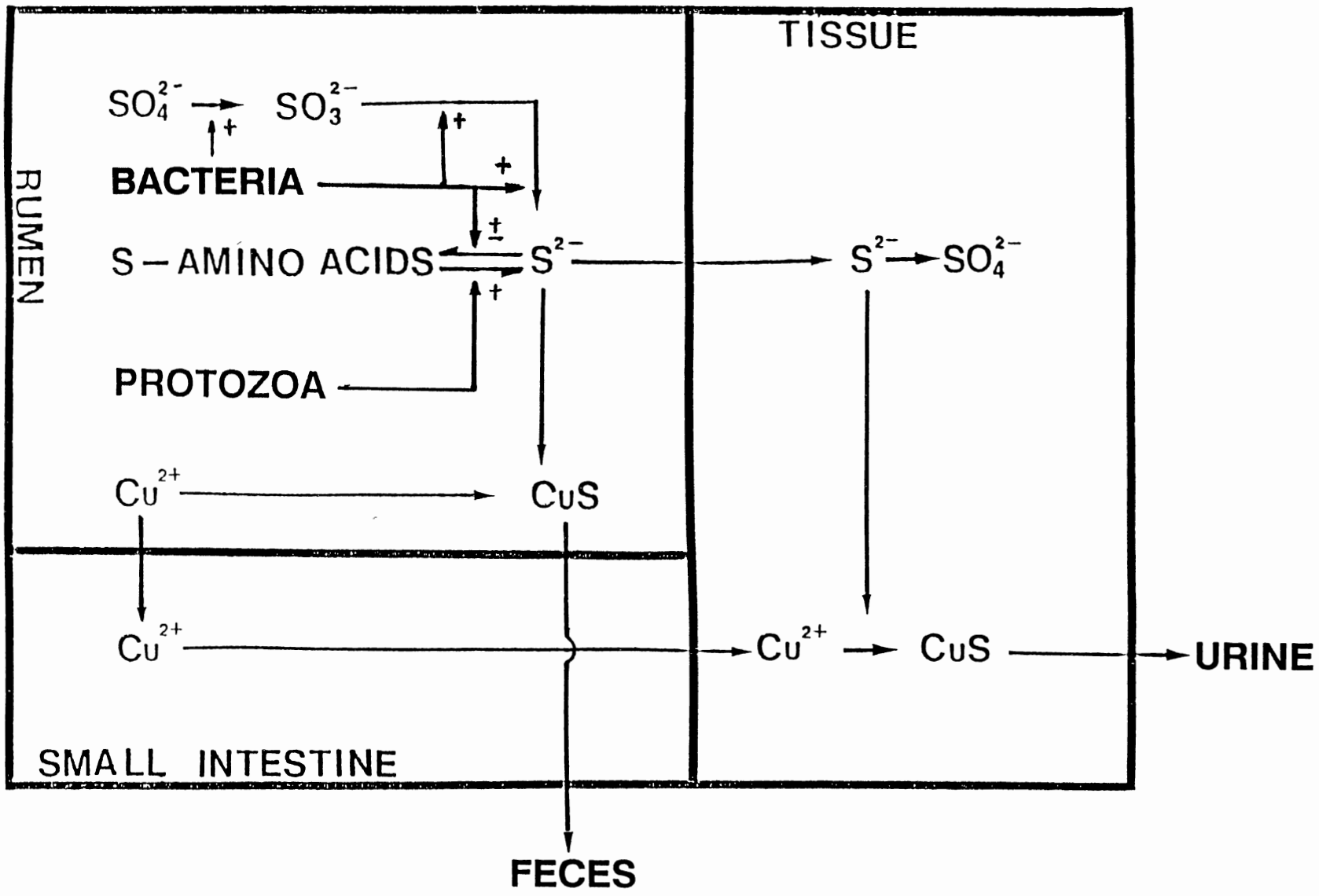

TISSUE
RUMEN
SO_4^{2-}
SO_3^{2-}
BACTERIA
S – AMINO ACIDS
S^{2-}
$S^{2-} \rightarrow SO_4^{2-}$
PROTOZOA
Cu^{2+}
CuS
Cu^{2+}
Cu^{2+} → CuS → URINE
SMALL INTESTINE
FECES

Figure 3. The updated molybdenum-sulfur interaction model. In this figure, MoO_4^{2-} is molybdate ion, A-SO_4 is adenosine-5'-phosphosulfate, and "C" is carrier. In the formula $RMoO_{4-n}S_n$, n =1, 2, 3, 4 which represents mono, di, tri and tetra thiomolybdate; R represents any ions which can associate with thiomolybdate. Others are the same as Figure 1.

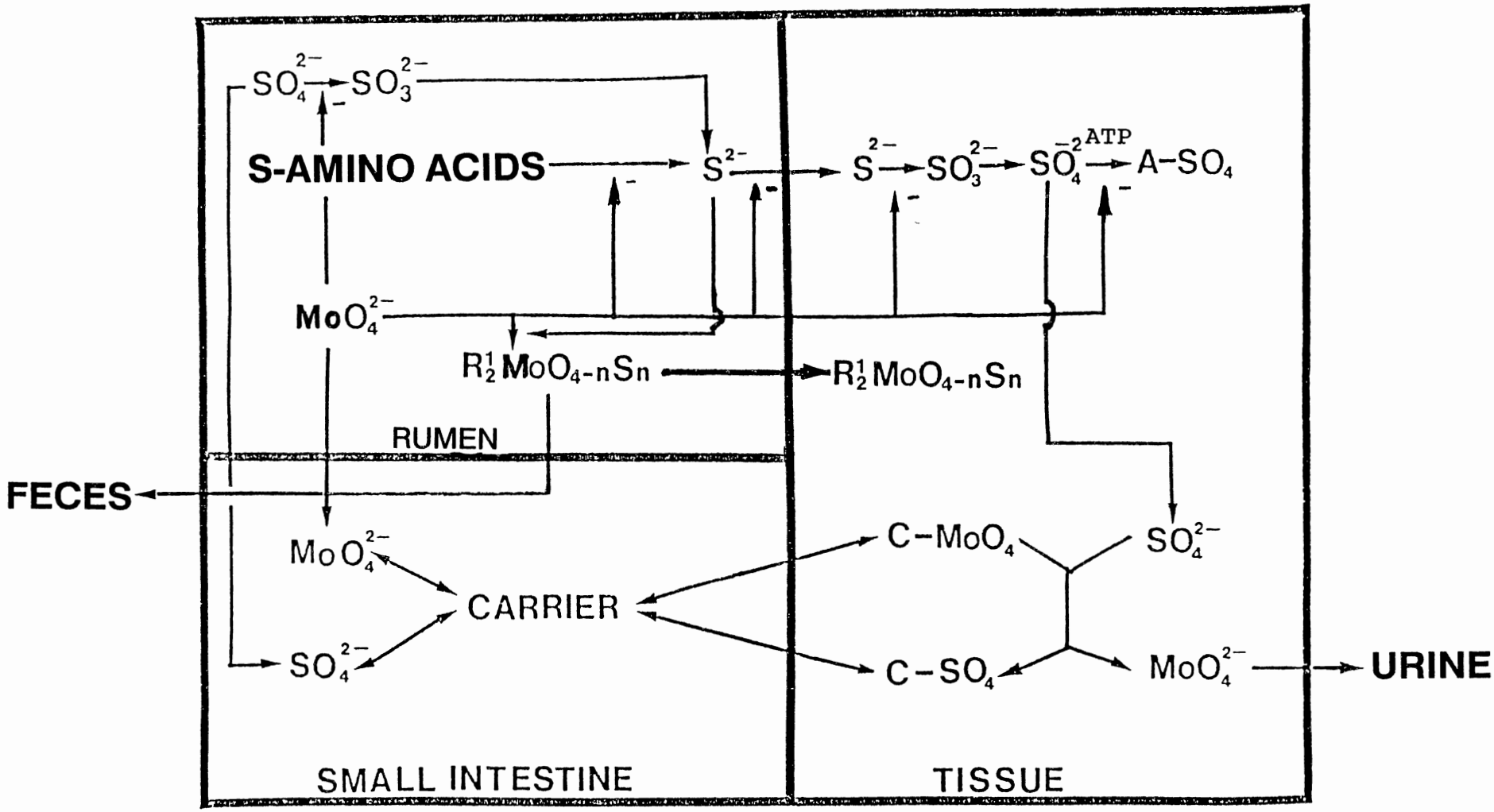
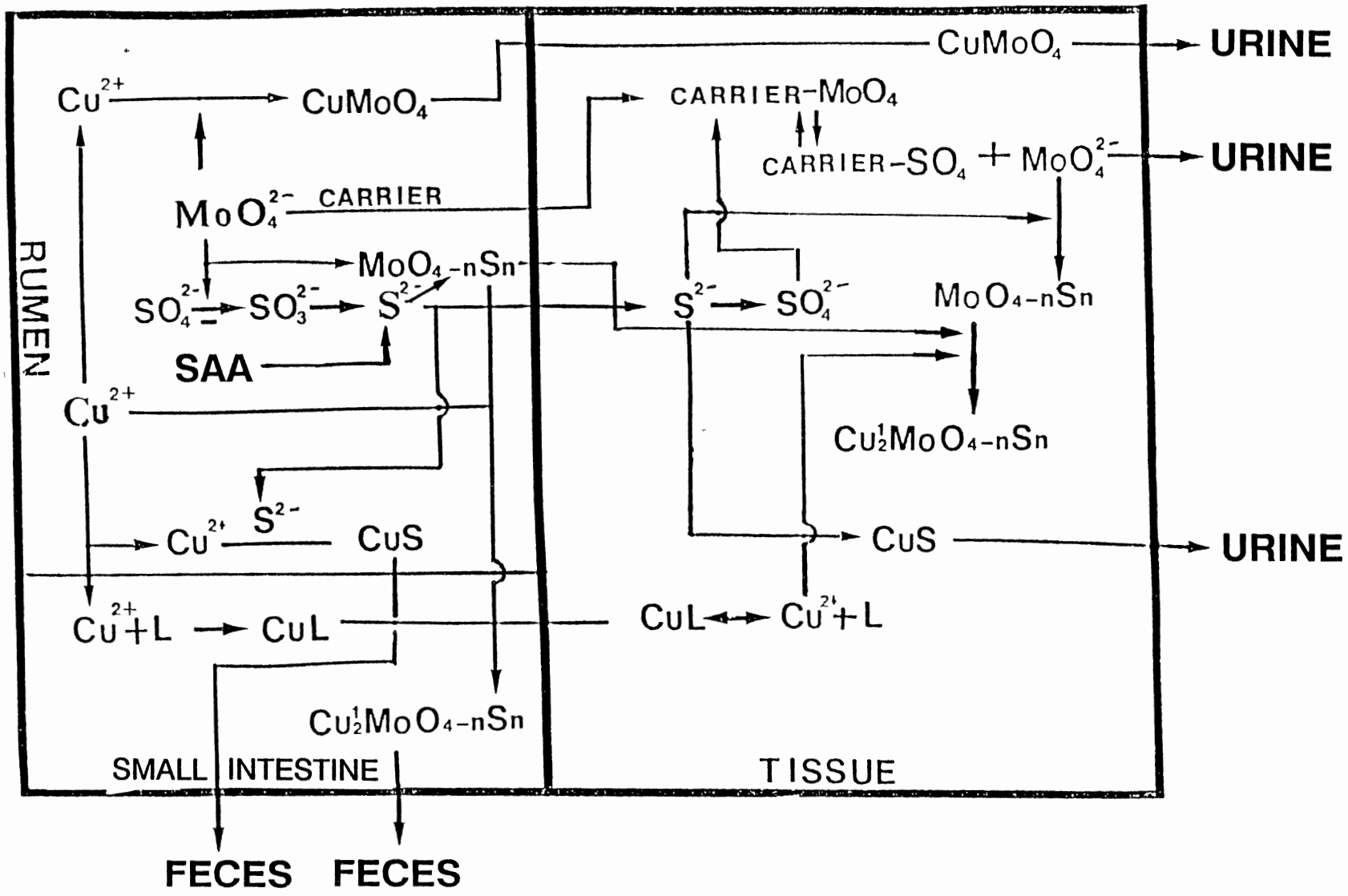

SO_4^{2-}
SO_3^{2-}
S-AMINO ACIDS
S^{2-}
S^{2-}
SO_3^{2-}
SO_4^{2-}
ATP
A-SO_4
MoO_4^{2-}
$R_2^1MoO_{4-n}Sn$
$R_2^1MoO_{4-n}Sn$
RUMEN
FECES
MoO_4^{2-}
CARRIER
SO_4^{2-}
C-MoO_4
SO_4^{2-}
C-SO_4
MoO_4^{2-}
URINE
SMALL INTESTINE
TISSUE

Figure 4. The updated copper-molybdenum-sulfur interaction model. In this figure, $CuMoO_4$ is cupric molybdate, SAA is sulfur-containing amino acids, L is ligand, C_2 is cuprous (Cu^+) or cupric (Cu^{2+}). Others are the same as Figures 1 and 3.


RUMEN
Cu^{2+}
$CuMoO_4$
MoO_4^{2-} CARRIER
MoO_4-nSn
SO_4^{2-}
SO_3^{2-}
S^{2-}
SAA
Cu^{2+}
S^{2-}
Cu^{2+} CuS
$Cu^{2+}+L$ CuL
$Cu_2^1MoO_4$-nSn
SMALL INTESTINE
FECES
FECES
$CuMoO_4$
URINE
CARRIER-MoO_4
CARRIER-SO_4 + MoO_4^{2-}
URINE
S^{2-}
SO_4^{2-}
MoO_4-nSn
$Cu_2^1MoO_4$-nSn
CuS
URINE
CuL $\leftrightarrow$ $Cu^{2+}+L$
TISSUE

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CHAPTER VIII

SUMMARY

Scope of These Studies

A total of 70 goats were used in the studies included in this dissertation. Responses of goats to supplemental dietary S were measured in mohair production and quality, milk yield and composition, body weight gain and feed efficiency. The metabolic effects of dietary S were evaluated at four levels: 1) the synthesis of ruminal bacterial protein; 2) plasma and ruminal metabolites; 3) blood acid-base balance; 4) mineral interactions (S, Zn, Cu and Mo). Methods in all these studies were focused on specific questions.

Findings and Conclusions

In the first experiment, eight male, castrated Angora goats were used in a repeated, simultaneous 4 X 4 latin square experiment to evaluate metabolic and mohair responses to sulfate supplementation. Goats were given ad libitum access to isonitrogenous diets containing .16% (basal), .23%, .29%, or .34% S (DM basis). Sulfur supplementation 1) did not affect feed intake or body weight; 2) quadratically increased grease and clean mohair production, grease and clean mohair staple strength, and staple length; 3) did not

affect other mohair characteristics, e.g. diameter, med fiber, kemp fiber, S and cysteine contents. Sulfur supplementation 1) quadratically increased ruminal pH, ruminal ammonia N, total S, organic S, protein S concentrations; 2) plasma organic S content; 3) retention of N and mohair S; 4) linearly increased urinary S output, but did not affect fecal S output; and 5) linearly increased S absorption and retention. Estimates of the metabolic fecal S, endogenous urinary S and biological value of supplemental S ($CaSO_4^=$) were .55 g/d, .48 g/d, and 37.3%, respectively. Calculated by regression, the optimum dietary S concentration for maximum clean mohair production was .267% of dietary DM, and the optimum N to S ratio was 7.2. These results suggest that the recommendation of NRC (1981) for S is inadequate to maximize mohair growth by Angora goats.

In the second experiment, thirty multiparous lactating Alpine does were used in a randomized complete block design to study the effects of sulfate supplementation on milk yield and composition, ruminal and blood metabolites, nutrient digestibilities and balances and acid-base balance. Does were given ad libitum access to isonitrogenous diets containing .16% (basal), .26% or .36% S (DM basis) for 15 weeks. Sulfur supplementation did not affect feed intake, fat-corrected milk yield or milk S content. However, does fed the .26% S diet 1) tended to have a higher persistency of lactation and 2) had a higher milk solids-not-fat

percentage during the last third of the study. Sulfur supplementation 1) resulted in quadratic decreases in ruminal ammonia N and plasma urea nitrogen, but linearly increased ruminal protein S concentrations; 2) linearly increased the apparent digestibilities of DM, OM, ash, ADF, and GE, but had little impact on blood acid-base status. Based on these results, we concluded that increasing S from .16 to .26% of dietary DM was beneficial for lactating Alpine goats during early lactation.

In the third experiment, thirty-two goat kids were used to study the S requirement for body weight gain and feed efficiency. Goats were individually fed isonitrogenous, isocaloric diets containing .11, .20, .28, or .38% S (DM basis) for 12 weeks. Sulfur supplementation 1) quadratically increased average daily gain and ad libitum DM intake, and tended to increase feed efficiency quadratically; 2) quadratically increased plasma lactate, but did not affect plasma sulfate and cystine; 3) tended to improve acid-base status of the animals as indicated by quadratic trends in plasma HCO_3^- and total CO_2 levels and 4) quadratically increased the urinary uric acid output, which presumably reflected synthesis of ruminal bacterial protein. Calculated by regression, average daily gain was maximum at .22% S (N:S ratio = 10.4:1), dry matter intake was maximum at .24% S (N:S = 9.5:1), and feed efficiency was maximum at .21% S (N:S = 11.1:1). These values substantiated the S

requirement for growing goats (N:S = 10:1) recommended by NRC (1981).

In the third experiment, we monitored the concentration of ruminal protozoa of Alpine and Angora kids, and measured mohair production and length. Finally, we compared the performance and metabolic responses between Alpine and Angora kids. Sulfur requirements for growth of Alpine and Angora kids did not detectably differ in terms of dietary S percentage (.22 vs .21%). Clean mohair production was not affected by added S, but mohair length tended to increase quadratically with sulfate supplementation. Average daily gain and DMI were lower for Angora than for Alpine kids (69.7 vs 94.7 g/d). Blood pH values did not differ in two breeds, but other criteria (HCO_3^-, total CO_2 content, base excess) differed substantially. Plasma glucose was lower, and plasma free cysteine concentration was higher for Angora than for Alpine kids. Ruminal L-lactate content and purine N content in isolated bacteria were lower, but ruminal ammonia N and sulfide S contents tended to be higher for Angora than for Alpine kids. Angora kids were faunated whereas Alpine kids were fauna-free in this experiment. Sulfate supplementation did not significantly affect the ruminal concentration of protozoa in Angora kids. The N:S ratio in isolated ruminal bacteria was lower for Angora than Alpine kids. The differences in performance and nutrient metabolism between Angora and Alpine kids can be ascribed

partially to inherent physiological dissimilarities and partially to environmental effects (faunated vs fauna-free).

Effects of S intake on Zn, Cu, and Mo metabolism from the first experiment were evaluated further. All diets contained 29.2 ppm Zn, 8.8 ppm Cu, and 1.0 ppm Mo. Sulfur supplementation 1) quadratically increased Zn absorption and Zn retention; 2) did not affect serum Cu and Zn concentrations; 3) quadratically decreased urinary Cu excretion; 4) tended to increase Cu absorption and net retention but 5) did not affect Mo metabolism. We interpreted these results to mean that at a deficient S diet, goats has low Zn absorption due to low production of bacterial S-amino acids. In contrast, excessive S results in ZnS precipitation which reduces zinc availability. Based on these results, we formulated a Zn-S interaction model to explain the mechanism of Zn absorption and effect of S. Using the results from this experiment and our other two experiments, we updated the models for S-Cu, S-Mo, and S-Mo-Cu interactions proposed by Huisingh et al. (1973).

Significance of the Studies

Our studies provide both extensive and intensive information about S metabolism in goats, specifically addressing 1) S requirements for mohair growth, milk production and composition, body weight gain and feed efficiency; 2) effects of dietary S levels on N, Zn, Cu and Mo utilization; 3) effects of dietary S level on plasma and ruminal metabolites, and blood acid-base balance. This

information helped broaden our understanding of S metabolism and utilization and its interaction with N, Zn, Cu and Mo metabolism. Averaged across the range of S levels used in each of these experiments, the optimum dietary S level in diets for lactating Alpine goats (.26% of dietary DM) increased fat-corrected milk yield by 4.5%, milk solids-not-fat content by 1.7% and total protein content by 4.1%. In adult Angora goats, the ideal S level (.27% of dietary DM) increased clean mohair production by 13.1%, staple length by 4.5%, clean staple strength by 8.1%, mohair cysteine content by 1% and mohair diameter by 1.7%. In growing goats, the ideal S level (.21% to .22% of dietary DM) increased body weight gain by 44.9%, feed intake by 15.7% and feed efficiency by 23.3%. In growing Angora kids, the ideal S level increased clean mohair production by 8.0% and staple length by 14.3%. Practically, these results have a strong economic impact.

Limitations and Future Outlook

Due to time and facility restrictions, several questions remain unanswered. Inorganic S (sulfate S) was used as the supplemental source of S in all diets and we ascribed all of our responses in animal performance to increased synthesis of ruminal microbial protein. An adequate level of dietary S is needed to satisfy the microbial population in the rumen. Because microbes have a N:S ratio of 12 to 15:1, the level of dietary S level needed by microbes probably is less than the animal's requirement for wool or mohair production

because such products have a N:S ratio between 4 to 5:1. Sulfate also is involved in carbohydrate and lipid metabolism. We detected an increase of ADF digestibility from supplemental S by lactating Alpine goats. Some S functions in mineral interactions and acid-base balance were explored, but many others remain unaddressed.

We did not analyze extent to which sulfide S is lost via breath or eructation because we did not have a reliable method. A slaughter trial was not employed in our studies, so we could not verify S retention data. Duodenal flow of microbial protein was not determined because surgical success of cannulation procedures was too low.

At present time, we do not know how extensively S supplementation affects the efficiency of microbial protein synthesis and the amino acid composition of ruminal bacterial proteins. We need to develop S metabolism and requirement models for ruminal microbes to further define the impact of S supplementation on the post-ruminal supply of S-containing amino acids. We also need to define the quantitative post-ruminal requirements for growth, lactation and optimum mohair production and quality to determine the potential responses to feeding ruminal escape source of S-containing amino acids.

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VITA

Kanhu Qi

Candidate for the Degree of

Doctor of Philosophy

Thesis: SULFUR: REQUIREMENTS FOR MOHAIR GROWTH, MILK YIELD AND BODY WEIGHT GAIN, AND EFFECTS ON NITROGEN, ZINC, COPPER, AND MOLYBDENUM METABOLISM IN GOATS

Major Field: Animal Nutrition

Biographical:

Personal data: Born in Shaanxi Province, China, May 3, 1961, the son of Si-Wen Qi and Gui-Ying Tan.

Education: Graduated from Northwestern Agricultural University, Xi'an, China in July, 1982, received Bachelor of Science degree with excellent research thesis; received Master of Science degree from Beijing Agricultural University, Beijing, China in July, 1985; completed the requirements for Doctor of Philosophy degree at Oklahoma State University in December, 1992.

Professional Experience: Worked for the Department of Animal Science at Beijing Agricultural University as an Assistant Professor from July, 1985 to December, 1988.

Professional Organizations: American Society of Animal Science, American Dairy Science Association.