Sulfate Supplementation of Angora Goats: Metabolic and Mohair Responses[1,2]

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ABSTRACT: Eight castrated male Angora goats were used in a repeated, simultaneous 4 × 4 Latin square designed experiment to evaluate metabolic and mohair responses of Angora goats to sulfate supplementation. Goats had ad libitum access to isonitrogenous diets containing a .16 (basal), .23, .29, or .34% S (DM basis), which yielded 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 prefeeding, 2, 4, and 6 h postprandial sampling times, ruminal pH, ammonia N, total S, organic S, protein S, and plasma urea N and 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 ($P < .001$) with increased S intake. Calculated by regression, the optimum dietary S concentration for maximum clean mohair production was .267% of dietary DM for a N:S ratio of 7.2:1, suggesting that the National Research Council N:S ratio of 10:1 is inadequate for Angora goats. The optimum level of digestible S was calculated to be .18% of the diet DM.

Key Words: Goats, Sulfur, Mohair, Metabolites, Nitrogen

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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 an increased 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). Therefore, more S may be needed for Angora goats than for sheep. Information pertaining to the S requirements of Angora goats for mohair growth and metabolic responses in blood or in the rumen of goats with S supplementation is limited. Therefore, an experiment was conducted with Angora goats 1) to measure

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the effects of S supplementation on mohair N and S yields, 2) to estimate the dietary S requirement of Angora goats for mohair growth, and 3) to evaluate the metabolic responses in the rumen and blood to S supplementation.

Materials and Methods

Animals and Diets. Eight castrated mature Angora goats ($\bar{x}$ ± SD BW = 47.8 ± 2.6 kg) were blocked into two groups according to BW and used in a 180-d experiment. A repeated, simultaneous 4 × 4 Latin square design (Cochran and Cox, 1957) was adopted. The eight goats were given ad libitum access to four treatment diets. These diets differed only in S content, which was added as $CaSO_4$. Calcium carbonate was used to balance the Ca contributed by $CaSO_4$. Silicon dioxide was added to maintain the concentrations of other nutrients at the same levels. 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 constant temperature (23 ± 2°C). Diets were fed once daily and water was available ad libitum. Before initiation of the experiment, animals were allowed to adapt to treatment 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 previous diet and to permit the goats to adapt to the new diet of the next period.

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 sheep 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 alter during the emergence time (the time required for the newly keratinized portions of fiber to move out of the follicles to the point at which they could be removed by 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 during the following 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. First, 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. Second, the reticuloruminal system for sulfate reduction requires a period of time to adapt to dietary sulfate (Lewis, 1954). To circumvent all these problems, the following approaches were adopted. First, all animals were kept indoors at 23 ± 2°C. Second, a period of at least 2 wk was allowed for adaptation to diets before the experiment and between successive periods. Third, fiber growth during this adaptation period was clipped and discarded. Fourth, 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,

Table 1. Composition of experimental diets[a]

Item	Diet 1	Diet 2	Diet 3	Diet 4
Ingredient				
Bermudagrass 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
Vitamins 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 mixture of monocalcium and dicalcium phosphates containing 17% Ca, 21% P.
[c]Containing (percentage): NaCl, 95.5 to 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.

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 < 60% of the diameter of the fiber; kemp fiber is a medullated animal fiber in which the diameter of the medulla is > 60% of the diameter of the fiber; medulla in mammalian hair fibers is the more or less continuous cellular marrow inside the cortical layer of most medium and coarse fibers; medullated fiber is an animal fiber that in its original state includes a medulla; ASTM, 1990c). 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) 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 3rd wk of each period. Feed, feces, and urine were analyzed for DM, total S, N, and GE. Feed and feces were also 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 4th wk of each period. At least 30 mL of blood was collected. Plasma was harvested immediately after sampling and stored frozen until it was analyzed.

Ruminal samples were procured via stomach tube at the same time as blood sampling. The first 20 to 30 mL of ruminal fluid was discarded to reduce salivary contamination and at least 50 mL of fluid was collected 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^{2-}) analysis (Fresenius et al., 1988). In addition, ruminal nonionized, volatile sulfide-S (H_2S-S) was calculated using the Henderson-Hasselbalch equation. The formula developed was as follows: $H_2S\text{-}S$ = sulfide-S × antilog(6.74 − pH)/[1 + antilog(6.74 − pH)], where 6.74 is the pK_a of sulfide-S ($H_2S \rightarrow HS^- + H^+$; $K_a = 1.8 \times 10^{-7}$; Bray and Till, 1975). The H_2S-S was an estimate of the amount of sulfide-S that can be volatilized and be easily lost 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 3rd wk.

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 the method of 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 the method of 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 1,000 × *g* for 5 min to remove feed particles and protozoa (Merchen and Satter, 1983). Ruminal and plasma samples were deproteinized using 20% trichloroacetic acid (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 the method of Mottershead (1971).

Ruminal VFA were analyzed using the procedures of Erwin et al. (1968). Plasma urea N was analyzed by the method of 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 as described by Visek (1968). The FAMN was an estimate of the amount of the total RAMN that 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 a Sigma kit (Sigma Diagnostic, St. Louis, MO).

Statistical Analysis. Data were subjected to ANOVA for a repeated, simultaneous 4 × 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 using 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 × diet interaction ($P > .20$) existed for the criteria analyzed. The statistical model included the effects of period, animal, diet, animal × diet interaction, sampling time, period × sampling time interaction, animal × sampling time interaction, diet × sampling time interaction, and the residual error. The effects of period, animal, and diet were tested using the mean square of the animal × diet interaction. Effect of sampling time was tested using the mean square of animal × 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 of S content of the diets and time of rumen and blood sampling using appropriate error terms. Because all criteria analyzed did not have diet × sampling time interactions ($P > .25$), time course data are not presented.

Determination of Sulfur Requirement. After a quadratic increase of clean mohair yield with S supplementation was confirmed, the sulfur requirement of Angora goats for mohair growth was determined by fitting a parabola equation between clean mohair yield (Y, grams per period) and dietary S contents (X, percentage) as follows: $Y = a + bX - cX^2$. Then, 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 were also 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, percentage) and midpoints of dietary S contents (X, percentage) as follows: $Y = a - bX$. 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 S content (.4 g/kg of 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 was doubled ($P < .05$) and apparent digestibility of OM was increased (39.3 vs 30.6%; $P < .05$). Differences 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 isoenergetic and isonitrogenous. The calculated digestibility of ash is similar among diets if the indigestible dietary SiO_2 is subtracted from the total ash. The intake of ME expressed as per unit of metabolic BW was similar across all diets, averaging 102.6 ± 4.1 kcal/kg $BW^{.75}$ (Table 2). Dry matter intake averaged 2.5% of BW, or 66.5 g/kg $BW^{.75}$.

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 ± .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 that wool S content was increased and wool N:S ratio was decreased. Qi (1989) reported that the major criteria for evaluating wool quality (strength, elasticity, and resilience) are highly correlated with the wool S content in wool of the same diameter (22.3 ± .14 μm). However, mohair is different from Merino wool in that mohair contains a higher percentage of medullated fibers,

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/(kg $BW^{.75}$ · 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

and the medulla layer contains a very low concentration of S-containing amino acids (Qi, 1988). Therefore, mohair S content might be lower. In summary, mohair production, staple length, and strength responded quadratically to the addition of S to the diet, whereas other traits were unaffected (Table 3).

Using clean mohair production as a dependent variable (Y, grams) and dietary S percentage as an independent variable (X, percentage), the parabola equation relating the two variables was as follows: $Y = 43.9 + 1448.7\ X - 2712.6\ X^2$ ($R^2 = .85$; $Sy \cdot x = 27.47$; $P < .0001$). Solving this equation for maximum clean mohair production, the optimum S content of the diet, (X) 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 the NRC (1981) recommendation (N:S of 10), which was 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 do sheep (Gallagher and Shelton, 1972). Huston et al. (1971) suggested that the 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 necessitate higher nutrient requirements for goats than for sheep.

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

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	882.0	.62	.9309	.2602	.7616
Med fiber, no./1,000	16.8	15.5	16.5	14.3	2.85	.6162	.8627	.6712
Kemp fiber, no./1,000	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 (percentage) = clean, dry mohair weight × (100 + 13.87)/grease mohair weight, in which 13.87% is the standard moisture regain for mohair;
[c]Dry mohair with 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.

increase in fecal S ($P > .20$) was apparent as intake of S increased (Table 4). However, the digestibility of S exhibited a linear ($P < .001$) response to S supplementation. Urinary S output exhibited a linear increase ($P < .01$) to 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%, and 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, sulfur digestibility was higher for supplemented S than for S in the basal diet (78.1 vs 59.9%; $P < .01$). Mohair S yield exhibited a quadratic response ($P < .01$), 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 ($H_2S \rightarrow HS^- + H^+$, $pK_a = 6.74$; Bray and Till, 1975). Ruminal fluid pH was approximately 6.4; 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^{2-} for synthesis of S-containing amino acids (methionine, cystine, cysteine, and cystathionine). Sulfur is also used for vitamin synthesis (thiamin 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). Most ruminal bacteria use sulfide derived from the dissimilatory pathway (Moir, 1979), and this 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% is 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. The regression equation of marginal efficiency of retained S used for mohair growth (Y, percentage) from midpoints of dietary S percentage (X, percentage) was as follows: $Y = 132.96 - 495.15\ X$ ($R^2 = .97$; $Sy \cdot x = 7.537$; $P < .11$). From this equation, the calculated requirement of dietary S percentage (X, percentage) for zero marginal efficiency of retained S for mohair growth (Y, percentage) was .269%, which was close to the value .267% previously calculated from the equation for maximal clean mohair yield. Similarly, the regression equation of marginal efficiency of intake S for mohair growth (Y, percentage) to midpoints of dietary S percentage (X, percentage) was as follows: $Y = 18.11 - 71.47\ X$ ($R^2 = .91$; $Sy \cdot x = 1.964$; $P < .20$). From this equation, the calculated requirement of dietary S percentage (X, percentage) for zero marginal efficiency of intake S (Y, percentage) was .253%,

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

Item	Sulfur, %				SE	Probability <		
	.16	.23	.29	.34		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

which was lower than the value obtained previously. This was attributed to a higher residual error of intake S than retained S.

Nitrogen metabolism data are summarized in Table 5. Although N intake, N digestibility, and 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 N:S ratio, the animal will adjust to this ratio by wasting N. Therefore, a decrease in efficiency of feed protein utilization is the principal effect of a S deficiency. The percentage of absorbed N retained was > 5% higher ($.10 < P < .20$) in goats fed .29% S diet than in goats fed other diets. Mohair N yield exhibited a quadratic increase ($P < .01$) with S supplementation. The percentage of retained N 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 and valerate concentrations increased quadratically ($P < .05$) by S supplementation. The acetate: propionate molar ratio was numerically higher ($P = .1862$) in the basal diet than in the S supplemental diets.

Ruminal fluid pH increased quadratically ($P < .05$) with increased S intake (Table 7). Edman (1988) indicated that the optimal range of pH for maximum cellulose digestion was 6.4 to 6.8. Mean ruminal pH was > 6.4 for all diets, with the highest value for goats fed the .23% S diet. Weston et al. (1988) also found that low dietary S concentration decreased fiber digestibility in sheep. Ruminal ammonia N and 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 RAMN 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 is observed when the ruminal ammonia N concentration is 23.5 mg/dL in the ruminal fluid, somewhat below the value we measured. A higher ruminal ammonia N concentration increases bacterial pro-

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

Item	Sulfur, %				SE	Probability <		
	.16	.23	.29	.34		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

tein 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 RAMN and FAMN in this trial seemed to be adequate for activity of ruminal bacteria.

Ruminal L-lactate concentration was numerically lower in the basal diet than in the S-supplemented diets ($.10 < P < .20$). Plasma L-lactate concentration was not affected ($P > .20$) by S supplementation. Whanger (1972) reported that lactate (L- or D-lactate not specified) accumulated in the rumen of sheep fed S-deficient diets, whereas only traces of lactate were found in the rumen of the 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 ruminal fluid could be considered as microbial protein. Protein-S should follow a similar pattern. The quadratic effect of dietary S on protein-S suggested 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 reports as 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 trend similar to that of total sulfide-S. According to Kandylis (1984), a ruminal sulfide-S concentration < 3.8 mg/L decreases bacterial growth. A low ruminal sulfide-S concentration also reduces the S-containing amino acid content of ruminal microbes (Weston et al., 1988). Our values were

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[a]	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

[a]Nonionized, volatile sulfide-S.

approximately three times greater than the sulfide-S concentration judged to be sufficient for microbial protein synthesis.

Sulfide derived from the reduction of inorganic S sources or from the dissemination of S-amino acids (Moir, 1979), which have not been used for protein synthesis, is absorbed very rapidly through the ruminal wall and some is lost with 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 rumen via saliva (Bray and Till, 1975). The S metabolism models presented by Doyle and Moir (1979) show that up to 40% of dietary S with an alfalfa diet and most of the supplementary methionine S are not used by the microbes. The observed range of ruminal fluid sulfide-S concentrations is between .6 and 288 mg/L (Bray and Till, 1975). Because many factors 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) that limits bacterial growth or fermentation as previously 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 increased quadratically ($P < .001$) with 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 dry matter, giving an ideal N:S ratio of 7.2. Based on the marginal efficiency of retained S for mohair growth, the optimal diet would have .269% S. Both values were higher in S than the current recommendation for a N:S ratio of 10. Mohair quality also 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 dry matter.

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