A Review of the Effects of Sulfur Nutrition on Wool Production and Quality[1,2]

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Summary

Clean wool contains 2.7 to 5.4% sulfur. The finer the wool, the more sulfur it contains. Sulfur is also an essential element in the sheep's body and is a component of important metabolites such as amino acids, vitamins and hormones. The mechanisms of action of sulfur-containing amino acids and/or inorganic sulfur supplementation in stimulating wool growth are: 1) it stimulates the anabolism of sheep; 2) it increases the supply of substrate available for keratin synthesis; and 3) it provides for optimal rumen microbial growth. The sulfur requirement of sheep is suggested to be 0.14 to 0.26% of their diet (dry matter [DM] basis) depending on the physiological stage of the animal (National Research Council, 1985). The recommended nitrogen-to-sulfur ratio is 10:1. When sheep are supplemented with sulfur-containing amino acids, both wool production and the sulfur content of wool increase; conversely, when sheep are selected for increased wool production, the sulfur content of wool decreases (McGuirk, 1983). Sheep from flocks selected for higher fleece weight tend to be more responsive to supplemental sulfur-containing amino acids than sheep from flocks selected for lower fleece weight, indicating that sulfur or sulfur-containing amino acids may be a limiting factor in wool production (Williams et al., 1972). The relationships among wool sulfur content, wool strength and resistance to compression deserve further study.

Key words: sheep, sulfur nutrition, wool production, wool quality.

Introduction

The rate of wool growth in sheep can vary over a wide range due to genotype and the influence of various physiological and environmental (nutritional) factors. Robards (1979) reported annual clean fleece weights for several breeds and crosses of sheep in many environments in Australia; most values fell in the range of 2 to 5 kilograms (5.5 to 13.7 grams per day). The maximum reported rate for Lincoln and Merino sheep was 22 to 23 grams per day of dry, clean wool (Daly and Carter, 1955; Hogan et al., 1979). This rate corresponds to an annual clean fleece production of about 9.4 kilograms. The wool growth rate of an individual sheep can vary considerably. Reis (1979) gave an example of a four-fold change in wool growth rate due to nutrition (supplementation with casein). The maximum rate at which sheep can produce wool and the range of variation possible are determined by its genotype. There are definite differences among breeds of sheep in their capacity to grow fiber and in various fleece characteristics. Likewise, within a breed there is considerable variation in the rate of wool growth among strains and individual sheep. For Australian Merinos, a comparison of the fine, medium and strong wool strains shows an increasing clean fleece weight as the wool fleece becomes coarser (Robards, 1979). In animals of similar size, various authors (Williams, 1979; McGuirk, 1983) have attributed differences in wool production to the efficiency of conversion of feed to wool, and not necessarily to differences in feed intake. Such claims are very difficult to prove, however, and clear-cut answers are not available. Apparent increased efficiency in wool production may be more directly related to a shift in metabolic priorities away from functions such as maintenance, growth, reproduction and lactation (Shelton, 1993). Genetically high-producing Merino sheep grow wool of a lower sulfur content and have lower concentrations of cystine and urea in plasma than genetically low-producing sheep (McGuirk, 1983). Williams et al. (1972) suggested that the availability

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of sulfur-containing amino acids limits the ability of sheep to produce wool, particularly those with a high genetic potential for wool production. The heritabilities of wool traits such as grease or clean fleece weight, number of follicles per unit area of skin, secondary-to-primary follicle (S:P) ratio, fiber diameter, staple length and crimp frequency are in the range of 0.3 to 0.6 (Brown and Turner, 1968; Yeates et al., 1975; Qi, 1986). This means that 30 to 60% of the variation in these traits is genetic while 40 to 70% is due to environmental effects in which nutrition is a primary factor.

Sulfur, like protein and energy, is very important to sheep and Angora goats for fiber growth. Sulfur is a component of methionine, cystine, thiamine, biotin, chondroitin, taurocholic acid, glutathione, insulin, glucogan and ACTH. Sulfur toxicity (National Research Council 1980; Kandylis, 1984) and deficiency (Qi et al., 1993) in sheep and goats have been reviewed previously. This article will focus on the following areas: 1) sulfur content, distribution and function in wool fiber; 2) the mechanism of action of sulfur-containing amino acids and inorganic sulfur in stimulating wool growth; 3) sulfur requirement of sheep; 4) the effects of dietary sulfur content on wool sulfur content and wool quality; 5) the influence of selection for wool production on wool sulfur content and interaction between selection and nutrition; 6) the effects of sulfur supplementation on wool diameter; and 7) meeting the sulfur-containing amino acid requirement through genetic engineering.

Sulfur Content, Distribution and Function in Wool Fiber

Clean wool is composed of the complex protein keratin which contains 20 amino acids in many polypeptides and has a sulfur content ranging from 2.7 to 5.4% of fiber weight. Most of the sulfur is present as cystine, with smaller amounts present as cysteine and methionine (McGuirk, 1983). Keratin is not homogeneous and the keratin proteins are usually grouped into low sulfur, high sulfur, ultra-high sulfur or high tyrosine proteins. These major protein groups are thought to be associated with different structural components of the cortical cells of the fiber. The low sulfur proteins are concentrated in the microfibrils, and the high sulfur proteins are concentrated in the matrix surrounding microfibrils. The high tyrosine proteins occur mainly in the matrix of the fiber cortex, and ultra-high sulfur proteins occur in epidermal scales of the fiber. Bradbury (1973) reviewed analyses of amino acids from the ortho-cortex and para-cortex of wool fibers and concluded that the para-cortex is rich in high sulfur proteins, while the ortho-cortex is rich in low sulfur and high tyrosine proteins. Cells in the medullary layer of wool fibers consist basically of low sulfur proteins which contain very little or even no cystine. High sulfur content and disulfide bond structure in fiber are the material basis of the physical and chemical characteristics of the wool. Sulfur-containing amino acids greatly influence fiber production, fiber elasticity, fiber strength and other textile processing and performance criteria; and sulfur-containing amino acids stabilize the tertiary and quaternary structures of wool protein molecules.

The Mechanism of Action of Sulfur-Containing Amino Acids and of Inorganic Sulfur in Stimulating Wool Growth

Reis and Schinckel (1963) reported the effect of infusing methionine and cystine into the abomasum of sheep on wool growth and composition and explored the mechanism of action of cystine and methionine supplements in stimulating wool growth. They found that infusing a sheep with 2.00 grams L-cystine or 2.46 grams DL-methionine (the sulfur equivalent) per day increased wool production by 35 to 130% and the sulfur content of wool by 24 to 35%. This finding stimulated research in this field. To date, researchers believe that the mechanisms of such results are as follows: infusing methionine into the rumen can increase the protein synthesis of ruminal bacteria. Sulfur-containing amino acids from the bacterial proteins and those infused into the abomasum stimulate the anabolism of animals, which is evidenced by increased weight gain. Cyst(e)ine may be the limiting amino acid for keratin synthesis and the infusion may simply increase the supply of substrate available for keratin synthesis (Martson, 1955; Reis, 1979). The mechanism may also include specific effects of cyst(e)ine or other sulfur-containing compounds in the follicle. The effect may be a stimulation of mitotic activity in the follicle bulb as there is much evidence that sulfydryl groups play an important role in mitosis (Reis et al., 1967). Other possible effects include increased production of co-factors important in protein and energy metabolism and stimulation of keratinization by the provision of sulfydryl groups. Methionine could stimulate fiber growth by supplying cystine through trans-sulfuration and in other ways. Methionine appears to have a special role as a chain initiator in protein synthesis and in stimulating the synthesis of RNA and of adenine nucleotides in the liver (Qi, 1988). Methionine has key roles in amino acid transport (Qi, 1988) and as a methyl donor (S-adenosylmethionine) in many reactions (Pegg and McCann, 1982). Experiments with methionine analogues (ethionine, methoxinine) support the view that some of the effects of methionine on wool growth are mediated via S-adenosylmethionine (Reis and Tunks, 1982; Reis et al., 1986).

Starks et al. (1953) found that lambs could utilize inorganic sulfur and that supplemental sulfur can increase nitrogen balance. Hale and Garrigus (1953) showed that sheep can synthesize cystine from sulfate, and to a lesser extent from elemental sulfur. Johnson (1971) reported digestibilities of 36, 70 and 78% for sulfur from elemental sulfur, sodium sulfate and L-methionine in lambs and retentions of 27, 56 and 70%, respectively. Seljeanski (1959) stated that lambs given 5.9 grams of potassium sulfate daily produced 6.6% more wool than lambs not receiving sulfate. Soviet Union workers (1982; as cited by Qi, 1988) reported that sheep supplemented with sodium sulfate to 0.25% dietary sulfur (DM basis) produced 17% more wool than unsupplemented sheep. Body weight gain and wool strength also increased. The basal diet was apparently deficient in sulfur.

Supplemental sulfur increased the utilization of urea as a source of non-protein nitrogen in ruminants (Allaway, 1970).

Whereas non-ruminant animals need sulfur-containing amino acids for growth, ruminants such as sheep are able to utilize inorganic sulfur. *Megasphaera elsdenni* and other ruminal microorganisms can effectively utilize inorganic sulfur to meet the requirement of their growth. The sheep then obtains sulfur-containing amino acids when the microorganisms pass to the duodenum and are digested. However, sulfur-containing amino acids originating from this source alone would not be adequate to supply the requirements for high-producing animals. An additional supply of sulfur-containing amino acids with ruminal escape protein such as feather meal and blood meal (Qi et al., 1993) in rumen-protected form (Bassett et al., 1981) or post-ruminally would be needed for the high wool-producing animals (Williams et al., 1972).

The Sulfur Requirement of Sheep

Several estimates of sulfur requirements have been proposed. The Agricultural Research Council (1980), basing its estimate on nitrogen supply, proposed that the dietary ratio of nitrogen-to-sulfur should not exceed 14:1 for sheep. The National Research Council (1985) suggested that dietary dry matter should contain a minimum of 0.14 to 0.18% sulfur for adult sheep, 0.18 to 0.26% sulfur for growing sheep and the nitrogen-to-sulfur ratio should not exceed 10:1. The Soviet Union National Standard (as referenced by Lu and Jiang, 1981), concerned that various animal classes have different sulfur requirements, recommended that the dietary dry matter for wool-type adult sheep should contain a minimum of 0.30% sulfur with a maximum nitrogen-to-sulfur ratio of 5 or 6:1; diets for meat-type adult sheep should contain a minimum of 0.25% sulfur with a maximum nitrogen to sulfur ratio of 6 or 7:1; and diets for growing sheep should contain 0.24 to 0.31% sulfur with a maximum nitrogen to sulfur ratio of 8 or 9:1. The recommended nitrogen-to-sulfur ratio is higher for growing than adult sheep not because growing sheep need fewer grams of sulfur, but because they require more nitrogen. In Australia, where sheep graze on improved grassland, farmers spread sulfur fertilizer to increase the sulfur content in the grass. Chestnut et al. (1986) observed that with orchard grass sulfur fertilization (sulfur at 132 kilograms per hectare from gypsum) not only increased the sulfur content in the forage, it also changed the composition and apparent digestibility of phenolic constituents of the grass.

Hogan et al. (1979) summarized research results concerning the conversion of nutrients to wool for the different genotypes of Australian Merino (Table 1). In most experiments, at least half the cyst(e)ine derived by intestinal absorption was converted into wool. The authors think the extent of incorporation of cyst(e)ine into wool may have been higher because it seems unlikely that all the methionine absorbed from the intestine would be converted to cyst(e)ine as the calculations assume. Hence the possibility remains that wool growth, even at the highest levels observed, was restricted by the supply of cyst(e)ine.

Sulfur requirement of sheep can be met by inorganic or organic sulfur. The maximum utilization of inorganic sulfur depends on the protein synthesis of rumen microorganisms. Durand and Komisarczuk (1988) pointed out that the amount of sulfur needed to meet microbial requirements in terms of concentrations in the rumen or of total dry matter content in the diet is inadequate. This is because sulfur availability in the diet is influenced by many factors, especially fermentable energy in the diet. Ruminal sulfur concentration is a result of a balance between supply, absorption, rate of passage and microbial utilization. This is particularly true because of the great magnitude of hydrogen sulfide

Table 1. Calculations on conversion of nutrients to wool in the different genotypes of Australian Merino.[a]

Wool, grams per 100 grams			Digestible organic matter, g/g wool growth	Wool cyst(e)ine, g/100 g cyst(e)ine absorbed[b]
Organic matter intake	Digestible organic matter intake	Total amino acids absorbed		
1.13	1.69	10.1	59.0	44.7 - 68.2
1.08	1.62	9.7	61.9	42.5 - 65.2
1.26	1.48	10.3	67.7	45.4 - 69.5
1.00	1.17	8.3	85.2	38.2 - 55.6
1.50	2.05	15.1	48.8	62.8 - 96.3
1.27	1.74	12.8	57.6	53.1 - 81.6
1.21	1.86	13.3	53.8	58.5 - 89.4
1.24	1.74	11.9	57.5	52.1 - 79.7
0.93	1.59	11.0	62.9	48.5 - 74.3
0.98	1.66	11.6	60.4	51.2 - 78.2
0.96	1.63	11.4	61.4	50.0 - 76.5
0.97	1.63	11.4	61.3	50.3 - 88.8
1.73	2.20	12.7	45.5	56.2 - 86.1

[a] Adapted from Hogan et al. (1979);
[b] Minimum and maximum values were calculated from possible range in cyst(e)ine content of wool (Reis, 1979).

absorption; therefore, the apparent optimal level of sulfide-sulfur (1.0 milligrams per liter of rumen liquor) previously suggested (Bray and Till, 1975) is very low and may lead to an underestimate of the requirement. Durand and Komisarczuk (1988) suggested that sulfur requirement of rumen microbes should therefore be assessed in terms of fermentable energy rather than in terms of total dry matter content of the diet.

Additional requirements for fiber production beyond the supply of microbial protein must be met by sulfur-containing amino acids. Reis (1979) reviewed the effects of sulfur-containing amino acids on the growth and properties of wool. He concluded that dietary supplements are usually ineffective because of degradation by rumen microbes, but abomasal, duodenal, parenteral, rumen-protected or through-drinking-water supplements of sulfur-containing amino acids can markedly alter wool growth rate. The effectiveness of supplements of sulfur-amino acids for stimulating wool growth is influenced by diet and the wool-producing capacity of sheep. For sheep receiving a moderate amount of a roughage diet, maximal responses in wool growth are obtained with an abomasal infusion of 2 to 3 grams per day sulfur-containing amino acids. Amounts larger than 6 grams methionine per day are less effective for stimulating fiber growth or may even depress it below pretreatment rates (Reis et al., 1990; Stephenson et al., 1990). The mode of action of sulfur-amino acids in stimulating wool growth requires more detailed study.

The Effects of Dietary Sulfur Content on Wool Sulfur Content and Wool Quality

Both the rate of wool growth and its sulfur content are influenced by availability of sulfur-containing amino acids. When supplements of cystine or methionine are infused into the abomasum of sheep, both wool production and sulfur content of wool are increased (Reis, 1979). The increase in sulfur content is due to increased production of high and ultra-high sulfur proteins. According to the two-stage theory of keratin synthesis in the wool follicles (Gillespie, 1983), the high-sulfur proteins of keratins may be synthesized by the stepwise addition of sulfur-rich peptides to precursors.

Wool growth is different from muscle and other tissue growth. When sheep are deficient in sulfur and energy, other tissues are mobilized in order to maintain wool growth at a certain level. Therefore, wool growth enjoys priority in the supply of amino acids over other non-fleece bearing tissues (Langlands et al., 1973). Furthermore, when sheep are supplemented with several amino acids, only cystine content in the wool is significantly changed with little or no change in other amino acids (Reis, 1979). Chemical analysis shows that the cysteine contents of low sulfur proteins, high sulfur proteins and ultra-high sulfur proteins are 6.0, 22.1 and 29.9%, respectively. The proportion of high sulfur and ultra-high sulfur proteins varies in wool. For example, the proportion of high sulfur proteins in wool can vary from 18 to 35% (Reis, 1979). As a result, wool sulfur content can be changed in response to dietary sulfur content.

Table 2. Correlation coefficients between the sulfur content and some physical characteristics of Chinese Merino wool.[a]

Physical characteristics	Mean ± standard deviation, X ± SD	Correlation coefficient with S content of wool, r[b]
Fiber strength, g	8.51 ± 1.51	+0.9666[b]
Elongation at break, %	43.05 ± 2.47	+0.7083[c]
Bundle strength, g/Denier	1.71 ± 0.18	+0.6888[c]
Work of rupture, g/cm	26.58 ± 4.94	+0.9528[c]
Specific work of rupture, g/Denier	0.54 ± 0.05	+0.5478
Initial modulus, g/Denier)	30.19 ± 4.83	+0.9252[b]
Elasticity at 10% elongation, %	53.37 ± 2.22	-0.1353
Crimp ratio, no./cm	3.23 ± 0.47	-0.2640
Whiteness, %	51.71 ± 1.31	-0.7373[c]
Scouring yield	49.57 ± 6.61	-0.3433

[a] Adapted from Qi (1989).
[b] $P < 0.01$.
[c] $P < 0.05$.

The Influence of Selection for Wool Production on Wool Sulfur Content and Interaction Between Selection and Nutrition

Selection for increased fleece weight has been shown to reduce the sulfur concentration in wool (Piper and Dolling, 1966; Reis et al., 1967; McGuirk, 1983; Qi, 1989). The effect is not entirely a dilution of a given amount of sulfur in a greater amount of wool, since total sulfur in wool is concurrently increased.

Selection for increased fleece weight may produce wool with some poorer processing characteristics due to the expected reduction in sulfur content and therefore fewer disulfide bonds and reduced fiber strength. Another important property related to intermolecular disulfide bonds is the ability of wool fibers to take and retain set, a property important in permanent pleating of worsted materials (skirts, trousers, etc.; Whiteley et al., 1975).

Qi (1989) reported that the sulfur content of Chinese Merino wool (average fiber diameter, 22.3 µm) was highly correlated with strength, elongation at break, relative strength, work of rupture, initial modulus and degree of whiteness in the same fiber (Table 2). McGuirk (1983) suggested that resistance to compression (the inverse of bulk) is positively correlated with sulfur content of the wool.

An interesting observation with respect to sulfur supplementation of sheep relates to the interaction between selection and nutrition. Williams et al. (1972) reported that responses in wool production and wool sulfur output to infusions of cyst(e)ine or methionine were much greater in sheep from a flock selected for higher fleece weight than in sheep from a flock selected for lower fleece weight (Table 3). The greater response in wool production indicates that the availability of sulfur-containing amino acids limits the productivity more severely for animals with a high genetic potential for fiber production.

The Effects of Sulfur Supplementation on Wool Diameter

For a particular sheep, the number of wool follicles actually growing fibers tends to be constant except during periods of severe undernutrition (Lyne, 1964). For non-medullated wool, the specific gravity of the clean fibers can be regarded as being constant (Connell and Andrews, 1974). The weight of wool grown by a sheep in a given period of time is therefore determined by the fiber diameter and rate of elongation of individual wool fibers. Downes and Sharry (1971) found that when the wool growth rate of Merino sheep was increased over a wide range (up to four-fold) by varying nutrition, the mean length of fiber growth per day (L) to mean fiber diameter (D) ratio (L:D) increased by about 10%. Reis (1992) reported similar results when amino acids or protein were infused in the abomasum of sheep. However, Hynd (1989) indicated that fiber length may increase more than fiber diameter as wool growth is increased by nutritional manipulation. Economically, it is desirable to increase wool production by increasing rate of elongation while holding the wool diameter constant. If fiber diameter is permitted to increase, the economic gain from increased wool production may be compromised because increased fiber diameter may reduce the value of the wool (Lupton and Shelton, 1988). By abomasally infusing lysine and methionine or zein, a protein which is devoid of lysine and tryptophan and contains a high proportion of leucine, Reis and Tunks (1976) and Reis (1979) changed the ratio of length-to-diameter and composition of wool. Significant increases (10 to 20%) in mohair production and mohair staple length were observed with negligible change (> 1 μm) in mohair diameter when Angora goats were supplemented with rumen-protected methionine or sulfate-sulfur (Bassett et al., 1981; Qi et al., 1992). Therefore, it does appear to be possible to increase fiber production while holding or even decreasing fiber diameter (i.e., improving fiber quality) through nutritional manipulation without changing follicle density.

Meeting the Sulfur-Containing Amino Acid Requirement through Genetic Engineering

Animal geneticists are researching additional methods to provide more sulfur amino acids to animals by introducing 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 only because mammals lack the pathways for cysteine synthesis other than by conversion from methionine. Bacteria synthesize cysteine from serine, an amino acid synthesized liberally in all living organisms. The two key elements in the pathway for cysteine synthesis from serine are shown in Figure 1. Genes that encode these two enzymes, isolated from the bacteria *Escherichia coli* (Boronat, 1984) and *Salmonella typhimurium* (Rogers, 1990), have been sequenced and studied for transfer to sheep (Franklin, 1988; Ward and Nancarrow, 1991). 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 cystine will be absorbed and transported to the wool follicles to be used for wool growth.

Conclusions

Wool production is characterized by a high demand for amino acids containing sulfur. Sulfur-containing amino acids and inorganic sulfur compounds offer the sheep industry potential for increasing efficiency of wool production, especially in sheep of high wool-producing ability. Differences in sulfur requirement and response to sulfur supplementation between fiber-producing sheep and breeds selected for meat production might arise because the fiber-growing sheep is relatively slow growing and late maturing and

Table 3. Response of genetically high and low fleece weight sheep to sulfur-containing amino acid supplementation.[a]

Treatment	Wool production, μg/cm²/day	Sulfur output, %	Sulfur content, μg/cm²/day
	High fleece weight		
No supplementation	734	2.99	22.2
2 g/day L-cystine	1,114	3.45	38.4
2.5 g/day DL-methionine	1,190	3.53	42.0
	Low fleece weight		
No supplementation	639	3.48	22.2
2 g/day L-cystine	714	3.77	26.9
2.5 g/day DL-methionine	757	3.74	28.3

[a] Adapted from Williams et al. (1972).

Figure 1. The two key elements in the pathway for cysteine synthesis from serine.

1: Serine + Acetyl-CoA $\xrightarrow[\text{serine transacetylase}]{}$ O-Acetylserine + CoA

2: O-Acetylserine + H_2S $\xrightarrow[\text{O-acetylserine sulfydrylase}]{}$ Cysteine + Acetate has been specifically selected for wool production. Dietary sulfur content and selection for increased fleece production have been shown to influence wool sulfur content, which in turn relates to the magnitude of several important wool characteristics. Research to date indicates a need to develop special nutritional strategies which include further consideration of sulfur if we are to reap optimal economic benefits from our sheep industry.

Literature Cited

Allaway, W.H. 1970. The scope of the symposium: outline of current problems related to sulfur in nutrition. pp. 3 - 4. In: O.H. Muth and J.E. Oldfield (Eds.) Symposium: Sulfur in Nutrition. The PVI Publishing Co., Westport, CT.

Agricultural Research Council. 1980. The Nutrient Requirements of Ruminant Livestock. pp. 166 - 168. Commonwealth Agricultural Bureau. Slough, England.

Bassett, J.W., B.C. Baldwin, Jr., M.C. Calhoun and R.H. Stobart. 1981. Plasma methionine and mohair response to dietary rumen-protected methionine in Angora goats. Texas Agric. Exp. Sta. PR-3904. College Station, TX.

Boronat, A. 1984. Location on the *Escherichia coli* genome of a gene specifying O-acetylserine (thiol) lyase. J. Gen. Microbiol. 130:673-685.

Bradbury, J.H. 1973. The structure and chemistry of keratin fibers. Adv. Protein Chem. 27:111-211.

Bray, A.C. and A.R. Till. 1975. Metabolism of sulfur in the gastro-intestinal tract. In: I.W. McDonald and A.C.I. Warner (Eds.) Digestion and Metabolism in the Ruminant, pp. 243 - 260. Univ. New England. Armidale, Australia.

Brown, G.H. and H.N. Turner. 1968. Response to selection in Australian Merino sheep. II. Estimates of phenotypic and genetic parameters for some production traits in Merino ewes and an analysis of the possible effects of selection on them. Aust. J. Agric. Res. 19:303-322.

Chestnut, A.B., G.C. Fafey, L.L. Berger and J.W. Spears. 1986. Effects of sulfur fertilization on composition and digestion of phenolic compounds in tall fescue and orchardgrass. J. Anim. Sci. 63:1926-1934.

Connell, J.P., and M.W. Andrews. 1974. The variability of the specific gravity of Australian wools and the implications for the airflow measurement of diameter. J. Text. Inst., 65:1-5.

Daly, R.A., and H.B. Carter. 1955. The fleece growth of young Lincoln, Corriedale, Polwarth and fine Merino maiden ewes under housed conditions and unrestricted and progressively restricted feeding on a standard diet. Aust. J. Agric. Res. 6:476-513.

Downes, A.M., and L.F. Sharry. 1971. Measurement of wool growth and its response to nutritional changes. Aust. J. Bio. Sci. 24:117-130.

Durand, M., and K. Komisarczuk. 1988. Influence of major minerals on rumen microbiota. J. Nutr. 118:249-260.

Franklin, I.V., CSIRO, Australia. 1988. Personal communication.

Gillespie, J.M. 1983. The structural proteins of hair: Isolation, characterization and regulation of biosynthesis. pp. 475 - 510. In: L.A. Goldsmith (Ed.) Biochemistry and Physiology of the Skin. Oxford Univ. Press. NY.

Hale, W.H., and U.S. Garrigus. 1953. Synthesis of cystine in the wool from elemental sulphur and sulphate sulphur. J. Anim. Sci. 12:492-496.

Hogan, J.P., N.M. Elliott and A.D. Hughes. 1979. Maximum wool growth rate expected from Australian Merino genotypes. pp. 43 - 59. In: J.L. Black and P.J. Reis (Eds.), Physiological and Environ-mental Limitations to Wool Growth. Univ. New England Publishing Unit, Armidale, Australia.

Hynd, P.I. 1989. Effects of nutrition on wool follicle cell kinetics in sheep differing in efficiency of wool production. Aust. J. Agri. Res. 40:409-417.

Johnson, W.H. 1971. Metabolism of radioactive sulfur from elemental sulfur, sodium sulfate and methionine by lambs. J. Anim. Sci. 32:778-781.

Kandylis, K. 1984. Toxicity of sulfur in ruminants: review. J. Dairy Science. 67:2179-2187.

Langlands, J.P., H.A.M. Sutherland and M.J. Playne. 1973. Sulfur as a nutrient for Merino sheep. II. The utilization of sulfur in forage diets. Brit. J. Nutr. 30:537-543.

Lu, X.W. and Y. Jiang. 1981. Sheep Science. Press of Agricultural Science. Beijing, China. pp. 205 - 209.

Lupton, C.J. and M. Shelton. 1988. Should we be selecting for finer wool? Texas Agric. Exp. Sta. Res. Cen. Tech. Rep. 88-2:1-12. San Angelo, TX.

Lyne, A.G. 1964. Effects of adverse nutrition on the skin and wool follicles in merino sheep. Aust. J. Agri. Res., 15:788-801.

Marston, H.R. 1955. In: J. Hammond (Ed.) Progress in the Physiology of Farm Animals, Vol. 2. Chapter II. Butterworths Scientific Publication, London.

McGuirk, B.J. 1983. Physiological and biochemical consequences of selection. In: W. Haresigh (Ed.) Sheep Production. pp. 556 - 558. Butterworths Press, London.

National Research Council. 1980. Mineral Tolerance of Domestic Animals. pp. 466 - 490. National Academy of Sciences. Washington, DC.

National Research Council. 1985. Nutrient Requirements of Sheep. pp. 15 - 16. National Academy of Sciences. Washington, DC.

Pegg, A.E. and P.P. McCann. 1982. Polyamine metabolism and function. Ame. J. Physic. 243:212-217.

Piper, L.R. and C.H.S. Dolling. 1966. Variation in the sulfur content of wool of Merino sheep associated with genetic differences in wool-producing capacity. Aust. J. Biol. Sci. 19:1179-1182.

Qi, K. 1986. A study on the genetic parameters and optimizing selection methods of the major traits for improving the excellent fine-wool sheep (now called Chinese Merino). Acta Agriculturae Universitatis Pekinensis. 12(2): 201-212.

Qi, K. 1988. The relationship of sulfur and wool production: A review. Chinese J. Sheep Goat Industry, No.1:15-18. Nanzhou, China.

Qi, K. 1989. The relationships between the sulphur contents and some physical characteristics of Chinese Merino wool and the influence of selection for wool production on the wool sulfur contents. Acta Veterinaria Et Zootechnic Sinica, 20(2):112-116.

Qi, K., C.D. Lu, F.N. Owens and C.J. Lupton. 1992. Sulfate supplementation of Angora goats: Metabolic and mohair responses. J. Anim. Sci. 70:2828-2837.

Qi, K., F.N. Owens and C.D. Lu. 1993. Effects of sulfur deficiency on performance of fiber-producing sheep and goats: A review. Small Ruminant Research (In Press).

Reis, P.J. 1979. Effects of amino acids on the growth and properties of wool. pp. 223 - 242. In: J.C. Black and P.J. Reis (Eds.) Physiological and Environmental Limitation to Wool Growth. Univ. New England Publishing Unit, Armidale, Australia.

Reis, P.J. 1992. Length growth and diameter relationships of Merino wool fibers. Wool Techn. Sheep Breed. XL(2):52-55.

Reis, P.J. and P.G. Schinckel. 1963. Some effects of sulfur-containing amino acids on the growth and composition of wool. Aust. J. Biol. Sci. 16:218-230.

Reis, P.J., D.A. Tunks, O.B. Williams and A.J. Williams. 1967. A relationship between sulfur content of wool and wool production by Merino sheep. Aust. J. Biol. Sci. 20:153-163.

Reis, P.J. and D.A. Tunks. 1976. The influence of abomasal supplement of zein and amino acids on wool growth rate and plasma amino acids. J. Agri. Sci. 86:475-481.

Reis, P.J. and D.A. Tunks. 1982. Inhibitory effects of ethionine, an analogue of methionine, on wool growth. Aust. J. Bio. Sci. 35:49-62.

Reis, P.J., D.A. Tunks, R.D.G. Rigby, S.G. Munro and R.W. Edols. 1986. Effects of methioxinine, an analogue of methionine, on the growth and morphology of wool fibers. Aust. J. Biol. Sci. 39:209-223.

Reis, P.J., D.A. Tunks, S.G. Munro. 1990. Effects of the infusion of amino acids into abomasum of sheep, with emphasis on the relative value of methionine, cysteine and homocysteine for wool growth. J. Agri. Sci. (Camb.). 114:59-68.

Robards, G.E. 1979. Regional and seasonal variation in wool growth throughout Australia. In: J.L. Black and P.J. Reis (Eds.), Physiological and Environmental Limitations to Wool Growth. pp. 1 - 42. Univ. New England Publishing Unit, Armidale, Australia.

Rogers, G.E. 1990. Improvement of wool production through genetic engineering. Trends Biotech. 8:6-13.

Seljeanski, V.M. 1959. Effect of inorganic sulphur on the growth of wool in lambs. Ovtsevodstvo, 11:20-22. As cited by M.L. Ryder in Wool Growth in 1968. Academic Press. NY.

Shelton, M. 1993. Personal communication.

Starks, P.H., W.H. Hale, U.S. Garrigus and R.M. Forbes. 1953. The utilization of feed nitrogen by lambs as affected by elemental sulfur. J. Anim. Sci. 12:480-492.

Stephenson, R.G.A., G.R. Suter, D.A. Pritchard and M.D.J. Martin. 1990. Studies of wool growth responses to 2-hydroxy-4-(methylthio) butanoic acid, Alimet, an analogue of methionine. Aust. J. Experi. Agri. 30:447-482.

Ward, K.A. 1984. The role of embryo gene transfer in sheep breeding programmes. In: D.R. Lindsay and D.T. Pearce (Eds.) Reproduction in Sheep, pp. 279 - 285. Cambridge Univ. Press, Cambridge, U.K.

Ward, K.A., I.R. Franklin and J.D. Murray. 1986. The direct transfer of DNA by embryo microinjection. Proc. 3rd World Congress on Genetics Applied to Livestock Production. pp. 6 - 19. Lincoln, NE.

Ward, K.A., J.D. Murray and C.D. Nancarrow. 1989. The current status of gene transfer in domestic animal breeding. J. Anim. Sci. 67(Suppl.):61.

Ward, K.A. and C.D. Nancarrow. 1991. The genetic engineering of production traits in domestic animals. Experientia 47:913-921.

Whiteley, K.J., M.E. Campbell, C. Siu and V.G. Kulkarni. 1975. Mechanical and chemical properties of wool fibers exhibiting extreme variations in chemical composition and crimp form. Proc. 5th Int'l. Wool Text. Res. Conf., Aachen, 4:57-66.

Williams, A.J. 1979. Speculation on the biological mechanisms responsible for genetic variation in the rate of wool growth. In: J.L. Black and P.J. Reis (Eds.) Physiological and Environmental Limitations to Wool Growth. pp. 337 - 354. New England Publishing Unit, Armidale, Australia.

Williams, A.J., G.E. Robards and D.G. Saville. 1972. Metabolism of cystine by Merino sheep genetically different in wool production. II. The responses in wool growth to abomasal infusion of L-cystine or DL-methionine. Aust. J. Biol. Sci. 25:1269-1276.

Yeates, N.T.M., T.N. Edey and M.K. Hill. 1975. Animal science: Reproduction, climate, meat, wool. pp. 299 - 352. Pergamon Press, Australia.