

A Review of Amino Acid Requirements for Fiber Growth of Sheep and Angora Goats¹

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Summary

Absorbed amino acid requirements for fiber growth in sheep and Angora goats were calculated based on the amino acid composition of keratin proteins in wool and mohair and on the maintenance requirements of the animals. According to these estimated amino acid requirements, bacterial protein is markedly deficient in amino acids containing sulfur (S), followed distantly by threonine, histidine and isoleucine. Supplementation with S-containing amino acids in a ruminally-protected form or postruminally for sheep and Angora goats has been inconsistent in stimulating fiber growth. This caused us to reevaluate the effects of amino acid supplementation on fiber growth in sheep and Angora goats. Reported adverse effects from an excess supply of methionine and/or lysine on fiber growth in sheep and Angora goats are reexamined from the perspective of an amino acid imbalance. Perhaps a lysine imbalance could increase fiber growth through elongation of the fiber length while maintaining a constant or decreased fiber diameter.

Key words: amino acid, fiber growth, requirement, imbalance, sheep, Angora goat.

Introduction

Amino acid requirements for optimum fiber growth have never been deter-

mined. Supplementation with amino acids and/or proteins for sheep (Reis, 1989; Stephenson et al., 1990) and Angora goats (McGregor and Hodge, 1989; Sahlu and Fernandez, 1992) in a ruminally-protected form or postruminally have resulted in different fiber growth responses depending upon the supplement levels and basal diets used. Researchers have tested various supplemental amino acids and/or protein levels seemingly at random. In some cases, supplementation with certain amino acids and/or proteins has reduced fiber production (Reis et al., 1990; Sahlu and Fernandez, 1992). However, most scientists have reported that supplementation stimulated fiber growth (Bassett et al., 1981; Reis, 1982; Stephenson et al., 1990; McGregor and Hodge, 1989) with increases in both fiber length and diameter (Reis and Sahlu, 1993). An increased staple length is desirable whereas an increase in diameter decreases fiber quality and value (Lupton and Shelton, 1988). Explanations for the various results generally have been limited to discussions of specific functions of individual amino acids (McGregor and Hodge, 1989; Reis et al., 1990; Stephenson et al., 1990; Sahlu and Fernandez, 1992).

Amino acid requirements of sheep and Angora goats could be estimated based on the theory of summation of amino acid requirements for mainte-

nance and fiber growth (Owens and Pettigrew, 1989). The adverse effects of excess supplementation with amino acids such as methionine and lysine may reflect an amino acid imbalance. Finally, a titration type of study is proposed that could verify the predicted amino acid requirements for fiber growth and test the hypothesis that fiber production can be increased by elongating fiber length without increasing fiber diameter.

Amino Acid Supply – The Primary Limitation for Fiber Growth

The maximum capacity of a sheep or Angora goat to grow fiber (wool or mohair) is determined by the animal's genotype. Genotype determines the maximum number, density and characteristics of fiber follicles. It also influences the competition between the skin and other tissues for nutrients (Black and Reis, 1979). Maximum genetic potential for fiber growth can be reduced by restricting the nutrient

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supply during fetal and early post-natal life (Black and Reis, 1979). In an adult animal, the rate of fiber growth is determined by physiological and environmental factors (Reis, 1982). Fluctuations in the supply of nutrients to the fiber follicles can alter growth rate and properties of fiber. Rate of fiber growth in an individual sheep can vary over a four-fold range as nutrient supply changes (Reis, 1982).

Wool and mohair growth generally are limited by amino acid supply to the skin. The energy requirement for fiber growth represents less than 10% of the basal metabolic rate in sheep and generally is not a limiting factor (Black and Reis, 1979; Black, 1987). Kempton (1979) concluded that 50 grams of absorbed amino acids per 1 Mcal of metabolizable energy (ME) was optimal for wool growth. Hynd (1989) confirmed that the maximum rate of wool growth was approached when protein flow to the abomasum was 150 grams per day in sheep fed energy at a maintenance level. The amino acid composition of mohair protein is closely analogous to wool protein and contains acetylated alanine as the N-terminal amino acid (Parris and Swart, 1975). In general, Angora goats are smaller but grow fiber at a higher rate than Rambouillet sheep (Gallagher and Shelton, 1972). Therefore, more amino acids may be needed by Angora goats than by sheep for maximal fiber growth (Bassett et al., 1981; McGregor and Hodge, 1989; Calhoun et al., 1990; Qi et al., 1992). Most studies (Black and Reis, 1979; Kempton, 1979; Black, 1987; Hynd, 1989; McGregor and Hodge, 1989) suggest that the major nutritional limitations for fiber production are: 1) the amount of amino acids available to the follicle for fiber growth; and 2) the composition of those amino acids.

Amino Acid Requirements for Maintenance, Fiber Growth and Importance of S-Containing Amino Acids

The amino acid requirements for optimum fiber growth have not been determined. Owens and Pettigrew (1989) suggest that the need for a specific amino acid to meet a targeted

performance could be estimated by summing the requirements for maintenance and performance. Such an approach should be particularly useful for animals with a relatively slow growth rate. Because maintenance comprises only a small fraction of the total amino acid requirement for rapidly growing animals such as rats or chicks, maintenance needs for amino acids are relatively unimportant. In contrast, for non-growing and adult animals, production is proportionally low; this increases the quantitative importance of maintenance. The maintenance requirements for amino acids in growing birds proved to be closely related to the amino acid composition of keratin ($r = 0.97$; Owens and Pettigrew, 1989), whereas the requirements for growth paralleled the amino acid composition of animal muscle (Owens and Pettigrew, 1989). Presumably, the absorbed amino acid requirements for maintenance and growth of ruminants can be estimated from information pertaining to non-ruminants (Owens, 1986). According to this methodology, we calculated amino acid requirements for maintenance of a 40-kg sheep or Angora goat (non-pregnant, non-lactating; Table 1). These values were adapted from two sets of experiments: one reported by Leveille et al. (1960) with chickens; and the other reported by Shin et al. (1991 and 1994) and Owens et al. (1994) with rats. The values from these two sets of experi-

ments are similar except for arginine and leucine. The difference in arginine requirements might be due to the inability of birds to synthesize arginine. Adult mammals synthesize arginine by way of the urea cycle. In contrast, birds excrete uric acid and body synthesis of arginine is low, so they require more arginine for maintenance. However, no information is available about whether extrahepatic tissues (especially skin) of sheep or Angora goats can synthesize arginine. The reason for the difference in these leucine requirements for maintenance is not known. We averaged the estimates from these two sets of experiments and regarded these averages as an estimate of amino acid requirements for maintenance. To estimate the full amino acid requirements of sheep and Angora goats, amino acids deposited in wool and mohair must be added to these values.

Astbury and Harris (as referenced by Lu and Jiang, 1981) summarized more than 40 reports on amino acid composition of keratin fibers from sheep and goats (Table 2). The average of these amino acid compositions should be useful as an approximation of the absorbed amino acid requirements of sheep and Angora goats for fiber growth. Unlike muscle protein deposition, fiber is a sink for amino acids; no turnover (breakdown and re-synthesis) of keratin protein occurs after keratinization (Qi, 1988). Deposited amino acids cannot be

Table 1. Calculated amino acid requirements for maintenance of a 40-kg sheep or Angora goat.

Amino acids	Requirement, grams per day ^a	Requirement grams per day ^b	Average, grams per day
Arginine	-3.54	2.40	-0.57
Histidine	0.37	0.80	0.59
Isoleucine	1.22	1.45	1.35
Leucine	1.13	2.48	1.81
Lysine	0.85	0.57	0.71
S-amino acids ^c	1.07	1.80	1.44
Phenolic amino acids ^d	1.56	1.19	1.38
Threonine	1.07	1.48	1.28
Tryptophan	0.19	0.38	0.29
Valine	1.13	1.22	1.18

^a Adapted from Shin et al. (1991; 1994) and Owens et al. (1994).

^b Adapted from Leveille et al. (1960).

^c Including methionine, cysteine and cystine.

^d Including phenylalanine and tyrosine.

remobilized during periods of amino acid deficiency (or imbalance) to support other physiological functions of the animal body. More research is needed to verify the predicted amino acid requirements for fiber growth.

The sum of maintenance and keratin requirements can be compared with the amino acid composition of ruminal bacteria (Table 3) to deter-

mine how many grams of bacterial protein need to be digested and absorbed to meet the demand for each amino acid. From such a calculation, the most limiting amino acids are pinpointed as being the S-containing amino acids. Reis and Tunks (1978) identified methionine, lysine, leucine and isoleucine as the most important amino acids for wool

growth. Postruminally infusing individual amino acids other than methionine, cyst(e)ine and lysine into sheep does not significantly affect wool production (Reis, 1979; Hynd, 1989).

According to the digestible dry matter intake (DMI) of sheep and Angora goats reported by Huston et al. (1988) and Huston (1994), the estimated bacterial protein production in the rumen of a 40-kg animal will reach 78 grams per day (National Research Council, 1985) when concentrations of sulfur, phosphorus and other nutrients do not limit bacterial growth (Owens and Qi, 1992). This amount of bacterial protein will meet requirements for all amino acids except for those containing sulfur. Supplementation of S-containing amino acids postruminally or with ruminally undegradable protein(s) having a high concentration of S-containing amino acids is necessary for maximal fiber production in sheep and Angora goats.

The Concept of Amino Acid Imbalance and its Application for Fiber Growth

Amino acid imbalance infers that the dietary amino acid composition is far removed from that required for optimal protein synthesis by the animal body. More specifically, Harper (1964) defined amino acid imbalance as a condition in which a

Table 2. Amino acid composition of keratin proteins.^a

Amino acids	Content, %	Range, %
Alanine	4.27	4.1 - 4.4
Arginine	10.35	6.0 - 10.4
Aspartic acid	6.92	2.3 - 7.3
Cystine	12.05	7.3 - 13.1
Glutamic acid	14.69	12.9 - 16.0
Glycine	6.50	5.6 - 7.8
Histidine	0.70	0.5 - 0.8
Leucine and isoleucine	11.30	9.7 - 11.5
Lysine and hydroxylysine	2.88	2.2 - 3.3
Methionine	0.71	0.2 - 0.9
Phenylalanine	3.75	1.6 - 4.0
Proline	6.63	4.4 - 7.2
Serine	9.86	9.4 - 10.3
Threonine	6.58	6.4 - 6.8
Tryptophan	1.25	0.7 - 1.8
Tyrosine	5.23	2.9 - 6.1
Valine	4.76	2.8 - 5.5
Total ^b	108.43	—

^a Adapted from Astbury and Harris as referenced by Lu and Jiang (1981).

^b The literature often lists total amino acids above 100% (105 to 112%) because hydrolysis of protein adds 18 grams to the molecular weight of each amino acid.

Table 3. Amino acid requirements for maintenance and fiber growth, and bacterial protein needed to meet these requirements.^a

Amino acids	Requirements			Bacterial protein	
	Maintenance, grams per day	Fiber growth, grams per day	Total, grams per day	Composition, grams per 100 grams ^b	Requirement, grams per day ^c
Arginine	-0.57	1.04	0.47	5.10	11.5
Histidine	0.59	0.07	0.66	2.00	48.5
Isoleucine	1.35	0.56	1.91	5.70	41.9
Leucine	1.81	0.57	2.38	8.10	36.7
Lysine	0.71	0.29	1.00	7.90	15.8
S-amino acids	1.44	1.28	2.72	3.89	95.8
Phenolic amino acids	1.38	0.90	2.28	10.00	28.5
Threonine	1.28	0.66	1.94	5.80	41.8
Tryptophan	0.29	0.13	0.42	1.38	38.0
Valine	1.18	0.48	1.66	6.20	33.5

^a For a 40-kilogram sheep or Angora goat growing 10 grams of clean, dry wool or mohair per day, equivalent to about 3.7 kilograms clean, dry fibers per year, which is the average production level of Texas sheep and Angora goats (Texas Agricultural Statistics Service, 1993). However, half of the sheep and Angora goats in Texas produce more than this level of fiber.

^b Adapted from Owens et al. (1994) and Shin et al. (1991, 1994).

^c Digestibilities of amino acids in bacterial protein were 0.73 for S-amino acids, 0.68 for histidine, 0.80 for the others (Owens and Qi, 1992).

dietary surplus of an amino acid exists, but the amino acid in excess is not the one that limits growth. An amino acid imbalance in animals can be created either by the addition of relatively small amounts of one or two amino acids or by the addition of a large quantity of a mixture of indispensable amino acids devoid of the growth-limiting amino acid (Mercer et al., 1989). When the surplus amino acid is catabolized, the metabolism of other amino acids in the body is increased. The most consistent physiological change is decreased feed intake. One biochemical change that occurs rapidly in animals fed an imbalanced diet is a change in their plasma amino acid patterns (Young and Fukagawa, 1988). The plasma concentration of the most limiting amino acid falls and feed intake is depressed. The altered plasma amino acid pattern may directly or indirectly reduce feed intake (Harper et al., 1970; Owens and Pettigrew, 1989). Depression of feed intake and growth are characteristic signs of amino acid imbalance. From a nutritional standpoint, an amino acid imbalance results from adding one or more non-limiting amino acids to a low-protein diet. Although the excess does not reach a toxic level, it depresses feed intake and growth. Supplementation with the growth-limiting amino acid enhances feed intake in non-ruminants (directly in diet; Harper et al., 1970) and ruminants (postruminally; Bassett et al., 1981; Calhoun et al., 1990). The initial metabolic response to an amino acid imbalance is stimulation of protein synthesis by the liver (Harper et al., 1970; Young and Fukagawa, 1988; Owens and Pettigrew, 1989). This decreases the size of the body pool of the limiting amino acids. The enzymes involved in the first step of protein synthesis have Michaelis constants (K_m) about 20 to 100 times less than those of the respective amino acid catabolic enzymes. These general properties enhance efficiencies of use of the limiting amino acid for tissue protein synthesis while providing the metabolic machinery for catabolizing the excesses of non-limiting amino acids. This occurs because, under normal conditions, the tissue amino acid concentrations fall between the K_m values for each respective cata-

bolic enzyme and amino acyl synthetase (anabolic enzyme). The idea of control of amino acid metabolism by enzyme characteristics (K_m) was discussed by Krebs (1972), who emphasized that excess free amino acids are not stored. The increased amino acid concentrations in blood after a meal automatically increases the rate of amino acid degradation. Adaptive increases of activities for most of the catabolic enzymes are not caused by increases of specific substrates, but by the total amino acids absorbed so that the high levels of non-limiting amino acids increase degradation of the limiting amino acids (Krebs, 1972; Anonymous, 1988). This is responsible for accentuation of the decrease in the concentration of the limiting amino acids in blood and muscle of animals during early stages of an amino acid imbalance. Based on the above discussion, we suggest that an amino acid imbalance in sheep and Angora goats might depress keratin synthesis. The specific effects of a particular amino acid imbalance on different proteins of keratin may vary. An amino acid imbalance could change the composition and other properties of fiber, which might improve fiber quality (i.e., reduced fiber diameter) if used wisely.

Effects of Methionine on Fiber Growth and Methionine Imbalance

Keratin protein is rich in cyst(e)ine but contains only small amount of methionine (Gillespie, 1983). Fiber growth requires an abundant supply of cyst(e)ine. Methionine provides cysteine via the transsulfuration pathway (Finkelstein, 1970); it can also be catabolized via transamination (Anonymous, 1988). At levels of methionine normally absorbed by sheep, about three-quarters of the methionine is converted to cysteine (Finkelstein, 1970).

Reis (1967), Reis et al. (1973, 1990) and Hynd (1989) all demonstrated that abomasal infusion of 1 to 3 grams of L-methionine per day stimulated wool growth in sheep on a maintenance plane of nutrition. Similar results were observed in Angora goats for mohair growth (Bassett et al., 1981; McGregor and Hodge, 1989;

Calhoun et al., 1990; Sahlou and Fernandez, 1992; Owens, 1993, unpublished data). Qi and Lupton (1994) reviewed the methionine functions for fiber growth in sheep and goats. In addition, Webb (1990) reviewed studies on the absorption mechanism of amino acids and concluded that methionine usually is absorbed very efficiently. Phillips et al. (1979) observed that moderate amounts of methionine stimulated the absorption of threonine when threonine concentration in the intestine was low. Similarly, Reiser and Christensen (1971) observed that intestinal absorption of basic amino acids (arginine, lysine, ornithine) were increased by supplementation with methionine. Because D-methionine can be converted to L-methionine in mammalian tissues (Reis, 1979), L-, DL- or D-methionine should be equally effective for promoting wool growth (Reis, 1989). Therefore, supplementation of sheep and Angora goats with DL-methionine may prove more economical than that with L-methionine (Owens and Qi, 1992).

Effects of methionine on fiber growth are dose-related. Supplementation with more than 3 grams per day has proved less effective than lower rates for stimulating fiber growth; dose rates higher than 6 grams per day have depressed fiber growth (McGregor and Hodge, 1989; Reis et al., 1990). Steele and Benevenga (1979) suggested that transamination products of methionine metabolism contribute to the adverse effects of high methionine concentration in rats. This pathway has been identified in sheep (Benevenga et al., 1983) which led Reis et al. (1990) to examine the effects of 3-methylthiopropionic acid (MTP) on wool growth of sheep. Infusion of MTP into abomasum had no effects on any components of wool growth (Reis et al., 1990). Therefore, the reduction in wool production from high amounts of methionine are not due to the MTP.

In rats, growth-retarding effects of excess methionine can be alleviated through feeding additional glycine which stimulates the hepatic transsulfuration pathway (Harper et al., 1970). However, the adverse effects of high

concentrations of methionine on wool growth were neither reduced nor prevented by glycine (Reis et al., 1990).

After testing and eliminating all the above concepts, Reis et al. (1990) still could not explain the adverse effects of a high level of methionine supplementation. We suggest that the adverse effect on fiber growth of excess methionine and, to a lesser extent, of cystine may be associated with an amino acid imbalance as defined by Harper (1964). Excess methionine may depress keratin synthesis by increasing amino acid catabolism whereas moderate amounts of methionine are beneficial. Christensen (1964) reported that excess methionine adversely affected cellular levels of other amino acids. This observation was supported further by studies of Phillips et al. (1979) and Webb (1990).

Effects of Methionine on Fiber Growth when Balanced with Other Amino Acids

Reis et al. (1990) showed that methionine and homocysteine were equally effective for enhancing wool growth when infused abomasally but singly in equimolar amounts. Equimolar amounts also have been administered when mixed with other amino acids. Reis et al. (1990) abomasally infused mature Merino wethers fed at maintenance with 45 grams per day of a mixture of ten amino acids. Wool growth was increased by 86%. When methionine in the mixture was replaced by an equimolar amount of homocysteine, fiber growth was reduced significantly. When betaine, folic acid and vitamin B₁₂ were added in an attempt to stimulate pathways of methionine regeneration, the fiber diameter, length growth and volume were appreciably increased, but wool growth remained reduced compared to when methionine was in the mixture. Mercer et al. (1989) suggested that three points are paramount when formulating an amino acid diet. First, total amount of available nitrogen; second, distribution of nitrogen between the indispensable amino acids (IAA) and dispensable amino acids (DAA); and third, relative concentration of amino acids within the indispensable amino

acid group. Studies with growing rats as a model indicated that DAA are synthesized from IAA at too slow a rate to support maximum growth. This means that an appropriate IAA/DAA ratio is important. In a growth trial with weaned rats, Mercer et al. (1987) found that when the IAA:DAA ratio fell below 0.14, animals lost body weight. Body weight gain was half-maximal at a ratio of 0.29 and body weight gain was maximized in the 0.9 to 1.0 ratio range. Higher ratios eventually reduced body weight gain. Following this idea, regeneration of methionine from homocysteine may be too slow to support maximum fiber growth (Reis et al., 1990). This situation also could induce an amino acid imbalance.

Effects of Lysine on Fiber Growth and Lysine Imbalance

The role of lysine in fiber growth is not clearly understood. According to Reis and Tunks (1978), lysine is not an important compound for the synthesis of wool protein because wool fiber is not rich in lysine (Table 1). Rogers (1964) reported that lysine is used primarily for synthesis of proteins in the inner root sheath, the area of the fiber follicle where fiber growth is initiated. Lysine concentration of the inner root sheath protein is about four times that of fiber. Busch (1965) reported that the importance of lysine for fiber growth may be related to its high content in histone proteins which are active in cell division.

Sahlu and Fernandez (1992) intra-peritoneally infused Angora goats with lysine (2 grams per day) and methionine (1 gram per day). Keratin contains about 3% lysine compared with 13% S-containing amino acids (Table 1). Because the lysine infusion level was higher than required for optimal fiber growth, an amino acid imbalance probably was induced. Clean mohair production (grams per 100 cm² of skin area) and mohair diameter both were increased by methionine infusion, but both were decreased by lysine infusion. However, fiber length was increased 22% ($P < 0.015$) by lysine infusion. Nitrogen balance (grams per day) was higher ($P < 0.05$)

in the control than in the lysine infused group.

Parsons (1990) suggested that excess lysine can elevate kidney arginase and decrease arginine synthesis which may depress growth; this has been shown in pigs and chicks. Keratin contains about 10% arginine, so a lysine-induced arginine deficiency may depress mohair production as in the study of Sahlu and Fernandez (1992). Decreased arginine synthesis and increased arginine degradation may reduce urea synthesis (Milner, 1985; Rogers and Visek, 1985). This could explain why plasma urea N was lower for the methionine and lysine infused groups than for the control group (Sahlu and Fernandez, 1992). If lower plasma urea had been due to improved nitrogen utilization, nitrogen balance should have been increased, not decreased as was observed.

A Hypothesis to Manipulate the Rate of Elongation and Diameter in Fiber Growth

Studies with mixtures of amino acids established that zein, a protein devoid of lysine and tryptophan, failed to stimulate wool growth. This was attributed to the absence of lysine in zein (Hynd, 1989; Reis, 1989). However, effects on wool growth were unusual. Length growth rate was increased but fiber diameter was reduced. The concentration of high-tyrosine proteins in wool was reduced (Gillespie, 1983). According to the two-stage theory (bulb cell division to form microfibrils and keratinization) of keratin synthesis in wool follicles (Gillespie, 1983; Hynd, 1989; Qi and Lupton, 1994), the high-sulfur proteins of keratin may be synthesized by the stepwise addition of sulfur-rich peptides to microfibrils in the keratogenous zone. The precise nutrient requirements of the cells in the bulb may differ from those in the keratogenous zone with the former being related to other body cells and the latter having a much higher requirement for the S-containing amino acids.

Hynd (1989) tattooed midside patches (10 cm-by-10 cm) on the bodies of two sheep fed a mainte-

nance diet. He infused the sheep via the abomasum with water for 14 days, zein (80 grams per day) for 14 days, then water for 21 days. Mitotic rate of bulb cells was estimated in skin biopsy samples. Total number of mitotic nuclei and cortical cell size (length, diameter, volume) were measured. Zein reduced the rate of proliferation of follicle bulb cells (Table 4). A deficiency of the amino acid lysine has a greater effect on bulb cell division than on keratinization, leading to less cells migrating from the bulb (Hynd, 1989). If these fewer cells migrated to the keratogenous zone and were supplied with sufficient S-containing amino acids per cell, larger cells and finally coarser fibers might be produced. On the other hand, if more cells migrated from the bulb as a result of lysine supplementation, but less than normal amounts of S-containing amino acids were available in the keratogenous zone, smaller cells and ultimately finer fibers might be produced. This hypothesis could explain the reduction in fiber diameter and increase in fiber length in the experiments with sheep deficient in lysine (Hynd, 1989) and Angora goats with excess lysine (Sahlu and Fernandez, 1992). The lysine levels imposed in the studies of Hynd (1989) and Sahlu and Fernandez (1992) were opposite extremes so that fiber production was reduced in both cases. Further studies are required to establish the effects of changing the ratio of lysine to methionine on fiber

growth in sheep and Angora goats. Hence, it may prove possible to increase fiber production by enhancing the rate of elongation while maintaining or even decreasing fiber diameter.

Conclusions

The absorbed amino acid requirements for maintenance and fiber growth in sheep and Angora goats were approximated by summing the average composition of keratin proteins comprising wool and mohair with maintenance requirements of animals not growing fiber. The effects of amino acid supplementation on fiber growth appear to be related to the absorbed amino acid composition and the specific requirements for individual amino acids in keratin synthesis of individual animals. A dose-related response in fiber growth usually is found when animals are supplemented with methionine. This phenomenon indicates that optimal fiber production requires an optimal methionine level; too little results in a deficiency, too much causes an imbalance. The effect of lysine supplementation on fiber growth is less clear. Both an optimal lysine level and an ideal ratio of lysine to methionine are required for optimal fiber growth. Lysine supply may alter fiber diameter. A titration study is required to examine the impact of lysine and methionine on fiber growth and quality in sheep and Angora goats.

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Table 4. Effects of zein on fiber growth, bulb cell division and cortical cell size.^a

Sheep, number	Treatment	Fiber length, μm per day	Fiber diameter, μm	Mitotic rate, nuclei per bulb per hour	Cortical cell size		
					Length, μm	Diameter, μm	Volume, μm^3
26	Pre-zein	312 ^b	19.7 ^b	20 ^b	102 ^b	4.9 ^b	643
	Zein	346 ^c	14.2 ^c	8 ^c	108 ^c	4.5 ^c	574
	Post-zein ^c	nd	nd	23 ^b	nd	nd	nd
27	Pre-zein	226 ^b	19.3 ^b	17 ^b	96 ^b	5.2 ^b	681
	Zein	287 ^c	16.2 ^c	7 ^c	101 ^c	5.0 ^b	663
	Post-zein ^c	nd	nd	12 ^d	nd	nd	nd

^a Adapted from Hynd (1989).

^{b,c,d} Differences within a column and within a sheep followed by different superscripts differ at $P < 0.05$.

^c nd = not determined.

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