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# SOMATIC NUTRIENT REQUIREMENTS OF RUMINANTS

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## INTRODUCTION

Ruminant species supply over half the meat and essentially all of the milk and animal fiber consumed by man, as well as being a significant source of draft power and fuel. The unique digestive and metabolic strategies of these animals make them particularly efficient in the conversion of food sources not suitable for human consumption. There are, however, some substantial inefficiencies in these strategies so that production per unit of available nutrient is usually lower for ruminants than for nonruminant domestic species. The correction or amelioration of these inefficiencies offers one of the most promising and attractive means of increasing food supplies from existing sources.



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The salient feature of ruminant digestive function is the massive anaerobic pregastric fermentation with accompanying physiological mechanisms; these sort and reprocess food to achieve maximum exposure of ingested food to microbial action. Through this process, complex polysaccharides such as cellulose are degraded, large amounts of microbial protein are synthesized, and water-soluble vitamins are produced. Thus, the nutrients presented for absorption differ widely from those ingested. The host animal must therefore be metabolically adapted to the utilization of the nutrients absorbed, not those ingested. This review examines the metabolism of the host animal as distinct from the microbiological symbiota, describes the ways in which this metabolism is organized to accommodate the nutrient supply, and provides a basis for devising methods of improving the efficiency of nutrient retention in ruminants. The term "somatic" denotes the aggregate of all tissues in the animal except for the associated microorganisms in the digestive tract, while "whole-body" is meant to describe somatic plus microbial nutrition.

Since interest in somatic nutrition is very recent, and because experimental methods are only now being developed to study the subject, it will be necessary to discuss methodology. It may also be necessary to draw a number of inferences from the comparison of whole-body metabolism with estimates of the microbial contribution.



## ENERGY REQUIREMENTS

The principal energy source for functioning ruminants is volatile fatty acid (VFA) (59). Indeed, very little available carbohydrate ever reaches the small intestine. Mono- and oligosaccharide are rapidly and completely degraded by rumen microorganisms, and complex carbohydrates, if digested at all, will be degraded to VFA. A fraction of native starch from seeds may escape rumen alteration and arrive at the small intestine but this amount is small and rarely exceeds 10% of the total starch fed, even when all-grain diets are fed (32).

In contrast, VFAs are produced in both the rumen and the hindgut and are absorbed directly from the organs to supply in excess of 90% of all the nonprotein energy used by the animal (59). This basic VFA economy is reflected in fundamental differences in energy metabolism. Blood glucose levels are low and relatively constant (63). Glucose tolerance and renal threshold are also very low (72). Insulin is less responsive to glucose influx, and blood glucose levels (44) are less responsive to insulin increases as compared to nonruminants. On the other hand, insulin levels respond very rapidly to propionate influx (44). These differences indicate that, not only is the major metabolic energy substrate different in ruminants, but also the mechanisms for control of metabolism and transport are not those usually considered.

The change from a glucose to a VFA economy occurs during the first few

weeks of life and is usually complete when the rumen begins to function. The rate at which the change to ruminant function is made can be altered somewhat by feeding and management, but blood glucose declines regardless of these changes and so appears to be independent of functioning rumination (56).

The glucose necessary for maintaining blood glucose levels, Krebs cycle intermediates, lactose synthesis, and other processes with obligatory glucose requirements is obtained by gluconeogenesis from propionate mostly (59), with some possibly obtained from glucogenic amino acids (9). There is very little fat in a ruminant diet, and producing ruminants deposit or secrete rather large amounts of fat, which is synthesized mainly from acetate. Hence, fat tissue, with its need for glycerol in fat synthesis, is probably a net user rather than a supplier of glucose to the economy (7).

There has been a great volume of work studying the relative efficiencies of utilization of individual VFAs (59). The current thinking is that, if there are adequate gluconeogenic precursors available, there is little difference in energetic efficiency of the three main VFAs. However, absorbed VFAs as a group tend to be utilized with only about 90% of the efficiency of glucose (43).

There are pathological conditions resulting from the relative scarcity of certain VFAs under certain physiological conditions. A lack of gluconeogenic precursors (i.e. propionate) during heavy lactation in dairy cows or late pregnancy in multiparous ewes can result in acetonemia with morbidity and even death. Conversely, a decreased proportion of acetate (which may result from high grain feeding) can cause low milk fat syndrome in dairy cows (38).

There appears to be little difference between ruminants and nonruminants in fasting heat production (FHP). Ruminant species were included in Brody's summary of FHP related to body weight and were not anomalous as a group (18). Indeed, sheep especially have, if anything, a lower FHP than the interspecies norm (77). However, the energy requirement for maintenance is usually considerably higher for ruminants than for nonruminants of similar size. For instance, the NRC digestible-energy (DE) recommendation for maintenance of an adult boar is 96 kcal/$BW^{0.75}$ kg/day (where BW stands for body weight) (52) while for an adult ram it is 192 kcal/$BW^{0.75}$ kg/day (53).

These comparisons suggest an unusually high heat increment of feeding (HIF). There are three main sources of this increased heat loss. The first, which is nonsomatic, is the heat of fermentation of the rumen and hindgut microorganisms, which, owing to their high metabolic activity, is considerable. The second component of HIF is associated with the physical act of eating and, to a lesser extent, rumination (76). This heat loss is in excess of what might be expected on the basis of the muscular work of prehension and digesta transport. It is accompanied, during eating, with some rather dramatic shifts in water compartmentation (23). The ruminant eats for a much longer time than most other species and, additionally, ruminates for an additional period of time (10).

It appears, then, that the heat loss associated with ingestion of food is a major source of energy inefficiency in the somatic ruminant.

The third component of HIF is the metabolic activity of gut tissue. Although gut tissue contains only 7% of the protein of the body, it accounts for 20% of the total heat production (76). Approximately half of this heat can be accounted for as the heat cost of protein synthesis. The fractional rate of protein synthesis is considerably higher for gut tissue than for any other major tissue in the body (76). The remainder is possibly due to substrate metabolism in gut tissue, which is a major site of substrate oxidation. Under most circumstances, even when animals are fed to achieve a significant amount of starch digestion in the small intestine, the gut is a net utilizer of glucose (34). There is also considerable conversion of propionate to lactate in gut tissue (35). Ruminants usually have a considerably greater weight of gut tissue in relationship to body size than nonruminant species. Thus, the high metabolic activity of gut tissue is a major contribution to the heat losses of ruminants.

As significant as these heat losses are, those associated with eating, ruminating, and gut metabolism, together with microbial fermentation heat, account for less than half of the total HIF (76). This suggests that the major loss of energy is associated with the basic metabolism in all tissues. While this is true of all species, the proportion of loss to total energy metabolized is higher for ruminants than for nonruminants. This has been ascribed to the lower efficiency of metabolism of VFA as compared to either glucose or long-chain fatty acid (17).

It has long been acknowledged that, even under the best environmental and dietary conditions, the efficiency of production of domestic ruminants is much less than that of nonruminants. Although some of these inefficiencies are related to the fibrous nature of ruminant feeds and the necessary fermentative losses in the rumen, a number of them are somatic in nature and may, perhaps, yield to dietary or environmental manipulations in order to improve the utilization of digested energy for productive purposes.

It is difficult to assign an energy requirement to somatic tissues as separate from the whole animal. Even HIF is composed of both microbial and somatic effects. Heat of fermentation is clearly microbial and heat production by gut tissues is clearly somatic, while the heat cost of eating is probably related to both. DE requirements, even when corrected for heat of fermentation, are higher for ruminants on an equal metabolic body size basis as compared to nonruminants (52, 53). Since the metabolizable energy requirements for maintenance vary greatly with energy level of intake and body composition (76), it is difficult to use this measure as an indication of somatic efficiency. As a consequence, the $K_m$ values presented by Blaxter (17) probably constitute the closest approximation of somatic energy use. It is suggested therefore, that the energy requirement for maintenance of somatic tissue is 10% higher for ruminant species than for nonruminants of comparable physiological age and size.

## AMINO ACID REQUIREMENTS

One of the most important influences of the pregastric fermentation of ingested food by ruminants is the very effective degradation of protein and the synthesis of microbiological protein from the degraded protein as well as from nonprotein nitrogen compounds such as urea. The process of microbial protein synthesis is so massive that the total protein requirement of producing animals can be met with microbial protein (74). Under practical situations, some dietary protein escapes degradation to be digested and absorbed post-ruminally, but microbial protein remains the major amino acid source for the host (46). In view of this, and considering the observation that the amino acid content of microbial protein is relatively unaltered by dietary conditions (14), it had long been considered a moot question to determine somatic amino acid requirements.

However, observations that post-ruminal infusions of methionine could increase wool growth and nitrogen balance (29) rekindled interest in this subject. It was seen that certain protein sources such as fish meal, blood meal, and corn gluten supported improved nitrogen retention and that these same properties could be bestowed upon other protein feeds by heat, aldehyde, or tannic acid treatment (25). These effects are associated with the ability of the feed protein to pass through the rumen fermentation process undegraded and yet be available for gastric and enteric digestion. This "undegraded" or "escape" protein has three possible advantageous properties. First, it may increase the total amount of amino acid nitrogen available for absorption since there is a limitation to the amount of protein that can be synthesized by rumen microorganisms. Second, even if all the nitrogen released by proteolysis in the rumen could be trapped by rumen microorganisms, the synthetic process diverts approximately 25% of the nitrogen into non-amino-acid compounds such as nucleic acids as well as into unusual amino acids that make no contribution to the protein metabolism. Third, the escape protein may alter the amino acid pattern of absorbed protein to improve its biological value.

Processes to protect individual amino acids from rumen degradation have been developed in order to manipulate the biological value of absorbed proteins (55). It has thus been demonstrated that the amino acid supply can, indeed, be manipulated in a variety of ways but results have so far been rather erratic. In making such manipulations, it is critical to know the somatic nutrient requirements for amino acids, since dietary alterations made in ignorance of the metabolic requirements are, at best, only speculative.

Clearly, the supply of essential amino acids available to somatic metabolism is that coming from the combination of microbial protein and undegraded food protein entering the post-ruminal digestive tract. The efficiency of utilization of this amino acid supply depends upon the digestibility of the individual amino acids and upon their relative proportions compared to the somatic requirements of the animal.

The amino acids that are metabolically essential (that is, not synthesized somatically) for the dairy cow, were shown by Black et al (15) to be fundamentally the same as for the rat. Arginine was synthesized in the animals but histidine was not. There were differences in the extent of incorporation of $^{14}C$ depending upon the energy substrate used for synthesis (16), but this gave no indication of the relative quantitative requirements for individual amino acids.

Ruminants respond to changes in amino acid patterns supplied post-ruminally (21, 42, 79). There is very little difference among protein sources fed orally unless they contain, or are treated to contain, large amounts of escape protein. However, nitrogen balance is improved when proteins of high quality for nonruminants, such as casein, are given directly into the post-rumen digestive tract. Conversely, poor quality proteins such as zein and gelatin given in this way generally depress nitrogen retention (42). The amino acid pattern found in sheep carcasses was much better utilized than a pattern similar to plasma free amino acids when these patterns were given intravenously (79).



## *Methodology*

It therefore appears that the somatic metabolism behaves much like the whole-body metabolism of a nonruminant and therefore could be studied using models similar to that used by Rose et al (62). However, the problem of ruminal amino acid synthesis must be resolved if reliable data are to be obtained. This has been approached in two ways. The pre-ruminant young has been used in studies of amino acid requirements (30, 78). Since the rumen in these animals is nonfunctional, the amino acids presented for absorption are essentially those ingested. Diets can therefore be altered to provide varying amino acid patterns to the animal. It is necessary, however, in the use of this model to assume that the somatic metabolism resembles that of the ruminating young. That is a very tenuous assumption in the light of the fundamental metabolic changes that accompany development of ruminating capacity. The changes in energy metabolism are well documented, but detection of alterations in amino acid utilization still awaits better methodology. If such changes are observed, the pre-ruminant model has little, if any, advantage over the use of nonruminant species such as swine. Additionally, the pre-ruminant is in a very transitory condition and occurs only during the milk-feeding period (40). Maintenance, gestation, or lactation requirements cannot be examined in pre-ruminant young.

The most promising technique in the investigation of somatic effects of amino acids is the use of post-ruminal administration of experimental regimens. Usual routes of administration have been abomasal, duodenal, or intravenous infusions. Using these infusions, nutrients can be supplied directly to absorption or utilization sites without undergoing microbial alteration. The infusions have been done in both the presence and absence of a functional rumen. If the

rumen is discharging digesta into the abomasum, the rumen effluent must be considered as the diet and the infusate as a supplement. This method has been used extensively to attempt to determine the limiting amino acids in the nutrient supply to ruminating animals under a variety of conditions (60).

Researchers studying amino acid adequacy are faced with the problem of choosing an appropriate indicator of response to changes in amino acid patterns. Theoretically, biological value is the absolute measure of the correspondence of a specific amino acid pattern to somatic requirements. However, it is very difficult to measure and, in the ruminating animal, is actually not a function of dietary amino acid supply, but is influenced by a great variety of factors (1, 5). Under conditions where protein degradation by rumen microorganisms exceeds protein synthesis so that appreciable ammonia is lost, the errors can be significant (3, 5). When amino acids or proteins are administered post-ruminally either intragastrically or intravenously, biological value can be determined and gives a good indication of the adequacy of amino acid supply. This technique has been employed by Asplund et al (8) and Storm & Ørskov (70).

Although it is not an absolute measure, nitrogen balance is very useful in comparing and titrating animal response to different amino acid patterns. Nitrogen balance is perhaps the most reliable and responsive measure available at this time (3). It has been used by most of those engaged in amino acid studies for ruminants. Most of the variation in nitrogen balance in a given experiment occurs in the urinary losses, specifically, urea losses. Consequently, urinary urea excretion has been used as a measure of protein adequacy. However, even in animals receiving their amino acids intravenously it was less precise and responded to a lesser degree than did nitrogen balance (71). Similarly, plasma urea levels are closely correlated with nitrogen balance but actual measurements were less useful than was nitrogen balance (71).

It has been proposed that plasma levels of free amino acids can be a useful indicator of the relationship of a given amino acid supply to its requirement. This was extensively reviewed by Bergen (13). The two-phase curve, with its inflection at the requirement, has generally corresponded with nitrogen balance and other data for many amino acids. Plasma free methionine (58, 71), threonine (58), and valine (48) have all responded as expected to graded levels of ingestion of these amino acids. However, lysine failed to respond with an increase in plasma levels of the free amino acid at intakes beyond those that produced maximum nitrogen balance (8, 58, 75). When phenylalanine was administered in increasing amounts in the absence of tyrosine, plasma free phenylalanine did not respond in any way to increasing infusion, but plasma tyrosine levels increased dramatically at the levels at which nitrogen balance indicated adequate phenylalanine supply (9). It appears, therefore, that responses in plasma free amino acids can be used for some amino acids but not for others.

The rate of oxidation of lysine has been used to indicate an excess of lysine (19). The increased oxidation rate observed for the amino acid may also explain the failure to observe the expected increase in plasma free levels of lysine at above requirement intake.

## *Indirect Studies*

The identification of limiting amino acids provides some inferences concerning potentially valuable supplementation. The most consistently limiting amino acid is methionine. In almost every instance where post-ruminal supplementation has been effective, methionine was the first limiting amino acid (60). There have also been some responses to lysine, especially as a second limiting amino acid (20, 70). Other amino acids have occasionally improved nitrogen retention. Among these are threonine (57), histidine (22), and phenylalanine (22, 24). However, even if the response to added amino acids can be titrated, the resulting values reflect only the inadequacies of the amino acid supply under the dietary conditions of the trial and not the somatic requirements of the host. Requirements can be approximated if some measure of the amino acid content of rumen effluent or abomasal ingesta can be made. Although ingesta sampling can be done rather simply, quantitative inferences are meaningful only if rates of digesta flow are measured. This involves the use of markers or of re-entry cannulae, which increases the cost and difficulty and reduces the precision of the determinations. Additionally, these techniques can be useful only if the amino acid being supplemented is clearly limiting under the dietary conditions of the study.

Nimrick et al (57, 58) infused a number of amino acids into sheep receiving a diet in which all the nitrogen was from nonprotein sources. They reported amino acid requirements as "supplemental amino acid needs" with the assumption that these values indicated the deficiencies of microbial protein. The data did, indeed, indicate which amino acids were limiting and the general order in which limitation occurred but, in the absence of data regarding the available amino acid supply from the rumen, cannot be considered to be somatic requirements.

Similar work with a variety of diets was reported for methionine by Shelling et al (65). In the latter experiment, response to methionine varied with the diets used. Fenderson & Bergen (28) used estimates of abomasal contents and abomasal flow rates in connection with response to supplementation with methionine, lysine, threonine, and tryptophan. They estimated requirements for methionine in growing steers but observed that the animal responded only to methionine, so that the requirements for the other three amino acids did not exceed the abomasal flow.

This general approach was more precisely pursued by Storm & Ørskov (67–70). These workers used isolated microbial protein administered in-

tragastrically so that "dietary" amino acid supply was controlled and known. The biological value of the dietary protein was determined and a mixed amino acid supplement given to bring the original diet to the value of 100%, based on the dietary intake. By serial deletion of individual amino acids, the order and extent of limitation for each was determined. This technique gave rational values for the appropriate requirement levels of the limiting amino acids, but values for those not limiting can be considered as simply not exceeding the levels in microbial protein.

## *Direct Studies*



Requirement estimates for all amino acids can be obtained by using chemically defined diets with crystalline amino acids. For ruminants, these must be administered post-ruminally and the rumen may not contribute measurable protein to the system. This state is achieved by a dual infusion method. Since the main energy substrate is VFA and the somatic tolerance for glucose is very low, a way must be derived to administer VFA. Intraruminal infusion of VFA accompanied by appropriate buffering has proven to be the most effective way of supplying energy in this form (59). This also has the advantage of keeping the rumen irrigated in the absence of any oral feeding with a resultant virtual cessation of protein synthetic activity.

In animals receiving energy by intraruminal infusion of VFA, intragastric or intravenous infusions of amino acids and other nutrients can be studied systematically with controlled and manipulatable dietary conditions. Using this model with intravenous amino acid infusions, data have been obtained for the somatic requirements of methionine (71), lysine and arginine (2, 8, 73) leucine (36), phenylalanine (9), valine (48), threonine (4), and tryptophan (unpublished data). In each study, the general design was the same. An amino acid mixture representing the most recent estimates of adequacy was used. This pattern began as the amino acid spectrum in sheep carcass (79) and was altered to incorporate the information from requirement trials as these were completed. The amino acid in question was deleted and added back at appropriate levels while the mixture remained isonitrogeneous with the addition or deletion of the required amounts of glycine. The level of amino acid that supported the highest nitrogen retention was taken to be the required level. Where appropriate, plasma free amino acid levels were also used to corroborate the nitrogen balance data. Trials were conducted at the energy level of 105 kcal per kg $BW^{0.75}$, which is an adequate maintenance allowance.

From these trials, a tentative requirement list for the essential amino acids for maintenance in the sheep was prepared (Table 1). The data, representing only a first estimation of these requirements, have been compared with figures for requirements of some amino acids obtained by other methods previously described and summarized by Lewis & Mitchell (39) (Table 1). It is observed

that there is substantial agreement for both lysine and methionine but that the estimates of threonine requirement obtained directly by infusion are lower than previous estimates. However, the previous estimates were made in animals with intact functioning rumens, which seldom supply less threonine than the required amount. It has already been shown that the requirement of most amino acids does not exceed the gastric supply.

The spectrum of amino acids obtained by intravenous infusion was tested for biological value using intragastric administration of casein enriched with amino acids to match the pattern listed in Table 1 plus isoleucine at the levels in casein. The biological value of this mixture, calculated from the regression of urinary nitrogen on nitrogen intake, was 103 ± 8%; it very closely approximated the pattern of requirement for sheep at maintenance. Corresponding values for casein alone and gelatin infused intragastrically were 87 ± 4% and 7 ± 7% (6).

Although there appears to be very efficient retention of this pattern of amino acids for maintenance, several questions remain to be answered:

1. Maintenance as defined by the experimental design includes wool growth. This function involves the selective incorporation into a nonrecycling pool and thus differs from the exact definition of maintenance.
2. The influence of nonessential amino acids is not fully explained. It is possible that, if nonessential amino acids were limiting, the nitrogen available from the deamination of surplus essential amino acids could be used for nonessential amino acid synthesis and give false high estimates for biological value. However, the improvement over casein of the supplemented casein suggests that this was not the case. The role and importance of both level and composition of the nonessential amino acids remain subjects for further work.



**Table 1** Comparison of estimates of amino acid requirements for ruminants

| Amino acid | Intravenous model (6) (mg/kg $BW^{0.75}$) | Other estimates (39) (mg/kg $BW^{0.75}$) | Intravenous model (6) (% of essential) | Factorial estimate (66) (% of essential) |
|---|---|---|---|---|
| ARG | 219 | | 9.9 | |
| HIS | <62.5 | | 2.5 | 2 |
| LEU | 375 | | 16.8 | 15 |
| LYS | 437 | 408–<545 | 18 | 7 |
| MET | 225[a] | 105– 207 | 7.2 | 3[b] |
| PHE | 250 | | 11.4 | 9[c] |
| THR | 187 | 260– 340 | 7.6 | 13 |
| TRY | <62.5 | | 2.8 | 4 |
| VAL | 187 | | 9.6 | 11 |

[a]No other source of sulfur amino acids was available.
[b]Methionine only. Total sulfur amino acids were 14%.
[c]Phenylalanine only. Total aromatic amino acids were 22%.

3. The use of intravenous amino acid administration begs the question of absorptive efficiency and possible digestive tract degradation. However, the fact that intragastric infusion was used to test the adequacy of the pattern determined by intravenous administration suggests that absorption influences were slight.

There is considerable evidence that the qualitative as well as the quantitative requirements for growth, lactation, and active reproductive functions may be different from those for maintenance, especially when maintenance includes wool growth. Thus, the data presented can probably not represent optimum amino acid patterns in producing animals. This criticism is valid, and concerted effort is needed to ascertain the requirements for producing ruminants. However, the figures for maintenance provide a useful beginning. First of all, maintenance is the only productive function that does not involve the deposition of tissue and, therefore is the only function in which the amino acid accrual cannot be measured. Perhaps some factorial system incorporating maintenance estimates and tissue accumulation, adjusted for incorporation efficiency, might prove useful in describing the somatic requirements for all productive functions.

This factorial method has most recently been attempted by Smith (66). He considered the amino acid composition of body tissues and the relative growth of each and calculated amino acid requirements from these values. His results are in substantial agreement with the values obtained by direct infusion studies (Table 1), but differ from the values obtained from sheep carcass alone. The requirement values for both the factorial and infusion methods vary from the National Research Council recommended values for swine (52) in that they are relatively lower in methionine and phenylalanine.

It is not known if amino acid metabolism differs between ruminants and nonruminants. This is largely a result of the paucity of information on specific amino acid metabolic pathways in ruminants, since amino acid supply is so difficult to control. There are, however, some indications that the control mechanisms and, perhaps, at least quantitative differences may occur. For example, branched-chain amino acids are released intact from muscle tissue in ruminants and the activity of enzymes associated with their degradation is markedly lower in muscle tissue when compared with nonruminants (41). In contrast, adipose and mammary tissue are relatively more active in branched-chain amino acid degradation in ruminants (26).

There also appear to be some differences in sulfur amino acid metabolism. The methionine requirement for sheep appears to be lower than would be expected on the basis of the content of sulfur amino acids in wool. There was no increase in that value in the absence of microbial protein or of exogenous cysteine (71). Benevenga et al (11, 12) observed that less than 10% of

methionine degradation occurred via transsulfuration in intact sheep. Thus the mechanisms and kinetics of cysteine biosynthesis in ruminants, especially sheep, would appear to be a very fruitful field for further studies. With experimental models now available, such studies should be undertaken.

## VITAMIN REQUIREMENTS

### *Fat-Soluble Vitamins*

There are no data to indicate specific needs, by microorganisms, for any fat-soluble vitamins and little reason to suppose that the ruminant differs from other mammals in its metabolism of these nutrients.

Vitamin K is synthesized by rumen microorganisms if natural feed supplies are otherwise deficient (47). Ruminants are fairly inefficient in the conversion of β-carotene to vitamin A (54) and there is some evidence to suggest that cattle have a specific β-carotene requirement as distinct from vitamin A (33). However, whole-body requirements would not appear to differ from the specific somatic requirements.

### *Water-Soluble Vitamins*

It has long been recognized that rumen microorganisms produce water-soluble vitamins (47). There have been no studies on the rate of destruction or incorporation of these nutrients. However, since in vivo studies always show a net increase in levels, it appears likely that supply will exceed demand under all normal conditions. The water-soluble vitamin requirements of pre-ruminant calves were studied some time ago. Deficiency symptoms for most of the B complex were demonstrated and optimum replacements determined (37). There were no substantial differences between calves and other nonruminant animals. However, it might be expected that the shift in the base of energy economy that occurs when the animal becomes ruminant might alter the requirements for at least those vitamins involved in carbohydrate metabolism.

There has been considerable recent interest in thiamin. Deficiency symptoms are observed when thiamin antimetabolites such as amprolium are fed or when natural sources of thiamin analogues such as bracken fern are eaten (27). More recently the condition of polioencephalomalacia or cerebrocortical necrosis was observed in animals fed high levels of rapidly degradable carbohydrates (64). This condition appears to be due to a thiamin analogue produced by an unusual rumen microflora rather than to a destruction and, hence, a simple deficiency of thiamin.

Using an infusion technique, Mueller & Asplund (51) were able to supply a thiamin-free diet to sheep. After a long period of time, blood lactate and

pyruvate were elevated and erythrocyte transketolase responded dramatically to thiamin pyrophosphate in deficient sheep but no alterations in central nervous system tissue were detectable. Moreover, all of these indications of deficiency were eliminated by supplementation with 135 mg $kg^{-1}d^{-1}$ of thiamin hydrochloride, a level similar to that usually recommended for nonruminants. The slow development of biochemical lesions and the absence of specific physical pathologies would suggest that the thiamin requirement is considerably lower than the levels supplemented.

The only other water-soluble vitamin to be studied in ruminants is niacin. There is some suggestion that supplemental niacin might be beneficial in very high producing animals such as rapidly growing calves and lactating cows in peak production, but the results are quite erratic. It has been suggested that niacin reduces the risk of acetonemia in dairy cows (31) but there is not very much metabolic evidence of this. It appears, however, that if the effects are real, the site of action is in the rumen and not the somatic tissues.

There is little reason to expect that somatic requirements for water-soluble vitamins exceed those observed in nonruminant species. It may even be that some of the requirements are lower. In any event, rumen synthesis appears to be adequate under an extremely wide variety of dietary conditions.

## INORGANIC NUTRIENTS

In contrast to the organic nutrients, where microbial alteration of structure can change the ingested nutrients to increase or decrease supply, there is no basis to assume that mineral nutrients will be augmented or decreased by passage through the rumen. Only three conditions might obtain in which somatic requirements would vary from the whole-animal requirements. The first would be an increase or a decrease in availability attributable to the function of rumen microorganisms. The second condition would be a requirement by the microflora exceeding that of the somatic metabolism. The third would occur when the rumen microorganisms required an element in order to produce a specific organic compound for the somatic metabolism.

The influence of the first two conditions can be examined using phosphorus as an example, while the third is epitomized in the incorporation of cobalt into cobalamine.

Phosphorus availability varies widely between species and between dietary sources. Phytate phosphorus is used with varying efficiency by a number of species, but the ruminant appears to be able to use this form of phosphorus essentially completely, with the rumen being the primary site of phytase

activity (61). However, Meredith & Asplund (unpublished data) demonstrated appreciable phytase activity in the small intestine of sheep. This activity increased during phosphorus deficiency, which indicates that the rumen is not the only source of phytate degradation. This results in an apparently lower whole-body dietary requirement for the element as compared with nonruminants, although this difference may only be due to the greater availability of dietary phosphorus. This destruction of phytate might in turn influence the availability of those trace elements that depend on phytate. It would appear, then, that recommended dietary allowances for phosphorus and trace elements, especially those that are traditionally inflated to compensate for lower availability, for the ruminant are certainly not greater and are perhaps less than those for nonruminant species.

The relationship between somatic and microbial requirements for phosphorus is more difficult to assess. There is considerable recycling of phosphorus to the rumen via the saliva and, although both salivary and rumen phosphorus levels are decreased in phosphorus deficiency, rumen levels are usually quite high. In a deficiency, one of the most striking symptoms is loss of appetite. It has long been debated whether this was due to decreased activity of rumen microorganisms or to somatic effects. Recent work by Milton & Ternouth (49) indicates that the lowered food intake is due to somatic influences. These researchers reduced recycling by exteriorizing the parotid salivary ducts and then feeding a phosphorus-deficient diet. Unsupplemented animals deprived of recycled phosphorus had only marginally reduced nutrient digestibilities but drastically impaired food intakes. Supplementation via the abomasum was just as effective in restoring food intake as was supplementation into the rumen. This supports the concept that food intake reduction is a somatic effect and that rumen microorganisms therefore do not have a higher phosphorus requirement than does the somatic metabolism. This is further supported by the observation that in vitro preparations perform optionally at phosphorus levels below those observed in the deficient state in this experiment (50).

Ruminants have an apparent whole-body requirement for cobalt. This is a result of microbial synthesis of cobalamine. The somatic system needs only cobalamine, and injections of cobalt are ineffective against a dietary cobalt deficiency. An absolute requirement of the microorganisms for cobalt has not been established. Growth and metabolite production by some species is influenced by cobalt supplementation (45), but there is no evidence that cobalt is involved in any reactions other than incorporation into cobalamine and numerous related analogues. Thus, we have a possible requirement of an element by the microorganisms but a requirement for the vitamin cobalamine specifically by the somatic tissue.

## SUMMARY

On the basis of existing information it is, perhaps, useful to propose tentative preliminary figures for somatic nutrient requirements (Table 2). Such a proposal may serve as a focus for research to clarify more precisely the somatic requirements for a given production function in a given species. The requirements, therefore, are presented as interspecies generalizations and are calculated per kilogram of metabolic body size for the maintenance of adult animals. Only those nutrients for which there are some experimental data are included, so the absence of a given nutrient is an indication that it has not been studied. The figure for energy was derived by subtracting from the metabolizable energy for maintenance those heat losses associated with bacterial action and with prehension and transport of food. The resulting value was then increased by an amount representing the relative inefficiency of VFA, as compared with glucose metabolism. Amino acid values are essentially those obtained by intravenous administration. Water-soluble vitamin values except for thiamin were not listed because they were not expected to differ from whole-body requirements. Thiamin data were based on the work of Mueller & Asplund (51).

The most obvious need is for definitive values for the amino acid requirements for productive functions and for water-soluble vitamin data. In the absence of such data, experiments with supplementation of these nutrients will continue to be haphazard and arbitrary.



**Table 2** Suggested somatic requirements for the maintenance of adult sheep

| Nutrient | Somatic requirement[a] |
|---|---|
| Metabolizable energy | 475 |
| ARG | 220 |
| HIS | 65 |
| ILE | 250 |
| LEU | 375 |
| LYS | 435 |
| MET | 225 |
| PHE | 250 |
| THR | 190 |
| TRY | 65 |
| VAL | 190 |
| Thiamin | 100 |
| Phosphorus | 140 |

[a]Metabolizable energy requirement measured in kcal/kg protein$^{0.75}$. All other nutrient requirements measured in mg/kg BW$^{0.75}$.

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