PROTEIN LIMITS TO PRODUCTION IN RUMINANTS

J. P. HOGAN*

Summary

Although the extent of protein synthesis in non-ruminants depends on the total amounts of nutrients available, the efficiency of protein synthesis is determined by the balance of essential amino acids and by the ratio of amino acids to energy absorbed from the digestive tract. There is a lack of similar information for ruminants. Data are presented for sheep fed on forages to show that the proportions of essential amino acids derived from the intestines are probably fairly well balanced for most types of protein synthesis except wool growth, for which the sulphur amino acids are grossly deficient. The ratio of amino acids to metabolizable energy derived following digestion is shown to change with the protein content of the diet. An indication is given of the meagre information available! on amino acid requirements for various productive processes, on the types of forages that could be eaten in sufficient amounts to meet these requirements, and on ways in which protein limitations to production can be overcome.

I. INTRODUCTION

A major part of animal production may be regarded as the synthesis of protein by the tissues in the forms of milk, meat, foetus and hair or wool. Protein synthesis in ruminants proceeds at about the rates indicated in Table 1, and the purpose of this paper is to consider how much dietary protein the animal needs to maintain synthesis at these rates. However, the requirements of an animal for any nutrient can be considered only in relation to other nutrients. Crampton (1964) has pointed out that there are good biological reasons why energy should be regarded as the primary nutrient and why the adequacy of other nutrients should be judged in relation to the energy supply. Evidence to support this claim has been obtained mainly from studies with poultry, rats and pigs, animals in which the proportions of nutrients derived from the digestive tract can readily be altered. From these studies, it is now realised that, although a major factor controlling production is the total amount of diet consumed, the efficiency with which nutrients are used and often the nature of the final product, will be determined by two other factors; these are, the ratio of digestible protein to energy and the relative proportions of essential amino acids in the digested protein (Agricultural Research Council 1963, 1967). The data in Table 2 for pigs and poultry indicate that changes occur in protein and amino acid requirements with differing physiological states. With these data in mind it is clear that the title of this paper

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*C.S.I.R.O., Division of Animal Physiology, Ian Clunies Ross Animal Research Laboratory, Prospect, New South Wales.

TABLE 1

Amounts **of** *nitrogen incorporated into protein during various forms* **of** *production in ruminants**

Product	Rate of Production	Protein Formed/Day (g)	Nitrogen (g/day)
Cow milk	18.2 kg/day	650	105
Ewe milk	1 kg/day	57	9
Steer gain	0.9 kg/day	142	23
Lamb gain	0.23 kg/day	35	6
Cattle hair	—	—	1.5
Sheep wool	4.5 kg clean/yr	12.5	2
Cattle foetus†	45 kg calf	1.81	29
Sheep foetus†	6 kg lamb	31	5

*Data obtained or calculated from Agricultural Research Council (1965).

†Average during last month of pregnancy.

can be redefined in terms of efficiency of conversion by asking the question "How can a diet be balanced so that any desired level of protein synthesis can be achieved with the minimal quantity not only of protein but of total diet". In other words, "How can a diet be balanced for maximum efficiency of production."

This question has been investigated extensively for poultry and pigs and information is readily available (Agricultural Research Council 1963, 1967). However, despite much study, progress along these lines with ruminants has been slow, mainly because of alterations to dietary components through microbial activity in the rumen. Because of this, it has not been possible until recently either to predict from dietary composition the nutrients derived by the animal following digestion or to know the extent to which nutrients such as amino acids added to the diet are altered in composition before absorption from the digestive

TABLE 2

Estimates **of** *requirements** **of** *non-ruminants for digestible protein? and essential amino acids‡*

	Pigs		Poultry	
	1.4 to 4.5 kg	9 to 20 kg	Chicks 0 to 4 weeks	Laying Hens
Valine	5.0	2.5	4.0	3.7
Cystine + Methionine	6.5	3.5	3.5	3.6
Isoleucine	6.5	3.5	3.8	3.3
Leucine	7.0	3.5	7.0	4.6-8.0
Phenylalanine + Tyrosine	5.0	2.5	6.0	4.6
Lysine	11.0	5.5	5.0	3.3
Histidine	2.5	1.0	2.0	?
Arginine	—	—	6.0	5.3
Threonine	4.5	2.5	2.8	2.7
Tryptophan	1.5	0.75	1.0	1.0
Digestible protein†	69	55	64	47

*Derived from Agricultural Research Council 1963, 1967.

†Digestible protein expressed as g/Mcal Metabolizable Energy.

‡Amino acids expressed as g/100 g crude protein (N x 6.25).

tract. The position is now somewhat improved although great gaps in knowledge still exist. In this review, it is intended to see the extent to which nutrients derived from the digestive tract of ruminants achieve a balance considered desirable for various physiological processes in non-ruminants. Data will then be presented on the quantities of nutrients that must be derived from the digestive tract to support given levels of production and on the amounts of forages that must be eaten to supply these nutrients. Finally, an indication will be given of ways of achieving a better balance of nutrients in a diet.

II. PROTEIN DIGESTION IN THE RUMINANT

Protein digestion in the ruminant must be considered in two parts involving first the microorganisms of the reticulo-rumen and second the enzymic digestion that occurs particularly in the small intestine. In practice, the effects of microbial digestion are most conveniently assessed by measuring the quantities of protein that pass from the abomasum, and in this article such data will be referred to as digestion in the stomach, that is rumen, reticulum, omasum and abomasum. The mechanisms involved in protein digestion in the stomach have recently been reviewed (Smith 1969). In brief, part at least of the nitrogen (N) that enters the rumen both from the diet and from endogenous sources is converted by the microorganisms to ammonia; part of this ammonia is subsequently re-incorporated into protein by the microorganisms while the remainder is largely absorbed from the rumen. The amount of protein that passes from the reticulo-rumen will be greater or less than that consumed depending on the balance between synthesis from dietary N + endogenous N, and ammonia absorption. Synthesis of protein in turn appears to be controlled by the availability to the micro-organisms of energy released during fermentation in the rumen (Walker 1965); Hungate 1966; Hogan and Weston 1970). With sheep fed roughage diets, about 60 per cent of the energy digested in the whole tract is apparently released in the rumen. Hence, the extent of protein synthesis will be related to the amount of digestible energy supplied by the diet; furthermore, since metabolizable energy (ME) forms a relatively constant proportion of digestible energy (Armstrong 1964; Graham 1969), it is not surprising, as the data in Figure 1 indicate, to find a relationship between the fate of dietary N and the balance between N and ME supplied by the diet. These data, recalculated from Hogan and Weston (1970), indicate that there is a net gain of N during passage of food through the stomach when the dietary N to ME ratio is less than about 12 to 14 g/Mcal i.e. when the diet provides less than about 75 to 90 g protein/Mcal ME. Conversely, a net loss of dietary N occurs at higher levels.

When estimating the quantities of amino acids released in the intestines, allowance must be made for the 20 per cent or so of nucleic acids and other non amino acid material in the crude protein (Ellis and Pfander 1965; Gausseres and Fauconneau 1965; Clarke, Ellinger and Phillipson 1966) and also for the approximate 78 per cent true digestibility of crude protein in the intestines (Hogan and Weston 1970). When corrected in this way, the data indicate (Figure 2) that the amino acids released in the intestines represent from 42 per cent to 127

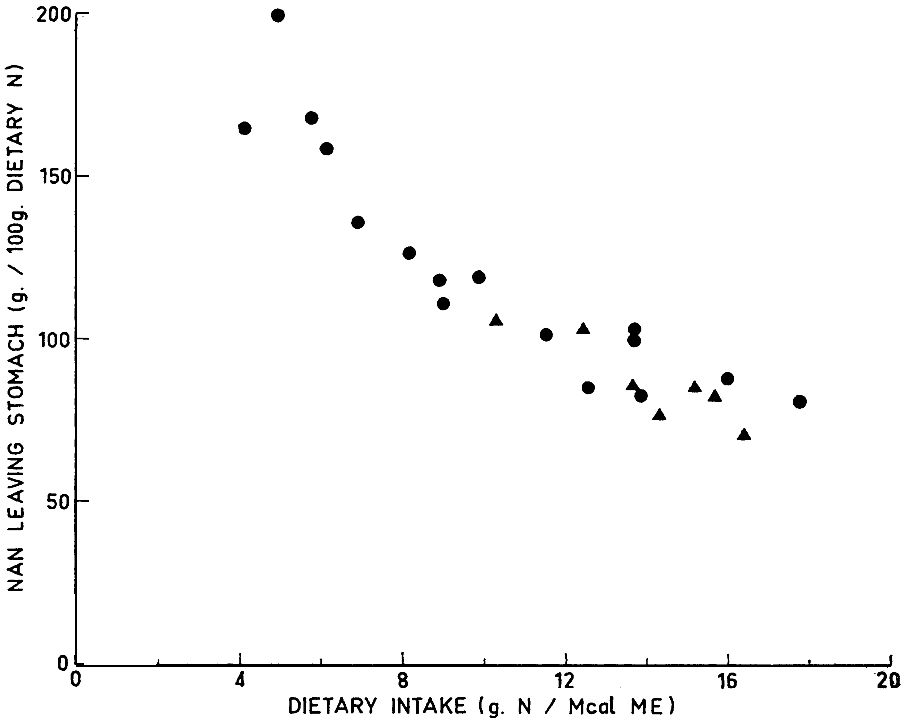

Fig. 1. — The effect of dietary composition (nitrogen (N) as a proportion of metabolizable energy (ME)) on the N in forms other than amonia (NAN) leaving the stomach. ● Grasses ▲ Legumes

per cent of the N intake. When expressed in relation to ME (Table 3), the data, grouped according to dietary protein content, indicate that amino acids released to ME (g/Mcal) range from 24 to 50. With the diet of lowest protein content, microbial protein synthesis was probably limited by lack of rumen ammonia and, hence a low ratio of amino acids to ME was observed. With the remaining diets, ratios of amino acids to ME were much higher and were less variable than the levels of dietary protein. However, in comparison with the recommended nutrient allowances for pigs and poultry, it appears that the balance between amino acids and energy in the digesta may be optimal only with the diets of highest protein content.

The amino acid mixture in the digesta that pass to the intestines is of relatively constant composition (Hungate 1966). The concentrations of essential amino acids in digesta from sheep fed nine forage diets are presented in Table 4. For comparison, data from the literature are given also on the levels of these amino acids in proteins from whole egg, milk, meat and wool. Whole egg protein is included because this protein is generally regarded as well balanced for growth of young animals. The pattern of amino acids in the digesta does not differ greatly from that in the animal products although cyst(e)ine + methionine, Lysine and histidine are proportionally lower than in meat and milk whereas cyst(e)ine + methionine levels are substantially lower than in wool. If these limitations were

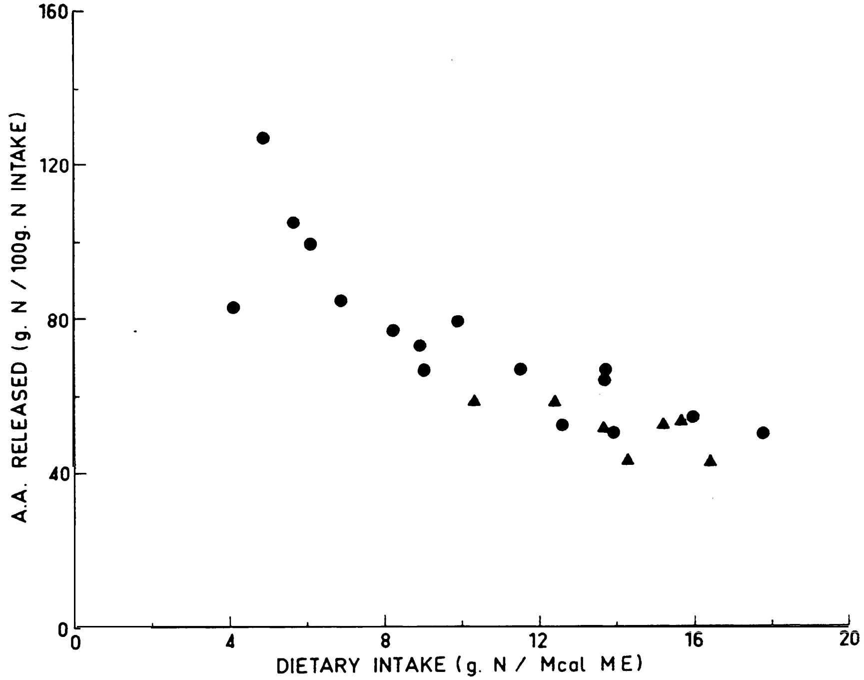

Fig. 2. — The effect of dietary composition (nitrogen (N) as a proportion of metabolizable energy (ME)) on the estimated release of amino acids (AA) in the intestines. ● Grasses ▲ Legumes

overcome, there should be a more efficient conversion to animal productions of amino acids absorbed from the intestine. Some support for this comes from the work of Reis (1969) who obtained substantial increases in wool growth and possibly some body growth by providing animals with additional cystine and methionine. The possibility that the supply of lysine may determine the efficiency of milk production is discussed by Bigwood (1960, 1963, 1964).

TABLE 3

The quantity of crude protein digested in the intestines relative to intake and the amino acids released relative to dietary metabolizable energy (ME) when various herbage diets were offered to sheep at levels approaching ad libitum. The herbages have been group within defined ranges of crude protein content. (Data recalculated from Hogan and Weston 1970)

Crude Protein in Diet (g/100 g OM)	Number of Diets	Digestion in Intestines	
		Crude Protein (g/100 g intake)	Amino Acids (g/Mcal ME)
5	1	117	24
6–14	7	112	38
16–22	6	75	43
25–32	9	66	50

TABLE 4

***Levels** of **essential amino acids in crude proteins from** a **variety** of **sources** (g/16 gN)*

Amino Acid	Whole Egg	Digesta†	Milk‡	Meat‡	Wool*
Valine	7.2	7.2	6.4	4.8	4.2
Cystine + Methionine	6.4	2.9	3.1	3.9	14.3
Isoleucine	7.7	6.2	5.3	4.5	8.2
Leucine	9.2	10.1	10.0	8.2	9.4
Phenylalanine	6.3	5.9	5.1	4.2	4.0
Lysine	7.0	7.1	8.2	9.1	3.1
Histidine	2.4	2.2	2.7	3.9	1.0
Arginine	6.6	5.6	3.5	6.1	10.1
Threonine	4.3	5.1	4.7	4.6	6.5
Tryptophan	1.5	1.5‡	1.2	1.2	1.5

Reference:
*Block and Bolling (1951).
†Hogan Weston, and Lindsay (1969 and unpublished data).
‡Bigwood (1960).

III. REQUIREMENTS OF NUTRIENTS FOR PRODUCTION

As mentioned earlier, sufficient data are available for pigs and poultry to permit general statements to be made on the total amounts of nutrients such as amino acids and energy required for maintenance and productive functions. Unfortunately, with ruminants there are virtually no reports in which quantitative studies of digestion have been made in parallel with studies of protein production. For the present purposes, however, calculations of the digestion of one roughage diet have been applied to results obtained by several workers at this laboratory for a variety of studies of maintenance and production. The aim has been to relate the amounts of amino acids released in the intestines to the levels of protein synthesis observed and, subsequently, to estimate the quantities of amino acids that must be derived from the intestines to ensure maximum protein synthesis. The diet, referred to as diet A, consists of equal parts of chopped wheaten and lucerne hays, contains 12-13 per cent crude protein and was chosen originally, as Reid and Hinks (1962) indicated, because it has a feeding value similar to clover hay. It has been estimated (Hogan, unpublished data) that the amounts of amino acids released in the intestines are equivalent to about one half the crude protein intake. Diet A as fed provides about 2 kal ME/g and, hence, the ratio of digested amino acids: ME, about 30 g/Mcal, is low in comparison with recommended ratios for pigs and poultry.

The calculations have been made following the approach used in studies of energy metabolism, viz. to estimate the requirements for maintenance and to add the estimated requirements for production. The daily maintenance requirements for a 32 kg (70 lb) Merino wether in moderate condition are met by 600 g diet A (Graham 1964a); larger sheep probably require about 800 g diet A for maintenance. These amounts would provide 6 to 8 g amino acid N and sustain wool production at about one third the maximal rate, i.e. about 0.6 to 0.8 g N/day (Reis and Schinckel 1964). An indication of the amino acids required for maximum wool growth can be obtained from the data of Reis and Schinckel (1964), in which amino acids above maintenance were converted to wool with an efficiency of about 12 per cent. Hence, the growth of an additional 1.6 g N/day in. wool would require the provision of a further 13 g amino acid N from the intestines, or about 19 to 2 1 g overall.

It is well known that the nuritional requirements of the ewe increase in late pregnancy, though the requirements for amino acids cannot be stated precisely. The energy needed by a 32 kg Merino ewe with a single foetus is probably provided by 900 g diet A/day (Graham 1964b); however, there is some evidence that the 9 g amino acid N supplied by that ration is not sufficient, because the N retained by the ewe, 3 g/day, is less than the estimated rate of storage of N in the foetus at term (Langlands and Sutherland 1968), without making allowance for the amino acids needed for wool production. It was suggested by Reid and Hinks (1962) that an adequate daily intake of diet A for 55 kg crossbred ewes with a single foetus in late pregnancy would be 1650 g, and for ewes with twin foetuses about 1900 g. Hence, the amounts of amino acids necessary to ensure adequate foetal growth in late pregnancy could range from perhaps 9 to 12 g N/day for small Merino ewes with a single foetus to 19 g N/day for large crossbred ewes with twins. Lack of amino acids in late pregnancy could result, apart from depressed wool growth, in small, poorly nourished lambs (Reid 1963), the type of animal particularly vulnerable to neonatal mortality (Alexander 1968).

Food intake in the ewe generally rises during lactation and this is clearly necessary to meet the nutrient requirements for milk production. It is not currently possible to estimate the extent of conversion of amino acids derived from the digestive tract into milk. In Graham’s (1964b) experiment, Merino ewes produced about 4 g milk N/day from the 12 g amino acid N supplied by 1200 g diet A. How much more amino acid N would be required to produce the additional 5 g N/day in milk expected of a Merino ewe (Corbett 1968) can only be guessed. If the efficiency of conversion was 100 per cent, 5 g amino acid N would be needed, bringing the total to 17 g. In reality, the amino acid requirement is likely to be much higher. Any limitations to milk production would be reflected in poor growth of the suckled lamb with consequent increased risks of ill thrift and weaner losses. In practice, the ewe probably attempts to compensate for dietary deficiencies during pregnancy and lactation by drawing on maternal tissue reserves. Even if completely successful, this must ultimately be associated with losses in productivity.

If it is assumed that the suckled lamb stores about 5 g N/day, the efficiency of conversion of milk N to lamb N would be about 50 per cent. After weaning, the lamb generally must function as a ruminant and it is unlikely that this efficiency of conversion can be maintained. Recently, R. H. Weston (unpublished data) obtained gains in crossbred lambs of about 6 g N/day (240 g/day weight increase) with a hay and concentrate diet that provided about 19 g amino acid N in the intestines. In adult sheep, tissue storage is important particularly to build up reserves. for use during pregnancy and lactation. Interesting data on growth in adult sheep have been obtained by Reis (1969) who supplemented, 800 g diet A by infusing 60 g casein into the abomasum to provide about 8 g amino acid N, or 50 g amino acids. Although the unsupplemented ration was adequate merely for maintenance, the supplement induced steady growth; the supplement added only about an additional 240 kcal ME to the 1600 derived from the diet, but the amino acids altered the ratio of digested amino acids to ME from about 30 to 54 g/Mcal. The data thus suggest that greater efficiency of utilization of nutrients can be achieved in ruminants as in non-ruminants if the ratios of amino acids to energy are correctly balanced.

Although these estimations are fairly tenuous, they suggest that for maximum protein synthesis, sheep and lambs require at least 19 g amino acid N/day. It is probable that the intake of diet A would generally not be sufficient to provide this amount of amino acids. However, other forages are clearly better able to meet the nutritive requirements as the data in Figure 3 indicate. Each point in Figure 3 represent mean data from 3 to 6 Merino wethers weighing 40 to 45 kg and offered dried grasses and clovers ***ad libitum.*** Some of this information is unpublished but the remainer appears as Weston and Hogan (1967, 1968a, b, c), Hogan and Weston (1967, 1969) and Hogan, Weston and Lindsay (1969). It seems that with immature forages, i.e. those of high crude protein content, the sheep can derive sufficient amino acids for most productive purposes; however, with forages whose organic matter comprises less than about 20 per cent protein, the supply of amino acids may not be sufficient for maximum production. The position is likely to be even less satisfactory in a grazing situation where food consumption may be

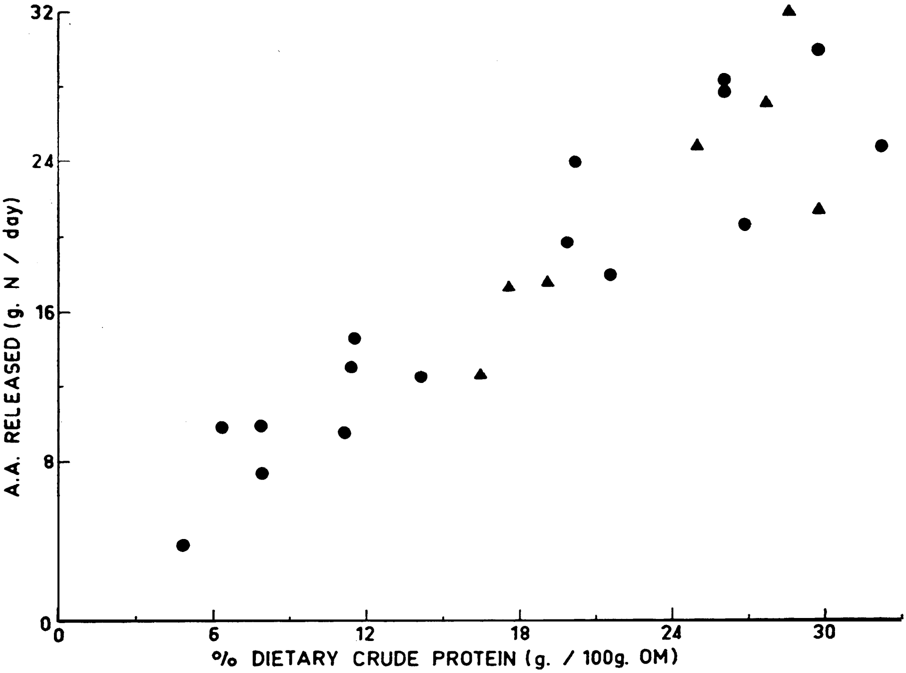

Fig. 3. — The effects of dietary composition on the estimated quantities of amino acids (AA) released in the intestines with sheep offered forage diets *ad libitum.*
● Grasses ▲ Legumes

further reduced by low forage availability (Allden 1962) and by social and environmental factors. Hence, a shortage of amino acids could easily be responsible for the submaximal levels of wool production during much of the year (Williams and Schinckel 1962) and especially during pregnancy and lactation (Corbett 1964, 1968).

IV. BALANCING DIETS

Earlier in this paper, the question was asked "How can a diet be balanced for maximum efficiency of production". The calculations presented to date suggest that additional amino acids may be required with many diets but the question arises regarding ways in which this amino acid supplementation can be achieved. Progress in this direction has been indicated by Ferguson, Hemsley and Reis (1967) who reported favourable responses in wool growth when diets were supplemented with casein protected by formalin treatment against digestion in the rumen. With similar material, Barry (1969) has reported improved birth weights and growth in lambs while R. H. Weston (unpublished data) and G. J. Faichney (unpublished data) have improved the growth rates of weaner lambs. There is also evidence that the treatment of a clover diet with formalin substantially improved its nutritive value for wool growth (Hemsley, Hogan and Weston 1970). The appraisal of this type of dietary treatment in both biological and economic terms is in its early stages but at least there is reason to believe that useful improvements can be made in those situations where dietary protein imposes limits to production.

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