

RELATIVE IMPORTANCE OF RUMINAL AND POSTRUMINAL DIGESTION WITH RESPECT TO PROTEIN AND ENERGY NUTRITION IN RUMINANTS¹

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The protein and energy nutrition of ruminants is briefly described in relation to rumen function. Protein nutrition is discussed in the context of satisfying the rumen microbial requirement for nitrogen, the host animal's requirement for protein and the integration of these two components. The level of dietary nitrogen required by the micro-organisms increase with the amount of fermentable carbohydrate available. The amount of nitrogen made available in the rumen will depend on the rumen degradability of the source. When the host animal's requirement is greater than the amount which can be provided by microbial synthesis within the rumen, then the balance must be provide by undegraded protein escaping rumen fermentation, and being digested post ruminally. The energy made available to the ruminant is chiefly in the form of the volatile fatty acids (VFA), and the efficiency of their utilization is discussed in the context of their production and utilization. Simple calculations demonstrate how the molar proportion of the VFA produced in the rumen dictate the efficiency with which carbohydrate energy is made available to the host animal. The greater the amounts of acetate and butyrate, the more energy is lost' as methane. The ability of the absorbed metabolises to provide glucose is dealt with briefly and it is considered chat under normal conditions there are sufficient glucose precursors. Recent work has been unable to demonstrate differences in the efficiency' of utilization of different mixtures of the VFA when these were infused into the rumen of sheep as the sole source of energy. It is concluded that within the range of the VFA produced by normal fermentation, differences in the efficiency of utilization of the VFA for fattening (kf) cannot explain the poor utilization for fattening of diets producing ahigh level of acetate.

Key words: Review, ruminants, protein, energy, metabolism

Protein and energy nutrition cannot be considered in isolation from each other. However it is easier to deal separately with the protein, energy interrelationship, and the composition of the energy yielding nutrients, and this is what I propose-to do in this paper.

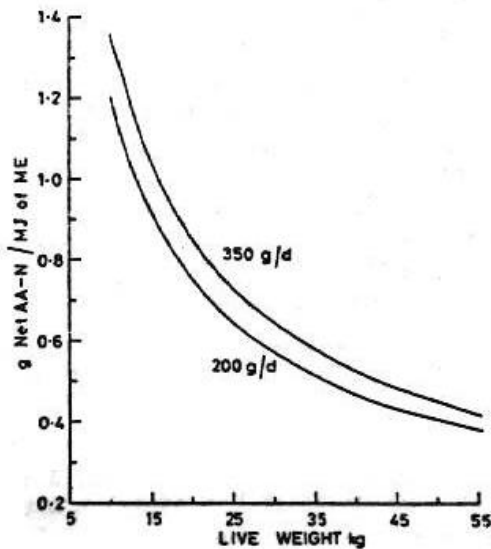
PROTEIN ENERGY RELATIONSHIPS

Protein: In order to discuss in detail the importance of ruminal and post-ruminal digestion, we must first discuss the protein needs of the animal. It is, of course, not possible in this article to review all the information that has recently become available on this subject. However an attempt will be made to discuss new principles. For more details recent review articles are referred to (Orskov 1970 1975 a b; Roy et al 1977).

¹ Paper given at the third annual meeting of the Dominican Centre for Livestock Research with sugar cane, 1978.

Until recently estimations of protein nitrogen (N) requirement had to be based mainly on data from nitrogen balance experiments, but there is now sufficient information to use changes in body composition to estimate the requirements of growing ruminants, and information on milk composition to estimate the requirements of lactating ruminants. It is also necessary to know the protein N requirement for tissue maintenance and a value for this has been given by Roy et al (1977).

Figure 1:
Net Amino Acid Nitrogen (Net AAN)
requirement of growing lambs.



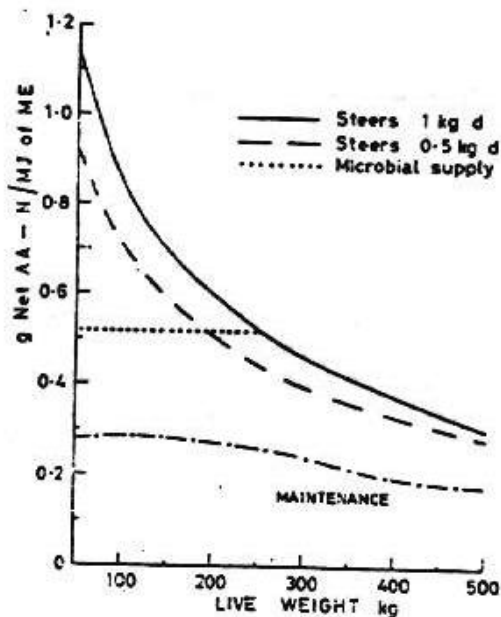
Let us first consider the growth of (Finish Landrace x Dorset Horn) lambs given adequate protein and energy to gain at either 350 or 200 g/d. Net Amino Acid Nitrogen (Net AA-N) requirement (ie N retained + N for tissue maintenance) in relation to metabolizable energy is plotted against liveweight in Figure 1. From this it can be seen, that as liveweight increases, the Net AA-N requirement/MJ* of Metabolizable Energy (ME) decreases. This is because as the animal grows, the composition of the growth alters (it contains more fat and less protein). The requirement at a rate of gain of 200 g/d is less than that for a liveweight gain of 350 g/d because the tissue N requirement for maintenance is much less than that for liveweight gain. Thus the dominant factor is the increased requirement relative to maintenance (zero growth), and not the lower proportion of protein deposited (relative to fat) at the higher rate of gain. Sex effects the composition of liveweight gain too, for entire male lambs contain more protein than females of the same weight (Andrews and Orskov 1976).

* 1 Megacalorie (Mcal) = 4.184 MegaJoules (MJ)

The requirements for males will therefore show a curve displaced to the left of that for females (i.e. more protein deposition, and hence Net AA-N requirement, at a given liveweight and given rate of gain). Previous nutrition can also have an effect, for lambs given a diet deficient in protein for a period, will have growth of a different composition (more protein) than lambs of a similar weight previously given a diet adequate in protein (Orskov et al 1976).

Microbial Protein: We must now consider the fact that the ruminant derives protein from two sources, namely microbial and dietary. In fact, one of the reasons for describing the protein need in relation to energy is that the microbial N is generally produced in relation to the amount of carbohydrate fermented in the rumen (see Orskov 1977 a, b). It is thus possible to estimate the contribution of microbial protein to the animal's need in the same terms used to define dietary protein. The philosophy of considering separately the microbial contribution (Orskov 1970) has led to the definition of the protein need of ruminants in two parts, microbial need, and host animal need. The microbial contribution of Net AA-N/MJ of BE has been summarized by Roy et al (1977). It is based on a microbial N production of 19.5 g N/kg DOM, of which 20% of the N is nucleic acids; 70% of this production is absorbed from the small intestine, and 75% of the absorbed N is utilized, giving 0.53 g Net Amino Acid N(Net AA-N)/MJ ME. In Figure 2, the Net AA-N need for Friesian steers gaining 0.5 or 1 kg/d is illustrated (Orskov 1976). The requirement decrease with increasing weight, and is less at lower rates of liveweight gain as with the lambs (Figure 1). The microbial

Figure 2:
Net Amino Acid Nitrogen (Net AAN) requirement
of growing steers.



contribution which is relatively constant is now superimposed. This approach is useful, because it can begin to define the growth periods in which protein in addition to the microbial contribution is required; i.e. where dietary protein has to be added in order to satisfy the requirement of the host animal. NPN can be used only to satisfy the microbial need for N, and not to satisfy any additional protein needed by the animal itself.

The concept adds simplicity to a description of protein requirements of ruminants, since the microbial requirement sets a lower limit for the N level than is required in ruminant diets. This is because, generally speaking, if N is limiting the rate of fermentation, then voluntary feed intake and feed consumption will be depressed. This is illustrated by Table 1 (from Mehrez and Orskov 1978) where whole barley was supplemented with different levels of urea. It can be seen that both digestibility and voluntary feed consumption increased with increasing levels of urea, until the optimum level was reached somewhere between 8 and 16 g/kg diet.

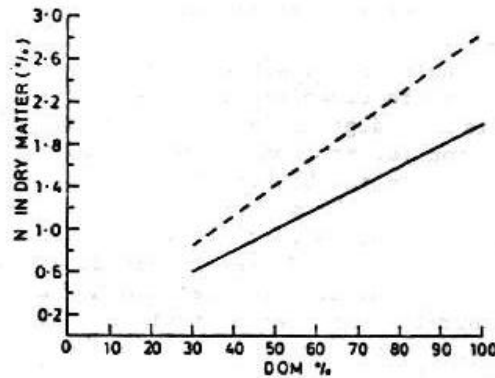
Table 1:
Effect of urea supplementation to whole barley on voluntary feed consumption and organic matter digestibility by sheep

Urea level g/kg diet	Feed Intake g dry matter/d/kg liveweight ^{0.75}	Digestibility of organic matter g/kg
	54.1	761
8	71.7	804
16	75.9	824
24	76.5	823
SE of means	4.0	29

From Mehrez and Orskov (1978)

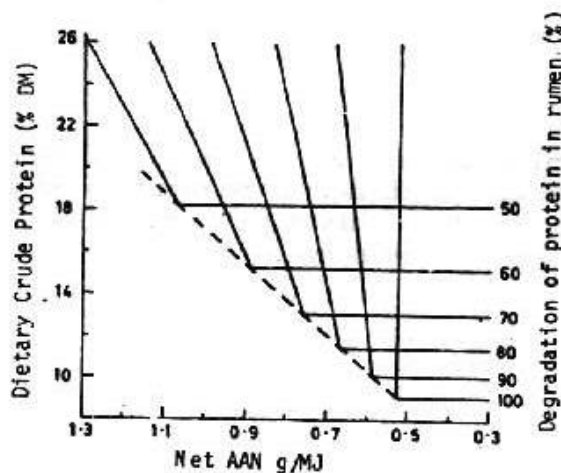
The N required to satisfy the rumen microbial requirement obviously depends on whether the dietary N is available to them. For instance, as might be expected, urea is superior to fish meal for the purpose of satisfying the requirement of the microbes, since fish meal is only partly degraded in the rumen (Orskov *et al* 1974). The microbial need also depends on the fermentability or digestibility of the diet. In Figure 3, the required concentration of N is based on a constant microbial need/MJ of ME. It can be seen that the dietary N concentration required increases with increasing digestibility of organic matter, and with decreasing degradability of the protein (N source). Therefore if the energy available is increased (e.g. with the NaOH treatment of straw) then the microbial requirement also increased. This was illustrated by recent work (Orskov and Grubb unpublished) where there was little or no effect of urea supplementation with untreated straw, but about 1.2% urea was required for maximum intake and digestibility for straw treated with NaOH.

Figure 3: Microbial Nitrogen requirement in relation to dietary digestible organic matter (DOM) assuming 100% (-----), or 70% (- - -) availability of N in the rumen



Integration of Protein Sources: We can now integrate the relative contributions of the microbial protein, and the undegraded dietary protein, as is shown by Figure 4. For this diagram it was assumed that the diet contained 75% digestible organic matter (DOM). The minimum protein concentration in the diet which is needed to meet the micro-organisms requirement at different levels of rumen degradability is shown by the broken line. Thus, the more degradable the protein, the lower is the amount required to meet the microbes need (about 10% if 90% degradable, and about 18% if 50% degradable). If protein of low rumen degradability is used, the greater will be its contribution to post ruminal digestion, sometimes (but not strictly correctly) termed 'by-pass' protein. Therefore, at the level required to meet the needs of the rumen

Figure 4: Relationship between dietary crude protein concentration and Net Amino Acid Nitrogen (Net AAN) availability as affected by the rumen degradability of the protein source



micro-organisms, the Net Amino Acid Nitrogen made available to the host animal will increase. Protein intakes above this level will only be useful as undegraded protein digested post ruminally, and this contribution is shown by the sloping lines above the broken line.

These levels are inefficient, since degradation in the rumen produces more nitrogen than the micro-organisms require. It should be noted that a protein source which is 100% degradable in the rumen will make no contribution to post ruminal digestion (other than the microbial protein synthesised), and therefore its line above the broken line is vertical. Thus the diagram in Figure 4 indicates what is the minimum dietary concentration of protein, and the degradability most suitable, for a given requirement by the host animal. For example, from Figure 2, we can estimate that a 100 kg steer growing at 1 kg/d will need about 0.8 g Net AAN/MJ ME. The minimum (and most efficient) concentration of dietary protein which can satisfy this, is given by the broken line in Figure 4, namely about 14% crude protein with a degradability of about 67%. If we use a protein of 90% degradability, insufficient will escape rumen degradation. If we use a protein of 50% degradability, insufficient will be degraded in the rumen to meet the requirement of the rumen micro-organisms. It should also be noted that by degradability is meant the average degradability of the dietary protein, and that a given degradability could be produced by mixing different nitrogen sources of different degradability.

For lactating cows (see Orskov 1977 a) the same principles apply. When the energy requirement is met, the animal can achieve a given yield of milk from microbial protein alone. At higher levels of milk yield, undegraded protein must enter the abomasum in order to meet the increase in N requirement.

The protein need for lactation is highest when the cows are in negative energy balance as is often the case in early lactation. This is because the dietary protein has to complement two sources of energy, dietary and mobilized fat, since very little labile protein is available (Orskov, Grubb and Kay 1977). As far as protein is concerned therefore, there are periods - depending on the stage of animal production - where post ruminal digestion of some dietary protein is required if maximum performance is to be achieved. The illustrations in Figures 2 and 3 assume a constant production of microbial N per unit of energy fermented. If this were lower, as may be the case with diets based on molasses or sucrose, then the length of periods in which there will be a requirement for undegraded dietary proteins will obviously increase.

Protein Degradation: In order to consider protein production requirement in the way described above, there is an urgent need for values for the degradability of different proteins. A description of disappearance of proteins in the rumen from basal diets and protein supplements using a polyester bag technique seems a promising tool to estimate this (Rodriguez 1968, Mehrez and Orskov 1977).

ENERGY YIELDING PRODUCTS OF DIGESTION

The energy yielding products of digestion in the ruminant are mainly the volatile fatty acids (VFA) which are absorbed almost quantitatively from the rumen (Hungate 1966). Usually the amount of protein absorbed is in excess of the host animal's requirement,

and the excess amino acids and nucleic acids are used as a source of energy. In some situations, particularly with the feeding of maize and sorghum, some starch may escape rumen degradation and be available for enzymic digestion in the small intestine. However, whereas for monogastric animals the main energy source is generally absorbed as glucose, for the ruminants it is the VFA.

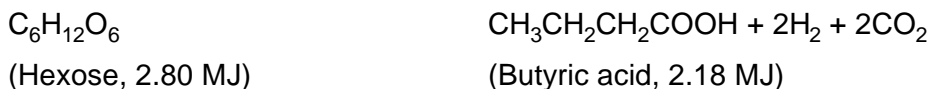
Glucose Requirement: From a basic knowledge of biochemistry, we know that a source of glucose, or 3-carbon units is required to ensure an efficient oxidation of acetate (whether absorbed directly, or from the metabolism of longer chain fatty acids). Glucose is also needed for the efficient synthesis of reduced NADPH for the synthesis of fat. Of the sources of energy produced by fermentation in the rumen, acetic and butyric acids cannot yield a net synthesis of glucose. Propionic acid, after conversion to succinic acid, can be used as a glucose precursor. Starch digested post ruminally is almost certainly absorbed as glucose. The amino acids which are in excess for protein synthesis are metabolized to yield both glucogenic and nonglucogenic energy in about equal quantities.

In order to discuss further the requirement for glucose it is useful to consider the Net Glucose Ratio (NGR) of the principal energy yielding nutrients absorbed (Orskov 1975). On a molar basis this is:

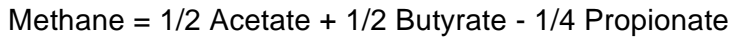
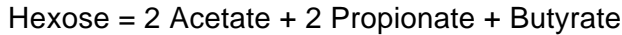
$$\text{NGR} = \frac{\text{Acetic acid} + 2 \text{ Butyric acid} + \text{Valeric acid}}{\text{Propionic acid} + \text{Valeric acid} + 2 \text{ Glucose}}$$

The NGR may influence energy metabolism and feed utilization in three different ways which will be briefly discussed.

1. Effect of NGR on the capture of the end-products of fermentation: First let us consider the conversion of dietary carbohydrate to VFA within the rumen, and the efficiency of that process. This is best illustrated by the simple stoichiometry of the rumen fermentation. Thus:

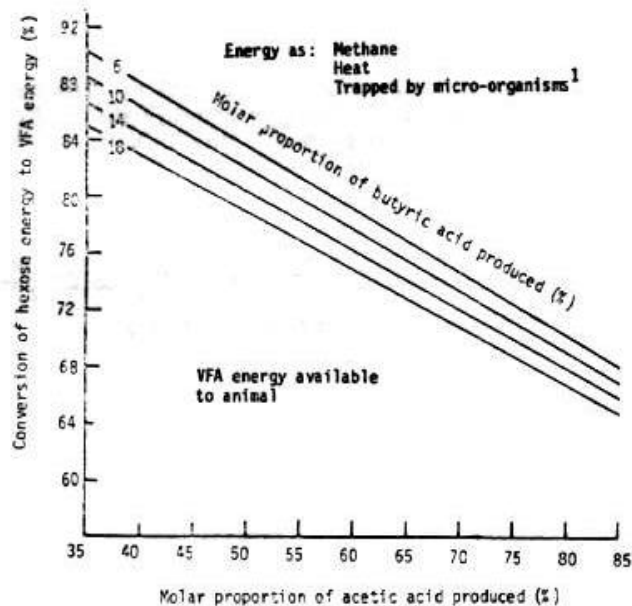


From these relationships it can be seen that more hydrogen is produced with the production of acetic acid. The production of propionic acid involves a net uptake of hydrogen and energy. This implies that from the point of view of the host animal, for the most efficient capture of energy by the fermentation process, a high proportion of propionate is desirable, since hydrogen which is converted to methane represents an energy loss. The relationships between the energy content of the hexose fermented, and the VFA and the methane produced, can be described by the following equations, which are derived from the four equations given above. Thus:



Using these equations, it is possible to calculate the relation between the proportion of acetic acid produced, and the conversion efficiency of hexose to VFA energy which is illustrated by Figure 5 (taken from Orskov 1975 b). The proportion of propionic acid in Figure 5 represents the difference between 100, and the sum of the acetic and butyric acid proportions. The figure clearly illustrates that the molar proportions of the VFA produced have an important bearing on the efficiency of the conversion of dietary carbohydrates to fermentation products which can be used by the host animals.

Figure 5:
Efficiency of conversion of hexose energy to VFA energy
relative to the molar proportions of acetic and butyric
acids produced



¹ Energy used in anabolic processes

2. *NGR and obligatory heat losses*: As mentioned previously, some glucose precursors are required for efficient oxidation, and efficient production of NADPH via the pentose-phosphate pathway. The fact that the proportion of acetic acid is generally highest with high roughage diets, which were associated with a lower efficiency of utilization of ME for fattening, led to investigations to determine if this low efficiency of utilization was associated with the utilization of acetic acid.

There has been a great deal of controversy on this subject, and this is by no means closed at the present day. There is probably general agreement that within a large range of VFA proportions, there is little variation in utilization at low levels of feeding - i.e. at or below energy maintenance. This is supported by feed evaluation work where differences in utilization of metabolisable energy are smallest at low levels of feeding. At higher feeding levels, there are distinct differences in the utilization of metabolisable energy, which is lower with roughage than with mainly concentrate diets. Since, in general, the proportion of acetic acid increases with an increasing proportion of fibre in the diet, it was a logical development to consider and test whether some of these differences could be explained by the differences in utilization of acetic and propionic acids. The early work carried out at the Hannah Institute in Scotland, using respiration calorimetry, showed that the heat losses were greater when a mixture high in acetic acid was infused into the rumen, than when a mixture low in acetic acid was given (see Blaxter 1962). Work at Reading, (see Orskov and Allen 1966) which compared different VFA salts in the diet and used carcass weight gain as the criterion, did not confirm the infusion work and suggested that high heat losses from acetic acid would occur only if the proportion of acetic acid absorbed was higher than that found even with roughage feeding. Hovell (1978) also showed this effect quite clearly by feeding different salts of VFA to lambs, and indicated a curvilinear response to an increasing proportion of acetic acid, i.e. at low proportions of acetic acid and was utilized with an efficiency equal to propionic acid, while a decreased efficiency was observed at higher proportions. Again this decrease was only apparent when the proportion of acetic acid was higher than that normally associated with roughage type diets.

The use of salts of VFA presents several problems; firstly, in order to achieve a level of dietary substitution which is measurable and meaningful, a large amount of cation has to be consumed, and secondly, since the molecular weight of acetic acid is lower than those of propionic and butyric acids, it is necessary to give more cations to animals receiving the acetate supplementation. Experiments involving either the incremental infusion of VFA, or the feeding of VFA salts, also suffer from the problem of possible interference with the utilization of the rest of the diet. The extent to which this may occur is almost impossible to measure.

In the past two years we have developed a technique (Orskov and Grubb 1977) which has enabled us to sustain growing ruminants (sheep) entirely by an intra-ruminal infusion of volatile fatty acids, and an intra-abomasal infusion of protein. This technique has overcome the problem of possible inaccuracy due to interference with the rest of the diet. We have carried out 60 respiration trials with two levels of infusion (at 450 and 900 kJ/kg D per day-equivalent to 108 and 215 kcal), and with molar proportions of acetic acid which ranged from 35 to 85%, and propionic acid proportions from 5 to 55%. (In practice the molar proportions of acetic acid may vary from 45 to 78%, and propionic acid from 12 to 45%).

The maintenance energy needs (and hence efficiency of utilization) did not differ between treatments (at 430 ± 0.02 kJ/kg^{0.75} per day). This is in agreement with the original Hannah work. The efficiency of energy utilization above maintenance is given by Table 2. The only significant difference was between the lowest acetic acid mixture (1) and the other treatments ($P < 0.05$). This suggests that for practical diets, for which VFA proportions are not generally outside the range of mixtures (2) to (5), differences in utilization of metabolizable energy for fattening cannot be explained by differences in the efficiency of utilization of VFA.

The results also suggest that for almost all diets fed to ruminants there are unlikely to be any problems of poor utilization due to lack of glucose or glucose precursors, and therefore attempts to increase post ruminal digestion of carbohydrate for the purpose of correcting a supposed deficiency of glucose or glucose precursors is likely to be of doubtful value.

Table 2: The efficiency of utilization of mixtures of VFA for energy retention (kf) by growing sheep

	Acid proportions (molar %)			% efficiency of energy utilization (kf)
	Acetic	Propionic	Butyric	
(1)	35	55	10	75 ± 5
(2)	45	45	10	65 ± 4
(3)	55	35	10	58 ± 4
(4)	65	25	10	61 ± 4
(5)	75	15	10	60 ± 4
(6)a	85	5	10	60 ± 10

a Studied at 1 and 1.5 times maintenance only

3. *NGR and partition of energy.* There is little doubt that NGR is important in this respect. It has been demonstrated quite often with dairy cows that a low NGR can result in low butterfat and milk yields. This is because the absorption of relatively high levels of glucose or glucose precursors cause the animal to 'switch' from mobilizing fat from its fat reserves (for milk synthesis) to actively depositing fat. This has important implications, for under (1) above it was concluded that the higher the NGR from the fermentation of carbohydrate, the higher would be the production of methane. It thus appears that in order to retain the most desirable partition of absorbed energy (in milk production), a reasonably high loss of methane has to be accepted.

A low NGR can seriously influence the composition of the subcutaneous fat in lambs and goats. Propionic acid in proportions greater than about 30 molar percent will give rise to a proportion of mono and all-methyl branched-chain fatty acids in the fat synthesised. This fat is softer than the fat usually is in these animals, and as such is unacceptable to the meat trade. However, so far, no problems of this nature have been found in cattle (Garton 1975).

Methods of altering the NGR of absorbed nutrients: It is possible to change the NGR either by altering the proportions of rumen VFA, or less commonly with starchy diets, to increase the extent of post ruminal digestion.

Alteration of NGR by changing VFA proportions:

Altering the proportions of roughage and concentrate: This is a very common method in temperate countries, and probably the most predictable. Increasing the proportion of concentrate will generally decrease the NGR (by increasing the proportion of propionate). The extent will depend largely on the quality of the roughage, the extent of processing of the concentrate and the level of feeding used.

Feeding level: Increasing the feeding level will generally cause a small reduction in NGR, but this change is difficult to predict since the change is also influenced by the feeding regime, type of feed and the eating patterns of the animals.

Processing of roughage: Processing by grinding will generally reduce the NGR, probably because it increases the rate of fermentation. The change in fermentation pattern is not very large, and will probably be less for poor quality than for high quality roughage. For instance, it will be less with straw than with dried grass.

Extent of processing of concentrate: Increasing the extent of processing of concentrate generally lowers NGR. In fact the change from processed to whole grain for lambs caused a sufficient change in NGR to eliminate the problem of the soft undesirable fat mentioned above.

Addition of buffer: With high concentrate feeding where rumen pH may be in the region of 5 to 5.5, the NGR can be increased by the addition of buffer such as carbonate or bicarbonate.

Methane inhibitors: With products which selectively inhibit methane production there is likely to be a decrease in NGR, i.e. an increase in the proportion of propionic acid.

Alteration of NGR by changing the relative importance of ruminal and post ruminal digestion: Post ruminal digestion of starch can be most readily encouraged by the selection of the type of concentrate used. Maize and sorghum starch, can therefore escape rumen fermentation in greater quantities, particularly at a high level of feeding. It is also possible to by-pass the rumen with solutions of glucose or lactose (e.g. whey) using the reflex of the oesophageal groove (Orskov and Benzie 1969) which causes the solution to pass directly into the abomasum in the same way as does milk in the suckling animal. In this case the protein or carbohydrate is truly 'bypassing' the rumen.

CONCLUDING COMMENTS ON THE RELATIVE IMPORTANCE OF RUMINAL AND POST RUMINAL DIGESTION OF PROTEIN AND ENERGY

Protein: From the discussion on protein nutrition it is evident that there are periods, depending on stage and type of production, where microbial N is insufficient to meet the protein need of the animal. For these periods post ruminal digestion of some dietary protein is required to achieve maximum performance. Thus there will be a response to digestible protein which escapes rumen fermentation and is digested post ruminally.

Energy: It would appear from the recent colorimetry experiments at the Rowett, and analysis of the literature, that for almost all practical diets, propionic acid and protein (amino acids) will provide sufficient glucose precursors for the glucose needed to ensure an efficient utilization of dietary energy. For this reason, attempts to increase the post ruminal digestion of starch in order to increase the absorption of glucose are likely to be of doubtful value.

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