

# EFFICIENCY OF FEED UTILISATION BY RUMINANTS

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## I. INTRODUCTION

Metabolisable energy content of a feed or its components has been used to assess its feeding value for ruminants. The demonstration that VFA energy could, at times, be used highly inefficiently when included in a roughage diet, led to the suggestion that feeds for ruminants should be evaluated in terms of their net energy. The establishment of calorimetry technology in nutritional research was a direct result of the apparent need to measure heat production in animals to develop systems of feed evaluation based on net or metabolisable energy. The formation in 1970 of "The Feeding Stuffs Evaluation Unit" at the Rowett Research Institute was the forerunner of the attempts to develop such a system of feeding standards (see Blaxter 1982). These systems have been developed with a narrow group of 'common' feeds with high digestibilities and usually high in protein. However, even on such feeds the relationship between measured metabolisable energy values and those calculated from chemical compositions, are poor. This led Blaxter (1982) to end a lecture given to the annual Nutrition Conference for Feed Manufacturers at Nottingham in the following way. "The two 'best' equations (relating observed and computed MEs) based on an entirely chemical approach do not seem as satisfactory as one based on physical measure of heat of combustion and the biological one of in vitro digestibility".

Since this time there has been a growing questioning of the accuracy and usefulness of prediction of feed requirements based on analysis and a calculated metabolisable energy values of a feed. This is emphasised much more where, low digestibility forages are being evaluated or where the husbander has little control over selection of the diet or, as in the case of grazing animals, has little knowledge of what an animal eats. More recently it has been suggested that the balanced nature of the nutrients absorbed are more important in determining intake and therefore nutritive value of a forage than its metabolisable energy content (Preston & Leng 1985).

Since the early 1970's there has been substantial research which showed that the utilisation of metabolisable energy of a diet is variable depending on its ingredients. The early observations of high heat increment when additional acetate was given to ruminants on top of a basal diet, have generally not been substantiated. The major conclusion is that the efficiency of utilisation of acetate is diet specific. Ørskov and Allan (1966) and Bull et al. (1970) showed the efficiency with which acetate was used for growth in sheep and cattle was not below expectation when added to a "high quality" diet. Over the last few years there has been considerable research effort to explain the differences between the early calorimetric work (see Blaxter 1962) and more recent studies (Hovell et al. 1976; Ørskov et al. 1979) on the efficiency of utilisation of metabolisable energy of VFA for body gain. This paper reviews the literature on the efficiency with which ruminants utilise VFA energy and strongly supports the concept that the level of glucose availability is critical for the efficient utilisation of the products of digestion for growth, milk production and reproduction.

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That the level of glucose availability is a major factor influencing the efficiency of utilisation of nutrients by animals is a contentious issue. For this reason a wide cross-section of research is taken to illustrate that the efficiency of utilisation of metabolisable energy by ruminants is dependent on both the quantities of glucose and amino acids and perhaps long chain fatty acid available in relation to the physiological state of the animal.

The overall concept is not new and there have been notable supporters in the past including Professor Max Klieber, who stated in 1960 that "metabolisable energy is not a homogeneous entity, instead it represents an assembly of nutrients or metabolites each of which is used with a specific efficiency for a particular productive purpose" (see Kronfeld 1982). In addition Linzell (1957) suggested that the rate of milk production was primarily effected by the glucose availability and Kronfeld (1976) suggested that milk yield is a function of glucose uptake by the mammary gland whereas the efficiency of milk production is a function of the uptake of long chain fatty acids. Leng and Preston (1976) postulated that the major limitation to growth and milk production in cattle fed sugar cane based diets was the availability of glucose.

The evidence that glucose, long chain fatty acids and amino acids are essential for efficient utilisation of feed for gain and milk production is discussed below.

## II. RUMINANT PRODUCTIVITY - BACKGROUND

Productivity of ruminants is a function of digestible feed intake and the efficiency with which the absorbed nutrients are used for productive functions. These are determined by:

- \* The capacity of the feed to support an efficient microbial milieu in the rumen.
- \* The capacity of the diet to supply the quantities and balances of nutrients required by the animal in different productive states.

A primary consideration for maximising intake is that the rate of fermentative digestion and the efficiency of microbial growth in the rumen is optimised. A deficiency of an essential nutrient for microorganisms will be reflected in (1) a lowered rate of digestion of feed; (2) a lower than optimum microbial growth efficiency in the rumen expressed as Y-ATP (g dry cells produced/mole ATP available) and (3) a lowered feed intake.

The capacity of a feed to supply the quantities of nutrients required in proportions that are balanced to meet a particular productive function depends on:

- \* Its potential digestibility and potential rate of digestion
- \* Its ability to support an efficient rumen, leading to a high microbial cell production relative to VFA and a high propionate production rate relative to acetate and butyrate.
- \* Its ability to provide additional dietary materials which bypass the rumen fermentation to balance the nutrients arising from fermentative digestion to meet the requirements of production.

The requirement for nutrients are highest in lactating and pregnant animals in the last 2-3 weeks before term, they are lower in growing animals and lowest with animals that are mature. Draught animals represent a special case but where they are fed on "low quality diets" they may also be limited at times by the balance of absorbed nutrients (see Leng 1985).

#### The availability of nutrients from a diet

The nutrients available for metabolism are:

- \* The products of fermentative digestion:
  - \* VFA which include acetate, propionate, butyrate and higher fatty acids
  - \* the digestible components of microbes synthesised in the rumen (which are about 60% protein),
- \* The dietary nutrients escaping the rumen and available for digestion in the small intestine, including:
  - \* bypass protein and starch providing amino acids and glucose
  - \* long chain fatty acids from dietary lipids.

#### Essentiality of nutrients for production

It is perhaps not surprising that nutrients that appear to be critical for efficient production in ruminants (essential amino acids, glucose and long chain fatty acids) are the same as the principal nutrients present in milk. For the young animal (considering the extremely high growth rates that can be achieved), milk probably provides the best balance of nutrients for growth (ie. they are highly efficiently used). Milk is also an effective supplement for young ruminants on solid food since suckling stimulates the oesophageal groove reflex and directs milk into the intestines.

#### Reauiement for dietary bypass protein

Although Virtanen (1966) was able to obtain considerable milk from cows fed semi-purified diets in which the only nitrogen was in the form of urea, production was not high and could be stimulated by feeding protein. In their studies, Virtanen and his colleagues also found it necessary to feed high levels of grain-starches and apparently some oil (fat) was given; both these components may have lowered the need for gluconeogenesis from amino acids (see later) sparing them for milk production.

It has been hypothesised that the effects of feeding a protein meal per se in dairy cow diets may be two-fold:

- \* On high quality diets there is an apparent increase in diet or fibre digestibility in the rumen (Oldham et al. 1985); this has been attributed to the continuous availability of amino acids and peptides which act as microbial growth stimulants. However, there is a possibility that urea simply increased rumen ammonia concentrations above a critical level which was limiting microbial growth. Urea supplementation, if it increased rumen ammonia levels could have stimulated the rate of starch digestion (Mehrez et al. 1977) which decreased rumen pH, and which in turn depressed cellulolytic activity where urea was the sole supplemental N source (see Terry et al. 1969; Mould et al. 1983).

\* Supplementary protein provides post-ruminal amino acids for absorption. Simple calculations (Burroughs et al. 1971) indicate that body growth requires more amino acids, relative to **energy**, than are produced in the **rumen** and a supply of dietary protein to the intestines is required to optimise milk production.

Ørskov (1970) summarised the situation in terms of availability of amino acids and energy and the ability of the microbial system in the **rumen** to provide these. This is shown in Fig. 1. The microbial ecosystem can supply a

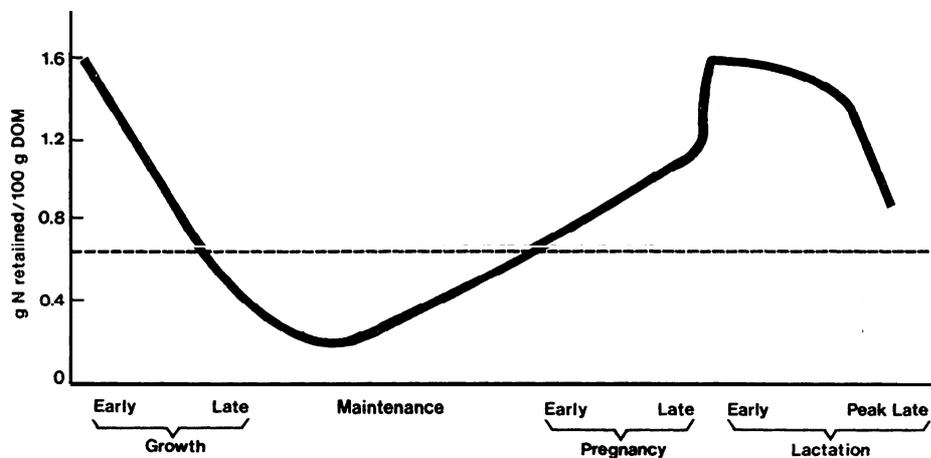


Fig. 1. Effect of physiological state on potential retention of nitrogen in relation to digestible organic matter intake.

suitably balanced protein to energy ratio in the products of fermentative digestion to support maintenance and the first two thirds of pregnancy but not moderate to high growth nor growth of the pregnant uterus close to term or moderate to high levels of milk production.

A deficiency of absorbed dietary amino acids for production will often limit feed intake and the efficiency of feed utilisation particularly in highly productive animals such as cattle in the last 60 days of pregnancy (Lindsay et al. 1982).

Roy et al. (1977) have attempted to describe requirements of the ruminants for amino acids in terms of the amounts of microbial and dietary protein that became available on a particular diet. This is based on a standardised and calculated microbial growth efficiency and a constant value for protein escape from the **rumen** for various feed components. This appears to be a major oversimplification, where these predictions of protein availability are applied to a variety of diets based on crop residues through to grain-based concentrates and highly digestible forages such as lucerne. This is discussed further below.

#### Microbial growth efficiency and the requirements for dietary bypass protein

Undoubtedly microbial growth efficiencies are variable depending on numerous factors, The factors that have been identified as being of major importance include:

- \* Deficiencies of microbial nutrients such as ammonia, sulphur, amino acids and peptides.
- \* Microbial species present in the rumen. In particular a large population of protozoa decreases the protein yield to the intestines (see Bird and Leng 1985, Veira et al. 1984).
- 3 Frequency of feeding. Hespell (1979) showed that rumen bacteria when starved, quickly lysed (some within 2 hours). In a mixed diet, soluble sugars are rapidly fermented and the organisms responsible may therefore grow and a proportion lyse according to availability of these soluble sugars. Feeding a concentrate diet six times daily as against once daily doubled the microbial growth yield from the rumen (Tamminga 1981).
- \* Rumen fluid outflow rate appears also to "control" microbial cell outflow from the rumen. Thus in cold stress, late pregnancy or lactation, digesta outflow rates from the rumen appear to increase and microbial growth yield appears to increase (Weston 1979; Kennedy and Milligan 1978).
- \* Physiological state, as well as effecting rumen microbial growth yields through the effects on digesta flow from the rumen, may also effect the overall digestibility of microbial and dietary bypass protein through increases in the capacity of the small intestine and increased enzyme secretions (see Oldham 1984). Thus the reported values for digestibility of microbial protein in the intestines have varied from 70-95% (see Leng and Nolan 1984).

The above factors indicate the uncertainty about the efficiency of microbial growth and therefore the availability from fermentative digestion of protein relative to energy (P/E). The theoretical variability of P/E with microbial efficiency is shown in Fig. 2. The point stressed here is that the theoretical values for the P/E ratio from fermentative digestion can change from about 10:1 to over 40:1 (g protein/MJ available energy) (Preston and Leng 1985).

Calculation of the ratio of protein/energy available for utilisation by ruminants, taking into account all the variables, clearly is not simply modeled.

### III. REQUIREMENTS FOR GLUCOSE

Glucose is required for a number of essential functions. Requirements change with physiological state in a similar pattern to the changing pattern of amino acid requirements (see Fig. 1 c.f. Fig. 3) (Leng et al. 1977). At the present time there are no analysis of feed that indicate the likely availability of glucose precursors from a feed given to ruminants.

It is the difficulty of predicting glucose requirements, the physiological and nutritional factors that effect this requirement and the estimation of glucose availability that appears to jeopardise systems of feed evaluation based on metabolisable energy.

This is an area in which there is considerable controversy and therefore the evidence for glucose being essential is discussed in more detail.

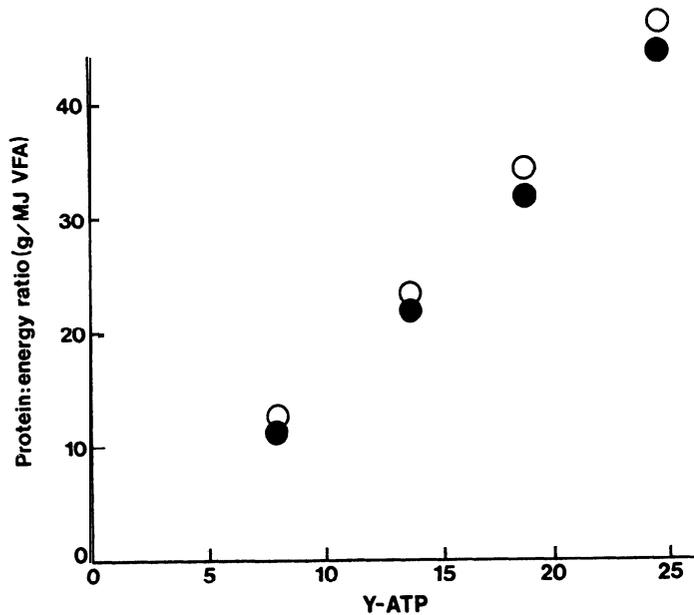


Fig. 2. The relationships between Y-ATP and the protein to energy ratio in the products of fermentation (o data for a fermentation pattern 70 acetate, 20 propionate, 10 butyrate; for a pattern 60, 30, 10).

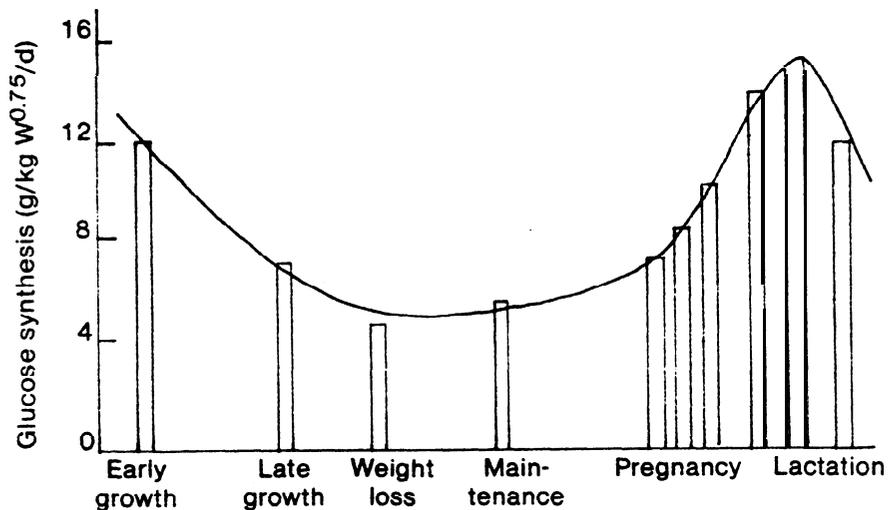


Fig. 3. Glucose synthesis rates in sheep in various physiological states (see Leng et al. 1977).

Background: Most dietary carbohydrates are fermented to VFA and microbial cell components in the **rumen** with the result that glucose absorption is **minimal** in **ruminants**. Glucose is largely synthesised from propionate (Leng et al. 1967), but amino acids may also contribute to **gluconeogenesis** (Lindsay 1980). In cattle on certain high grain diets appreciable, but variable, quantities of starch escape fermentative digestion (Waldo 1973). **Maize,**

sorghum and rice appear to have a capacity to escape microbial activity in the rumen, and therefore to be digested in the small intestines and absorbed as glucose when included in a diet for ruminants. Small amounts of starch absorbed in this way could be detrimental where glucose availability is precariously balanced since it could actually suppress glucoeogenesis (see Leng 1970).

Although some of the amino acids arising from digestion of dietary and microbial proteins can be converted to glucose they probably represent a minor source of glucose on diets that support a high propionate fermentation (e.g. grains) in the rumen. Under certain conditions, however, where glucose requirements are high (as in fattening animals on diets low in fat) and/or where propionate production in the rumen is low, amino acids could be used extensively for glucose synthesis. Propionate is the major precursor of glucose and probably accounts for 80-90% of the glucose synthesised in maintenance fed animals (Cridland 1984).

The requirement for minimum quantities of glucose for efficient use of absorbed nutrients is inferred from a number of different research approaches. The major ones are summarised below.

#### Evidence from growth studies

Forage diets: Corbett et al. (1966), in a classical calorimetric study, demonstrated that in Scotland the spring pasture was more efficiently used for fat synthesis by sheep than that grown in the autumn. In the context of this discussion important differences were the higher propionate concentration in the VFAs in the rumen of animals on spring pasture. The energy retention of sheep on diets of spring or autumn pasture is shown in Fig. 4.

Recently MacRae et al. (1985) have demonstrated that an infusion of casein (30 g/d) per abomasum into sheep given autumn harvested dried grass at a feeding level equivalent to maintenance or 1.5 times maintenance increased the efficiency of utilization of the herbage from Kg 0.45 to Kg .57 and those authors suggested that this response was a result of the increased availability of glucose synthesised from the amino acids.

Thomson (1978) found that the efficiency of utilization of ME for bodyweight gain in cattle was higher for a concentrate/forage diet based on maize and forage (clover or grass) than for barley and forage even though the metabolizability of the DM (ME/DM) was the same on all diets (Table 1). One explanation is the proportionately greater post-ruminal digestion of maize compared with barley. Clover, as compared to grass based diets, was also more efficiently used by the animal. There is higher protein (more bypass) and generally there appears to be a higher fat content in legumes than in grasses indicating the likely relative nutrient availabilities on the two diets. In addition, maize contains up to twice the content of oil found in barley.

○, spring herbage      ●, autumn herbage      ▲, fasting heat production

The composition of the pastures is shown below:

	CP	CF	EE	Ash	NFE
spring pasture	13	30	2.5	6.7	48
autumn pasture	16	29	3.3	9.5	43

VFA properties in the rumen were as follows:

	Ac.	Prop.	But.	Higher Acids
spring pasture	66	24	7	3
autumn pasture	72	17	8	3

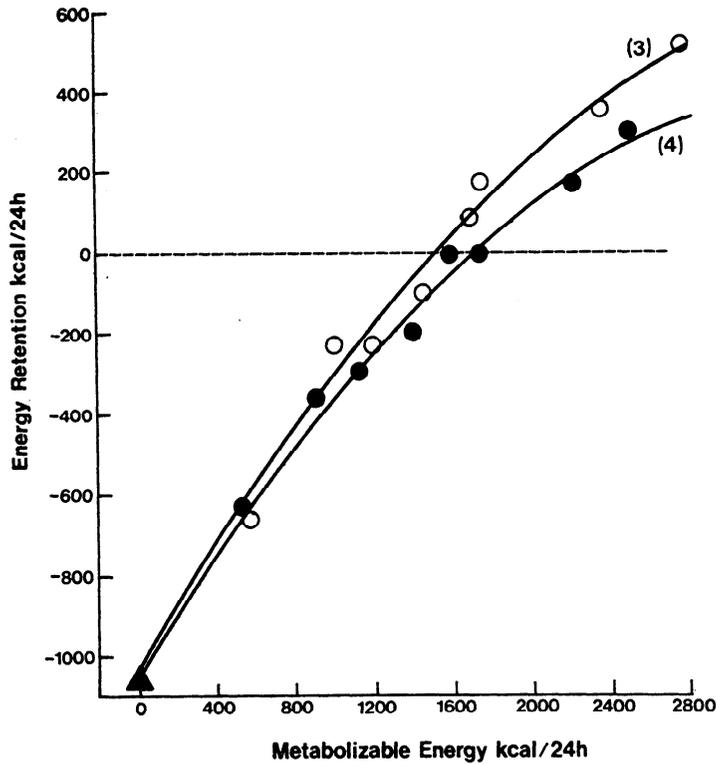


Fig. 4. Relationship between metabolisable energy intake and energy retention (kcal/24 hr) (after Corbett et al. 1966).

Table 1. Efficiency of utilization of metabolizable energy for fattening cattle (kf) according to the nature of the ingredients in the diet. The ration combinations containing maize grain and clover forage were used more efficiently than those containing barley grain or ryegrass forage (from Thomson 1978).

Forage/grain	Energetic efficiency (kf%)
Ryegrass + barley	36
Ryegrass + maize	42
Clover + barley	44
Clover + maize	50

Further evidence for an inefficient utilization of feed being related to propionate concentrations in the rumen arises from the studies of Tudor and Minson (1982) which showed that pangola grass was used more efficiently than setaria grass for tissue synthesis in sheep even though both were fed at the same rates and had the same apparent digestibility (Table 2). The authors mention higher concentrations of propionate in rumen fluid of sheep on pangola as one possible explanation for the difference. It is also feasible that microbial growth efficiencies were higher on the pangola grass diets or that the grasses differed in the quantities of fat they contained.

Table 2. The metabolizable energy in pangola grass is used more efficiently for fattening sheep than is the energy in setaria grass, even though both grasses had the same concentration of metabolizable energy in the dry matter (from Tudor and Minson 1982)

Grass species	ME (MJ/kg DM)	kg (%)
Setaria	8.0	17
Pangola	8.1	28

Undoubtedly acetate given in quantities representing a significant proportion of the ruminant's intake is used with a variable efficiency. Acetate given to a fasting animal or when the basal diet is roughage is "burnt off" to some extent since heat increment is high (Armstrong and Blaxter 1957; Armstrong et al, 1957; Tyrell et al. 1979). However when given in a concentrate diet acetate is much more efficiently used by the animal (Rooke et al. 1963; Ørskov and Allen 1966a; Hovell et al. 1976; Tyrell et al. 1979). These conclusions are illustrated by the research of Tyrell et al. (1979) which is shown in Fig. 5.

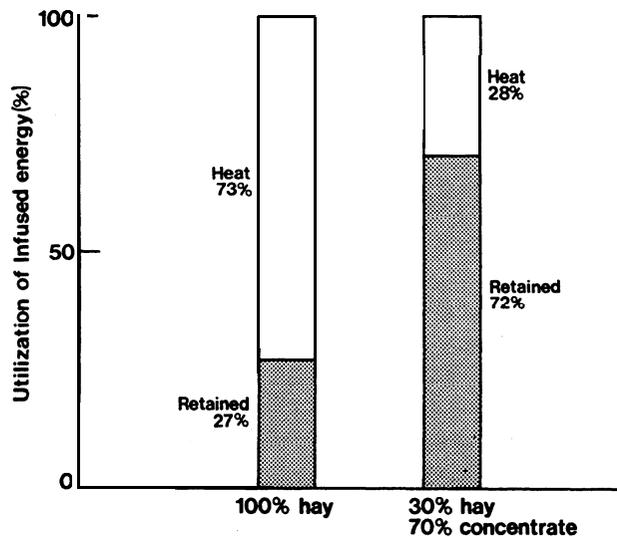


Fig. 5. Effect of the basal diet on the efficiency of utilisation of acetic acid infused into the rumen of cattle. The highest retention of energy was on the diet rich in glucose precursors (Preston and Leng 1984 adapted from Tyrell et al. 1979).

### Evidence from infusion of metabolites

Economides et al. (1978) examined the interaction between dietary bypass protein (fish meal) and abomasally infused glucose in lambs fed a basal diet of sugar/oaten chaff supplemented with urea. Feed intake and growth rates were increased by supplements of bypass protein. Glucose infusion had no effect on feed intake but increased liveweight gain and feed conversion efficiency (Table 3).

Table 3. The effects of bypass protein (fish meal) and glucogenic energy (glucose infused into the abomasum) on feed intake, growth rate and feed conversion in lambs fed a basal diet of sugar/oat chaff (rumen fermentable carbohydrate) (Economides et al. 1978)

Fish Meal Glucose	(% (g/d)	0		6	
		0*	0*	80	80
Feed intake	(g/d)	890	1140	770	1070
Liveweight gain	(g/d)	100	200	130	260
Feed conversion	(g/g)	8.9	5.7	5.9	4.1

\* Infusion of 0.9% N<sub>a</sub> Cl

#### Acetate clearance

Early studies in Australia, aimed at examining the role of glucose as a priming substrate for the TCA cycle (ie. providing oxaloacetate), used acetate clearance rate as a measure of glucose sufficiency (Table 4). The data show that, almost always, acetate clearance was most rapid on those diets likely to have a high glucogenic capacity (ie. diets high in protein or maize; or where it could be expected that propionate would be a high proportion of the rumen VFA). The rate of clearance of injected acetate on the lucerne hay diet was highly correlated ( $R^2 = 0.98$ ) with feed intake. The increasing level of intake could be expected to lead to greater escape of potentially glucogenic nutrients.

The suggestion from this work is that there is a close correlation between the ability of an animal to clear acetate and the availability of glucose. Ruminants must control blood acetate within physiological limits, and therefore feed intake and fermentation rate must match the animal's ability to utilise acetate which is dependent on the availability of glucose provided that the acetate is being used for fat synthesis. This hypothesis should be tested since acetate clearance rate is relatively easy to measure.

The other point arising from these considerations is that the intake of a particular feed will be maximised when nutrient availability is "balanced" with requirements. Therefore, the ability of the animal to clear acetate could be used as an index of the "balance" of the absorbed nutrients. This relationship could be especially useful in grazing studies to identify the effects of supplements.

Table 4 Acetate clearance in sheep on diets of high or low glucogenic potential. Acetate clearance is defined as the time for half an injected dose of acetate to be cleared from blood (after Reid 1958; Jarrett and Filsell 1960; Egan 1965; Weston 1966)

	Diet (g/d)	Glucogenic potential	Acetate clearance
600	lucerne hay	++	21
1200	lucerne hay	++++	15
600	lucerne (40)/ maize (50) peanut meal (10)	+++	21
1200	" " "	+++++	13
520	Wheat straw/ wheaten chaff	+	29
360	wheaten chaff		
540	lucerne chaff		
900	cracked maize	+++++	9
350	lucerne		
350	cracked maize	++++	19
	wheaten chaff/ lucerne chaff	++	21
700	wheaten chaff	++	
300	wheaten chaff/ 300 wheat straw	+	26
800	wheaten hay chaff	++	21
	Green pasture (ad lib)	++++	9
	Dry pasture (ad lib)	+	20
800	lucerne chaff	++++	7
800	wheaten hay chaff	++	18
510	oaten chaff low-N	+	25
	high-N*	+++	4
417	oaten chaff	++	48
525	oaten chaff + casein (37g) per duodenum	++++	37

\* Fermentable N

The "superior" nutritive value of propionic acid compared with acetic acid, observed in the original work of Armstrong and Blaxter (1957 and Armstrong et al. (1957) with starved mature sheep, and Armstrong et al. (1958) with feeding sheep, and the absence of differences in efficiency of use of these two VFA acids in the experiments of Ørskov and Allen (1966) can also be explained in terms of the glucogenic potential of the basal diet. The diet used by Armstrong et al. (1958) was dried grass (low glucogenic potential) whereas Ørskov and Allen (1966) gave the different VFA mixture to animals fed mainly on barley grain (high glucogenic potential).

Evidence for the essentiality of glucose on low-fat diets

The need for glucose for high efficiency of feed utilization appears to be more obvious where the diet is low in lipid and/or when the animal is growing at a fast rate and is close to maturity (ie. is fattening). The evidence from this is discussed below.

Diets based on molasses: Fattening systems for cattle on molasses based diets supplemented with bypass protein, supported levels of growth comparable with those on grain based diets (Preston et al. 1967). Molasses-fed animals, however, had a lower feed conversion efficiency and a lower carcass fat content (Redferne and Creek 1972). In contrast, only low to moderate levels of milk production were attained when maize was replaced by molasses in a diet fed to dairy cows (Fig. 6). The level of milk yield was closely related with rumen propionate proportions and in addition the diet was extremely low in fat (Clark et al. 1972).

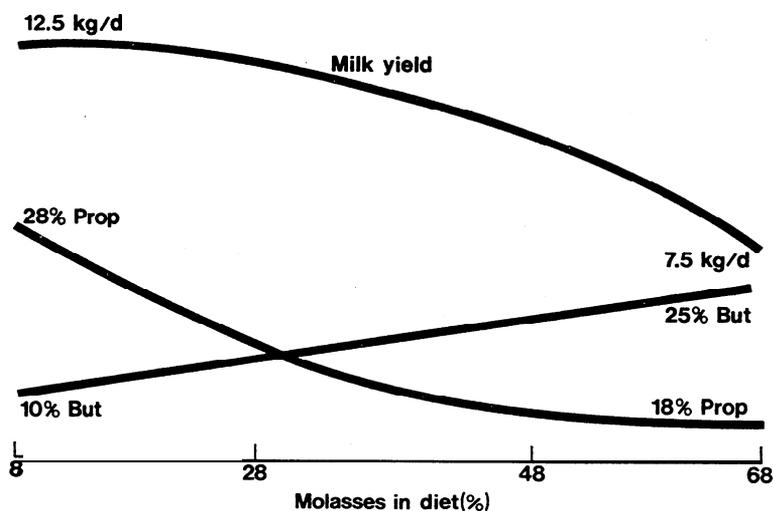


Fig. 6. Effects of replacing maize with molasses on the pattern of rumen frementation and milk yield of Holstein cows (Clarke et al. 1975).

Diets based on sugar cane: Rice polishings with a large proportion of broken rice grains and oil (1248%) was a better supplement than cassava root meal (low in fat) for growth of cattle on sugar cane based diets (see Preston et al. 1976). The starch in rice polishings escaped rumen fermentation almost totally (Elliott et al. 1978), whereas the starch of cassava root meal was

fermented rapidly in the **rumen** (Santana and Hovell 1979). Glucose entry rates were higher in cattle fed sugar cane based diets when supplemented with rice **polishings**, rather than cassava root meal (Ravelo et al. 1978). On these diets the rice **polishings** provided considerable fat in addition to bypass protein and starch.

Supplementary maize grain (with good **rumen** escape characteristics and with a relatively high content of oil) improved feed conversion efficiency in cattle fed sugar cane pith whereas the same amount of molasses energy (completely fermented in the **rumen** containing no fat) depressed feed conversion efficiency (Donefer cited by Pigden 1972).

Evidence from animals fed by intraruminal and intragastric infusions

Strongest evidence for the thesis comes from the studies reported by Ørskov et al. (1979) where growing lambs nourished by infusion of **VFA** into the **rumen** and infusion of **casein** into the abomasum (no lipids were given) increased their nitrogen retention as the proportion of propionic acid in the infused **VFA** was increased (see Fig. 7). The effects were the same in sheep fed at maintenance or twice maintenance. Similar experiments reported in preliminary form also support the concept of glucose increasing the efficiency of body protein gain (Girdler et al. 1985).

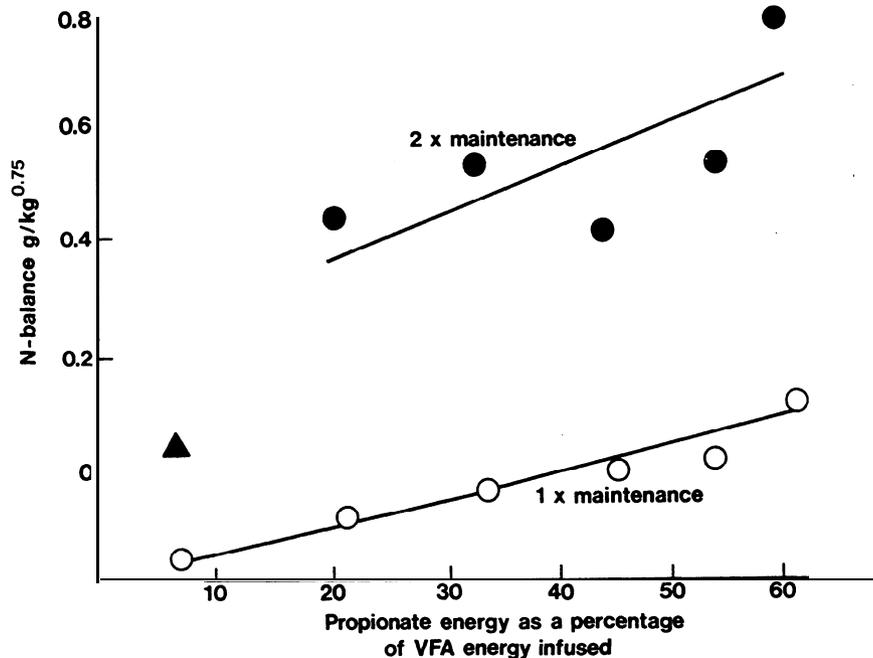


Fig. 7. Relationship between proportion of glucogenic energy in the mixture of **VFA** infused into the rumen of sheep and the **N** retention (the sheep were nourished by **VFA** infused into the rumen and **casein** infused into the abomasum at calculated rates for maintenance and twice maintenance (Preston and Leng 1985 - adapted from Ørskov et al. 1979).

In the studies of Blaxter and his colleagues (see Blaxter 1962), there was apparently a positive linear relationship between the molar proportions of propionate in **rumen** **VFA** and the efficiency of utilization of metabolizable

energy above maintenance for fattening of sheep (see Fig. 7). As these animals were of mature body size they were presumably fattening, as compared to the lambs in Ørskov et al. (1979) experiments which would have been depositing mainly proteinaceous tissues and water.

A comparison of the data summarised by Blaxter (1962) with the results obtained by Ørskov et al. (1979) with young lambs nourished by infusion of VFA into the rumen and casein into the abomasum, is given in Fig. 8. The data clearly show that N-balance (Fig. 7) (proteinaceous tissue deposition) was stimulated in young animals as the proportion of glucogenic energy increased.

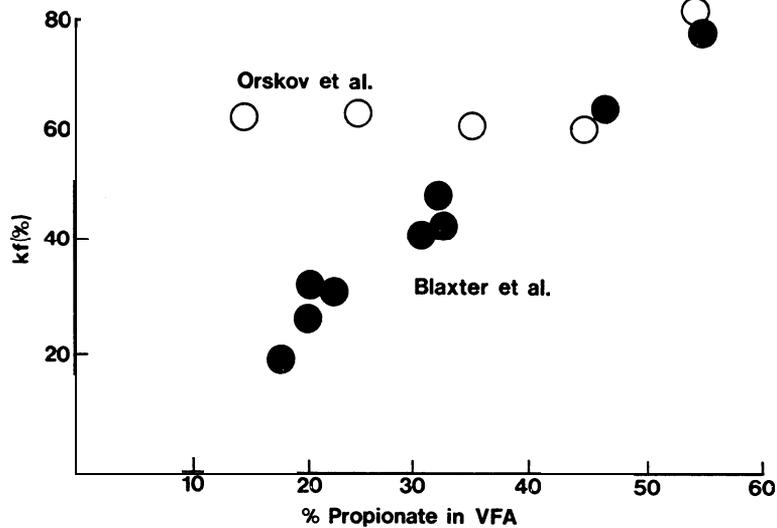


Fig. 8. Relationship between the molar proportion of propionic acid in the rumen VFA and the efficiency with which metabolisable energy consumed above maintenance is used for tissue synthesis (Preston and Leng 1979; the data are adapted from Blaxter 1962, assuming that the molar proportion of butyric acid was only 10% of the total VFA) (see Preston and Leng 1985).

There is obviously less need for glucogenic energy in the growing animal when the body tissue gain is high in protein rather than lipid. The highly efficient use of both dietary energy and protein at the highest glucogenic energy to total energy ratio in the nutrient (ie. where the two sets of data coincide) is clearly the optimum balance of nutrients for maximum efficiency of growth (ie, a G/E ratio of 53% and a G/P ratio of 54 kJ/g). The optimum balance of these nutrients, however, would be dependent on the P/E ratio which is 10 for the infusions into young lambs (Ørskov et al. 1979). A P/E ratio of 10 represents an efficiency of microbial growth in the rumen equivalent to approx. Y-ATP of 7 which is relatively low (Leng 1982).

Further evidence for the essentiality of glucose  
from studies of milk production

Kronfeld (1982) in his discussion of the metabolic determinants of milk production in the relatively high yielding dairy cow, has highlighted that:

- \* Rate of milk synthesis is a function of mammary uptake of glucose.
- \* Efficiency of milk synthesis is a function of the uptake of long chain fatty acids by the mammary gland.

The evidence presented for these statements are that:

- \* Enzyme activities in the mammary gland are not rate limiting (Hartmann 1969).
- \* Milk secretion in the perfused udder of goats varied directly with the perfusate concentration of glucose but not with the concentrations of amino acids or acetate (Hardwick et al. 1967; Linzell 1967).
- \* In ketotic cows, milk yield responded linearly to stepwise increments of infused glucose (Kronfeld 1970).
- \* The amounts of glucose passing through the blood pool in lactating cows (Kronfeld 1982) was linearly related to milk production.
- \* The uptake of glucose by the mammary gland, measured using blood flow rates and A-V differences (Hartmann and Kronfeld 1973; Kronfeld et al. 1968), was 72 g/kg milk produced. A similar value was reported in goats by Annison and Linzell (1964).
- \* The partial efficiency of milk production was increased when grain replaced concentrates in a diet and the level of propionate in rumen fluid increased relative to acetate and butyrate.

#### IV. INTERRELATIONSHIPS BETWEEN REQUIREMENTS FOR LCFA AND GLUCOSE

Part of a ruminant's requirements for glucose is undoubtedly that needed to be oxidised to allow fat synthesis to occur, therefore the need for glucose is a function of the level of fat in a diet. This is an important area since it emphasises the role of dietary fat and its analysis in feed evaluation systems and therefore considerable background information is given.

##### Long chain fatty acid synthesis and catabolism

Background: Long chain fatty acids are rapidly released from feed glycerides in the rumen by bacterial lipase. In the rumen, long chain fatty acids may be hydrogenated to give saturated acids but are otherwise unchanged and are efficiently absorbed from the small intestine following their movement down the tract in digesta. Lipid may contribute approximately 1-10% of the Dry matter of a forage consumed depending on the species, its maturity and the components consumed.

Metabolism of long chain fatty acids in the animal results in endogenous acetate production (Annison and White 1962). The long chain fatty acids of the diet are efficiently incorporated into body tissues and into milk fat. Thus the lipids of adipose tissues become unsaturated if unsaturated long chain fatty acids are added directly to the abomasum (Ogilvie et al. 1961) or fed as "protected" fats (Scott et al. 1970).

Lindsay (1970) demonstrated a negligible synthesis of long chain fatty acids from acetate in sheep on a maintenance diet. He provides evidence in subsequent publications to support the concept that lipids of adipose tissue arise **mainly** from the uptake of circulating long chain fatty acids which are of dietary origin (Lindsay 1983) a concept that is supported by Thornton and Tume (1984).

Long chain fatty acid synthesis is only likely to occur quantitatively from acetate where animals have either a low availability of dietary fat or a low protein to energy ratio in the nutrients absorbed from the alimentary tract where the fat deposition may act as an energy **sink**.

Lipogenesis from acetate requires considerable ATP and therefore fat synthesis is accompanied by considerable heat generation.

Whilst fat synthesis from acetate almost certainly requires glucose to be oxidised most of adipose tissue long chain fatty acids **probably** arise from dietary fat. On the other hand only half the fat in milk fat (about half the C<sub>16</sub> and **all** the C<sub>18</sub> fatty acids) arise from dietary fat, the rest is synthesised from acetate and butyrate (ie. half the C<sub>16</sub> and all the C<sub>4</sub>-C<sub>18</sub> fatty acids) (see Linzell 1968). The mammary gland **has** developed **mechanisms** for generating some of the NADPH for fat synthesis from acetate which do not require glucose oxidation (see later),

The relationship between glucose oxidation and fat synthesis from acetate

The interrelationships are illustrated in Fig. 9. The process of synthesis of palmitate from acetyl CoA is shown below.

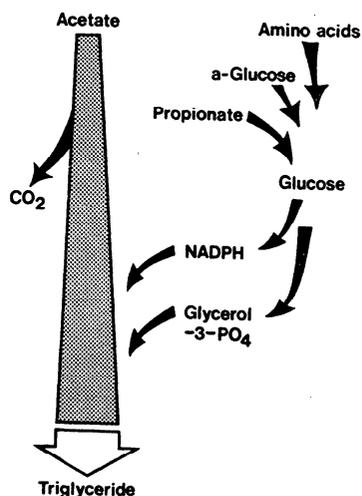
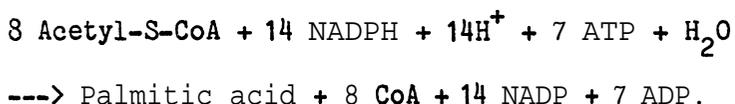
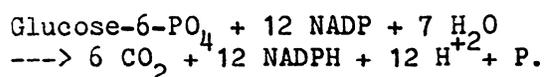
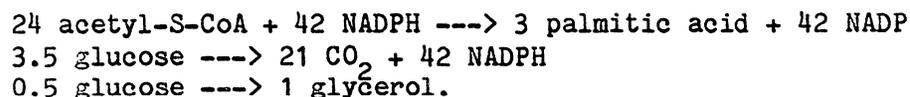


Fig. 9. Diagram of the relationships between availability of glucogenic precursors and pattern of acetate utilisation (from Oldham 1983).

The NADPH is formed in part, via the phosphogluconate pathway from glucose in which 1 mole of glucose-6-phosphate is oxidized to CO<sub>2</sub>.



Thus, for every 8 moles of acetate converted to palmitic acid, 14 moles of NADPH are needed. If this arises from glucose oxidation then 1.17 moles of glucose are oxidised via the phosphogluconate pathway. In addition, 1 mole of glycerol-phosphate is needed to esterify three moles of palmitic acid and this arises from glucose. The overall reaction for the synthesis of tri-palmitin is as follows:



Thus, where glucose provides the NADPH, 4 moles of glucose are oxidised to synthesize 1 mole of tri-palmitin or 89 g of glucose are used in the formation of 100 g of fat.

It appears that in adipose tissue glucose oxidation provides most of the NADPH for fat synthesis. There is, however, evidence (Baumann and Davis 1975; Moore and Christie 1981) that a proportion of the NADPH (up to 50%) for long chain fatty acid synthesis in mammary tissue may arise through other reactions than the phosphogluconate pathway (eg: dehydrogenation of isocitrate to 2-oxoglutarate) but relative contribution of this pathway has not been truly quantified (Vernon 1981).

There are three situations where fat may be more extensively synthesized from short chain VFA. These include:

- 3 in immature animals when the dietary protein to energy (P/E) ratio is low and the fat deposition becomes an energy sink. Fat synthesis may thus adjust the protein to energy ratio in residual nutrients for tissue growth.
- \* When fat is a small proportion of the diet, such as occurs on diets based on molasses and cereal straws.
- 3 When acetate availability is increased suddenly, such as by intravenous infusion (unbalancing the protein/energy ratio). In this case considerable energy is used in the synthesis of fat, leading to increased heat production.

The need for glucose therefore depends, to a large extent, on the amounts of long chain fatty acids absorbed.

Another point is that if glucose requirements are increased by the need to synthesise fat (eg. because of the low availability of dietary long chain fatty acid) this could lead to excessive demand for glucose and an increased deamination of amino acids to maintain glucose availability. Thus the requirements for dietary bypass starch or protein may be increased where propionate production in the rumen is low and where dietary fat is low. This is typical of crop residues and dry mature pastures. If long chain fatty acid synthesis is limited by glucose availability, the animal would have to

increase heat production by "burning off" acetate in futile cycles (essentially uncoupled oxidative phosphorylation) and/or it would decrease its feed intake. Thus the availability of long chain fatty acids could be a determinant of the level of "requirements" for glucose and indirectly essential amino acids. If the level of availability of lipids is low the inability to synthesis fat could result in reduced voluntary feed intake because of a slow clearance of acetate. These effects may be different in the growing as compared to the fattening ruminant.

## V. INTERACTIONS AMONG NUTRIENTS

The major conclusion that arises from the above discussion is that it is the balance among the three major groups of nutrients (amino acids, glucose and long chain fatty acids) which determines the efficiency with which the metabolizable energy is utilized for a particular productive purpose (eg: work, growth, reproduction and lactation) and the rate of production.

The requirements for amino acids are well recognised. The roles of glucose and long chain fatty acids have become more apparent as a result of the increasing understanding of the constraints to animal production on so-called "low quality" diets (Leng and Preston 1976; Preston and Leng 1980; Leng and Preston 1985; Preston and Leng 1984), although the role of dietary fat in dairy cow diets has received considerable attention and has focussed on glucose and long chain fatty acid requirements for milk production (see Kronfeld 1982; Palnquist 1984).

There are two important conclusions which arise from development of the understanding discussed above. That is that:

- \* Neither the system of proximate analysis nor the more recent version based on detergent fibre analysis can predict the balance of critical nutrient availability to the animal,
- \* Nutrient requirements for a particular productive purpose, expressed in terms of metabolizable energy do not take into account the interactions among the critical nutrients. The efficiency of utilization of metabolizable energy is a function of the availability of these nutrients.

New approaches to feeding standards and feed evaluation are needed which predict the outcome of digestion and metabolism and provide guidelines as to how the available feed resources can be manipulated so as to optimise the efficiency of their utilization. It is proposed that the nutritive value of a particular feed is probably best assessed by measuring metabolic indicators of the efficiency of rumen fermentation (say microbial biomass?) and of the efficiency of use of nutrients (say acetate clearance?). Both aspects need to be researched.

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