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Forage Evaluation in Ruminant Nutrition

Forage Evaluation Using Measurements of Energy Metabolism

Christopher K. Reynolds

Department of Agriculture, The University of Reading, Earley Gate, Reading, UK

INTRODUCTION

Considering the evolutionary adaptations of the ruminant digestive tract, the fundamental importance of forages in ruminant nutrition is self-evident. In wild ruminants and many extensive ruminant production systems, forages often provide the sole source of dietary energy and protein. In these situations forages are often harvested solely by the animal, but forages may also be mechanically harvested and conserved for use during seasonal changes in forage availability. In more intensive systems seeking maximum production, forages may be fed in conjunction with cereals and other concentrated energy or protein sources, but even in high-yielding dairy cows a minimal level of dietary fibre is required for the maintenance of rumen function and health. In these cases the effectiveness of by-product fibre sources in maintaining rumen function is often evaluated relative to grass or legume forages (e.g. Clark and Armentano, 1997). In a similar manner, the first feeding standards for cattle developed by Thaer in 1809 compared the nutritive value of feeds and expressed requirements relative to the fattening value of 'good meadow hay' (Flatt *et al.*, 1972).

Even before the development of Thaer's hay equivalent system, ruminant nutritionists and husbands sought to develop comprehensive systems for evaluating and expressing the nutritive value of forages and other feeds relative to their ability to meet specific animal requirements. In the intervening years a number of systems have evolved, but the need for refinement and improvement of current feed evaluation systems is as important today as 200 years ago. Current systems for evaluating the nutritive value of forages for specific production requirements are an improvement over their predecessors, largely on account of collective and integrated experience and technological advances, but they do have limitations. The ideal system of feed evaluation was described by Flatt *et al.* (1969a) as the 'Holy Grail' of animal nutrition, where as for religion, a variety of approaches are used around the world, each believed by its users to be the one 'true' system.

Many of the current 'official' feeding systems compare the energetic value of forages based on their relative ability to meet the animal's requirements for net energy (NE) at a standardised level of intake or a specific physiological state. These systems are based on calorimetric measurements of energy balance within animals fed individual feeds or combinations of feeds, although in practice the energetic values of many feeds are estimated using other approaches. This approach has been the subject of much criticism, in part owing to the inability of current approaches to predict production responses in terms of intake, product composition or nutrient partitioning. Energy is not a nutrient per se thus NE approaches represent an amalgamation of the metabolism of a variety of compounds into a single entity, combustible energy, which

is measurable at specific points of loss or gain within the animal. This simplification of complex biological reactions is both a strength, in terms of applicability and versatility, and a weakness in terms of predictability. Many now believe the newer 'religion' of mathematical modelling of nutrient metabolism will ultimately illuminate the path to predictable response, but in application such models will need to be 'fed' using practical criteria for evaluating individual feeds. Although highly desirable, and the justification for untold sums of research funding, the one 'true' system capable of predicting production responses to changes in feed composition is as elusive today as the Grail for the crusaders.

This chapter will consider the use of energy balance measurements for forage evaluation within the context of current feeding standards and research, as well as the limitations and merits of the approach, with an inevitable bias towards the author's background and previous employment.

HISTORICAL PERSPECTIVES

The work of Thaer and Einhof led to the development of the first 'official' hay-equivalent feeding system and was the basis of the 'Weende' system of feed analysis. This analytical approach was the basis of a 'Total-Digestible Nutrients' (TDN) system of feed evaluation and livestock rationing whose origins were at the Weende Experimental Station in Germany in 1860 (Flatt *et al.*, 1972). The TDN approach which developed was used for rationing dairy cattle in the USA until it was replaced as the 'official' National Research Council (NRC) system for rationing energy in dairy cattle by the NE for lactation (NE_l) system (NRC, 1971). However, the TDN system is still widely used throughout the world. Indeed, because of the difficulties of obtaining measurements of energy balance in dairy cattle, many of the tabular values of ME and NE_l used in the current NRC publication (NRC, 1989) are based on TDN values, often obtained in sheep or steers.

Even as the digestible nutrient approach was being developed it was realized that digestible nutrients were not equal in terms of the production they could support and that losses of nutrients other than those in faeces also must be accounted for. In many instances, these differences were due to the efficiency of utilisation of metabolizable energy (ME) for NE gain. Net energy systems for rationing ruminants are based on measurements of energy metabolism and balance, obtained by measuring metabolizable energy (ME), by subtracting energy losses as urine (UE) and combustible gasses (GE) from digestible energy (DE), and by measuring either heat energy (HE) loss or energy retained as product (RE). The use of calorimeters for measuring HE and NE balance by a number of individuals in Europe and the USA led to the development of two NE energy systems in the early 1900's. Kellner's starch equivalent system, used widely in Europe, and Armsby's estimated NE system in the USA, which ultimately had limited use as an adjunct to the TDN system. However, both of these systems were based on a limited data base of experimental measurements. The limitations of the TDN and Starch Equivalent systems, and the paucity of their data base, eventually lead to the development of the current NE systems in use today, which were based on an explosion of animal calorimetry studies beginning in the late 1950's. A driving force behind the establishment of a calorimetry facility for dairy cattle at the US Department of Agriculture's Research Center in Beltsville, MD was the scientific debate over the reasons TDN from

concentrates supports higher milk production than TDN from forages (Huffman *et al.*, 1952). Conjoint with the development of large data bases on NE metabolism in farm animals, chemical methods of feed evaluation were also developed and refined in an attempt to explain and predict animal responses to changes in diet composition and quality. At the Beltsville laboratory these efforts led to the simultaneous development of the NE_i system for rationing dairy cows and the neutral detergent fiber (NDF) system for analytically describing fibre fractions in feeds (Goehring and Van Soest, 1970). The NDF approach was a leap forward in the evolution of chemical procedures for forage evaluation (Reid, 1994), but the need for enlightened approaches to assessing forage and feed quality and predicting their effects on animal production are as relevant today as for Thaer.

METHODOLOGY

Techniques for measuring energy metabolism have been described and critiqued in numerous reviews and books (e.g. Flatt, 1969; Blaxter 1971; McLean and Tobin, 1987). As mentioned previously, there are two general approaches to determining NE. One is to measure or estimate HE and calculate RE by subtracting HE from ME, the other is to measure RE, but a measure of ME will also be required to estimate HE. Since the days of Lavoisier's ice calorimeter (McLean and Tobin, 1987), measurements of HE have been obtained using calorimeters that house the experimental subject. Two approaches have typically been used, direct measurement or indirect estimation of HE. As the name implies, direct calorimeters obtain direct measurements of the HE dissipated by the animal, using a variety of technological approaches such as measuring the difference in the temperature of water entering or leaving a jacket surrounding the chamber, or thermocouples. Indirect approaches include estimation from respiratory exchange or carbon and nitrogen balance. Carbon and nitrogen balance simultaneously estimates RE, but still requires measurement of carbon dioxide and methane losses.

Owing to the historical complexities of direct calorimeters, especially for use with large ruminants, the majority of the calorimeters in use in the later half of the 20th century have been indirect calorimeters. These can be either closed or open circuit, but the problem of removing large quantities of moisture and carbon dioxide in closed circuit systems has meant that most of the calorimeters used for large ruminants are open circuit. In open circuit systems estimates of respiratory exchange are obtained by measuring the difference in gas concentration between incoming and outgoing air and the flow rate of air through the chamber. These measurements are then corrected for effects of temperature, barometric pressure, humidity and the residual volume of the chamber (Flatt, 1969). Heat energy can then be estimated based on relationships between nutrient oxidation and heat production, with adjustments for the type of nutrient oxidized based on carbon dioxide production and urinary nitrogen loss. For ruminants, further adjustments are made for incomplete oxidation of carbohydrates based on methane losses. The constants for these relationships were recommended by an European Association of Animal Production (EAAP) sub-committee on constants and factors (E. Brouwer, K. Blaxter, K. Nehring and W. Wohlbier) and condensed into a single equation reported by Brouwer (1965).

Which ever approach is used to determine HE, complete energy balance measurements also require the measurement of DE and UE, using digestion trials, and

GE, using respiratory exchange. Gaseous energy losses are mostly represented by methane, but in some cases hydrogen and ethane also may be lost (Flatt, 1969). Digestion trials and measurements of HE may be conducted simultaneously if the calorimetry system employed is suitable for separation and collection of faeces and urine, or obtained on separate occasions. If this is the case then effects of level of intake and feed quality must be considered carefully as changes in intake can have immediate effects on HE, as well as DE and ME. This is especially a problem in evaluating forages, where day to day variations can be substantial depending on the source, method of harvesting and conservation and experimental management.

Another approach to estimating NE is to use comparative slaughter techniques. To determine RE over a period of time the body composition of 2 groups of animals is determined, at the beginning and at the end of a prescribed experimental period. Digestible energy is determined separately, with GE often estimated. This has obvious limitations for lactating animals, but indirect (specific gravity) estimates of changes in carcass composition are the basis of energy feeding standards for growing beef cattle in the USA (NRC, 1996). However, numerous comparisons between comparative slaughter and respiration calorimetry have found that estimates of HE are higher, thus NE is lower, when measurements are obtained by comparative slaughter (Johnson, 1986; Waldo *et al.*, 1990). There are a number of reasons for this discrepancy. One concern with the use of calorimeters is that they require the subject to be confined in a sealed chamber for extended periods, which can elevate HE by causing stress if proper adaptation is not employed. More importantly in the comparison of respiration and comparative slaughter calorimetry, activity is limited when animals are confined to chambers, thus maintenance costs and HE are reduced. Another concern with digestion trials and balance approaches is that errors of measurement are cumulative, thus losses of energy and nitrogen during faecal, urine and scruff collection tend to cause overestimation of their retention in the animal (Martin, 1966). The confinement of animals in chambers also means that traditional respiration calorimetry approaches can not be used to measure NE of animals under field or grazing conditions.

Other techniques can be used to estimate respiratory exchange or RE in subjects that do not require total confinement, but at the expense of the precision which can be achieved with a rigorously operated chamber system. Examples include head chambers or face masks, which would not estimate total GE and also require restriction of activity. Approaches that have been applied to the study of grazing ruminants include tracheal cannulas or isotope dilution procedures. Tracheal cannulation techniques for measuring energy exchange of ruminants have a history extending over a 100 years (Flatt, 1969). Attempts to use the techniques for measurement of HE in grazing cattle (Flatt *et al.*, 1958) and sheep (Young and Webster, 1963) have been successful, but concerns about the weight of equipment the animal is required to transport and the effects of the cannula on animal health have limited the use of the technique. As for facemasks, the approach does not measure total GE and carbon dioxide loss.

Isotope dilution procedures can be used to estimate body carbon dioxide production, using labelled carbon dioxide (Corbett *et al.*, 1971) or doubly labelled water (McLean and Tobin, 1987), or body composition (Andrew *et al.*, 1995; Crooker *et al.*, 1998). The doubly labelled water approach is widely used in studies of energy

metabolism in 'free-living' humans and appears an attractive option for studies in grazing ruminants, but the agreement between this approach and established calorimetry procedures has not justified the widespread adoption of the procedure. One concern with the use of labelled water dilution in ruminants is the effect of the large and variable gut and milk pools on the dilution profiles obtained (Crooker *et al.*, 1998).

Practical Considerations

The limited application of alternative procedures has meant that the evaluation of the energetic value of forages and their effects on animal energy metabolism have largely been obtained using chamber calorimeters and conserved forages. Measurements for fresh herbage have been restricted primarily to zero-grazing, which has often required the freezing of large quantities of fresh material to ensure consistent quality over the course of the experiment. However, like other methods of conservation, freezing has effects on forage quality (Minson, 1990). In addition, the cost and difficulties of maintaining calorimeters for large ruminants has meant that measurements from sheep are often used to provide tabular values of the ME or NE value of forages for cattle. However, digestibility and metabolisability of a variety of feeds is higher in sheep than cattle due to comparative differences in rumen function (McDonald *et al.*, 1995). Similarly, effects of level of intake are an important consideration, especially when using tabular values from maintenance fed sheep for rationing lactating dairy cows (Tyrrell and Moe, 1975).

Measurements of HE are not required to estimate ME, and some NE systems assign energy values to feeds in terms of ME, then use constants for the efficiency of ME use for a productive function in rationing the animal to arrive at NE (Alderman and Cottrill, 1995). Thus in evaluating forages, a ME value is used as the term of reference. Calorimeters are expensive and labour intensive to operate, but if calorimeters are not available, then a digestion trial may be conducted and methane losses estimated. The equations derived by Blaxter and Clapperton (1965) based on DE and intake level are often used for this purpose. However, for dairy cows a summarisation of data by Moe and Tyrrell (1979) found that GE losses were best predicted from amounts of digested soluble residue (the more soluble and readily digested carbohydrates), hemicellulose and cellulose. In a more recent analysis of data from cattle obtained at Beltsville, the equation of Moe and Tyrrell (1979) predicted methane output more closely than any others available (Wilkerson *et al.*, 1994). However, this agreement may reflect the fact that both data sets were obtained in the same laboratory using similar types of feeds. Another concern is the effect of feeding fats on methane production, which may not be adequately addressed in the prediction equations currently available. There are numerous other approaches for the prediction of ME based on laboratory analyses, which are addressed in other reviews (eg Barber *et al.*, 1989; Alderman and Cottrill, 1995). A major concern for the evaluation of conserved forages is the ability to determine volatile components of ensiled material at feeding. Whether fed fresh or conserved, in practise forage quality varies considerably from harvest to harvest, or even day to day, thus the need for rapid, accurate and economical lab-based methods of assessing forage energy value.

In contrast to most concentrates, the energetic value of many forages can be determined by feeding the test forage as the sole diet component. However, this is often not the case in studies with higher yielding dairy cows. In the case of comparisons or determinations for concentrates (eg. Andrew *et al.*, 1991), or for forages fed to lactating dairy cows (eg Casper *et al.*, 1993), substitution trials are often conducted (Armsby and Fries, 1918; Tyrrell and Moe, 1975). A variety of approaches can be used, but often in measuring ME or NE values for a specific diet component all other components of the diet are kept as constant as possible whilst only changing the test component. This can be extremely difficult to achieve if attempts are made to equalize parameters such as crude or rumen degradable protein, ME, minerals or fibrous components such as NDF or acid detergent fibre, but represents a creative challenge for the researcher. The associative effects of combining feeds on their digestibility and metabolisability are due to a multitude of factors, such as energy and nitrogen interactions within the rumen, pH, intake and other effects on microbial dynamics. However, these effects must be considered in interpreting substitution trials and applying tabular energy values for individual feeds in diet formulation (Tyrrell and Moe, 1975; Moe, 1981).

DIGESTIBILITY

Of the losses of dietary energy measured in determining energy balance, the most variable is faecal energy loss, thus DE accounts for the largest proportion of the variation in NE between diets and feeding criteria. In summarizing the results from 543 energy balance trials, Moe *et al.* (1972) found that DE accounted for 86% of the variation in NE measured. Digestibility of forages is determined largely by structural factors such as the degree of lignification, but also influenced by factors such as physical processing, level of intake, diet protein concentration and other associative effects within mixed diets (McDonald *et al.*, 1995). All of the factors that determine digestibility then have a major impact on the ME which the ruminant can derive from a specific feed.

A particular problem in formulating rations for dairy cows is the effect of intake on diet digestibility. A number of studies have shown that increasing intake reduces dry matter (DM) digestibility, but the response varies with the type of diet fed. For example, in heifers fed pelleted diets containing either 75% lucerne hay and 25% concentrates or the inverse proportions, increasing intake from just above maintenance to nearly twice maintenance levels numerically depressed the digestibility of the 75% concentrate diet to a greater extent than the 75% lucerne diet (Reynolds *et al.*, 1991a). By increasing rate of particle passage from the rumen, pelleting tends to both lower overall digestibility and exacerbate effects of intake level on digestibility. However, similar responses have been observed in lactating dairy cows fed lucerne hay-based diets differing in concentrate level (Tyrrell and Moe, 1975). These observations have suggested that increasing the level of cereals in the diet exacerbates depressions in digestibility with increasing intake, but the response is not consistent across all studies (Tyrrell and Moe, 1975). Of the diet components measured, cell wall components are often most affected. Many of the associative effects of grain feeding on cellulose digestion are known to be associated with, if not mediated by, depressions in rumen pH (Mould *et al.*, 1983). If feeding grain and subsequent effects on rumen acid load reduces cellulolytic activity of the rumen, then the increased rate of passage with increased intake may have a greater impact on cell

wall digestion than in the absence of starch in the diet. Increasing intake reduces methane production to a greater extent as the proportion of concentrate in the diet is increased (Blaxter and Clapperton, 1965), which reflects shifts in the microbial population of the rumen.

One consideration is that studies specifically designed to measure effects of intake level on digestibility often compare the relative digestion of diets in lactating dairy cows at maximal intake and nonlactating animals at maintenance (Tyrrell and Moe, 1975). These comparisons are appropriate considering that many tabular values for DE, TDN or ME were obtained in steers or sheep, but tend to magnify the problem relative to changes that may occur across a range of intake within a group of lactating cows. For example, Bines *et al.* (1988) found that the digestibility of grass hay-based diets was lower in lactating cows than in immature, dry cows, but that within lactating cows moderate variations in level of intake had no effect on diet digestibility. This was especially true as level of concentrate in the diet increased. However, elevation of intake did depress digestibility in the nonlactating cows. This suggests that either the response to intake level is curvilinear, or that physiological factors other than level of intake per se may play a role in the lower digestibility of diets fed to lactating cows compared to dry cows.

It has long been known that there is a positive relationship between dietary crude protein (CP) concentration, DM digestibility and ultimately intake level in ruminants (Schneider and Flatt, 1975). Averaged across a number of studies, the response is roughly .01 units of digestibility (1%) for each unit change in diet CP% up to 16%, or higher (Oldham and Smith, 1980). The response appeared to be similar in USA and UK studies, although it was suggested that the response might be lower for diets with higher digestibility and CP content. This was more often the case in the UK studies surveyed, where diets tended to have a higher digestibility than USA diets because of the use of high digestibility grass silages (Oldham and Smith, 1980). Increases in DM digestibility with increasing diet CP content can be attributed to the innately high digestibility of protein, or positive effects on microbial fermentation and digestion in the rumen (Tyrrell, 1980). Intake responses may be a result of both increases in digestibility and metabolic effects of improved amino acid supply (Oldham and Smith, 1980). Abomasal infusions of protein are as (or more) effective than dietary protein supplementation in improving grass silage intake (Chamberlain *et al.*, 1989), however this response might be attributed to increased transfer of urea nitrogen to the rumen. In lactating dairy cows fed maize silage-based diets, feeding urea restored DM digestibility as effectively as an iso-nitrogenous amount of soybean meal, but only increased DM intake 1.3 kg/d, compared to an increase of 5.9 kg/d when soybean meal was fed (Tyrrell, 1980). It is known that urea is less effective than protein as a nitrogen supplement in dairy rations (Clark and Davis, 1980). This suggests either; 1) a protein, peptide or amino acid effect on microbial growth in the rumen; 2) a metabolic effect of amino acids absorbed from rumen undegraded feed protein in the small intestine; 3) negative effects of excess ammonia in the rumen or tissues such as the liver (Clark and Davis, 1980; Reynolds, 1992). For USA dairy rations, the effect of diet CP level on milk yield is greatest when CP content is below 14%, but continues to have a diminished effect as CP content increases to as high as 20% (Clark and Davis, 1980). In the UK, the response of DM intake to increasing diet CP content was on average .34 kg/unit increase in CP% across all diets surveyed (Chamberlain *et al.*, 1989).

RETENTION OF DE AS ME

Unquestionably, digestibility accounts for the largest variation in ME or NE value of forages. However, forage type and quality can also influence the efficiency of DE use for ME, as well as the use of ME for RE. Methane losses are really digestive losses, but are not accounted for when apparent digestion is measured solely by faecal output. Factors affecting methane output are related primarily to the availability of digestible carbohydrate fractions, rumen turnover and microbial population dynamics (Moe and Tyrrell, 1979). In addition to methane, UE losses are the other determinant, albeit a small one, when calculating the amount of DE available as ME in measurements of energy balance. Urine energy losses are determined primarily by urea, which accounts for more than 70% of urine nitrogen (Blaxter and Martin, 1962). However, other metabolites such as hippurate also contribute to the energy content of urine, such that the relationship between N and energy content varies with the diet fed (Blaxter *et al.*, 1966). Regardless, factors which increase liver urea production, such as excess rumen degradable nitrogen, increase UE losses and have a small effect on the ratio of ME/DE. The ratio of ME/DE is normally quite high, especially for diets fed to lactating dairy cows (87%; Flatt *et al.*, 1969b) where GE losses as a proportion of intake energy are lower than for nonlactating animals fed poorer quality diets at lower intakes (Blaxter and Clapperton, 1965). However, these differences are small, with GE and UE losses combined normally accounting for less than 15 to 20% of DE.

EFFICIENCY OF ME USE FOR RE

Forages Compared to Cereals

The lower efficiency of ME retention for forages compared to cereals was clearly demonstrated by Kellner in the development of the Starch Equivalent NE feeding standards over a hundred years ago (Armsby, 1903; Table 1). Oxen fed a supplement of straw or meadow hay had a higher HE increment than when fed an equivalent amount of ME from starch. This was related to the low digestibility of the forages, as alkali treatment of straw dramatically reduced the HE increment when it was fed (Kellner as summarized by Armsby, 1903). However, studies by Armsby and Fries (1918) in steer 'J' found a similar NE value for corn starch and alfalfa hay, which was lower than the value for starch reported by Kellner. This discrepancy may have been the result of differences in the basal intakes used in these studies, as the efficiency of utilization of ME for maintenance is greater than the efficiency of ME utilization for growth (Blaxter and Graham, 1955). In addition, there were differences in the correction factors used in calculating the results. These and other conflicting results, often from studies using very limited numbers of observations (i.e. 1 animal), added confusion to the debate over the reasons for differences between the use of TDN from alfalfa compared to corn for milk production. The debate was also clouded by the recent discoveries of a number of vitamins as essential nutrients (Huffman *et al.*, 1952). As mentioned, this debate in part led to the establishment of the Beltsville calorimeters and the conduct of a series of trials comparing the NE value of diets varying in alfalfa hay and concentrate (corn, soybean and bone meals) proportion fed to lactating dairy cows. Initial work compared isonitrogenous diets containing 100, 75 or 50% estimated NE from alfalfa hay (100, 84 and 63% alfalfa hay on a DM basis; Coppock *et al.*, 1964a). They observed clear differences in the ratio of HE/ME

across the 3 diets. When the ME required for maintenance was assumed (131 kcal/kg^{.75}) and tissue energy losses or gains were adjusted to zero using efficiency constants, the efficiency of utilisation of ME for RE was 54, 61 and 65% for the 100, 84 and 63% hay diets, respectively. Later studies compared similar diets containing 60, 40 or 20% alfalfa hay (Flatt *et al.*, 1969) in trials which included the legendary cow Lorna (who achieved a milk yield of 49 kg/d whilst in the respiration chambers). At higher levels of concentrate inclusion (60% or more) there was no effect of level of forage in the diet on the efficiency of ME use for RE, but clear effects on the partitioning of ME between milk and TE. Thus in lactating cows, the inclusion of relatively small amounts of concentrate improved the efficiency of ME use for NE_l, but there was little effect of further dilution of the forage component of the diet above minimal levels of concentrate normally fed to dairy cows in practice. For this reason, the effects of diet forage to concentrate ratio on the efficiency of ME use for NE_l are acknowledged, but considered too minor to merit inclusion in the NE_l rationing approach (NRC, 1989). As the efficiency of ME use for tissue and milk energy synthesis is similar in lactating dairy cows, the NE_l standards do not attempt to distinguish between the 2 processes (Moe *et al.*, 1972).

Forage Type

In addition, type of forage can also affect the amount of ME lost as HE, and conversely NE (RE) gain. An often-used model in this regard is the comparison of grasses and legumes, where ME from grass is typically used less efficiently than ME from legumes. In growing cattle, the use of ME for RE was lower for orchard grass silage than for alfalfa silage (Varga *et al.*, 1990; Waldo *et al.*, 1990). Similarly, dairy cows fed diets based on orchard grass silage consumed less DM, had higher HE/ME ratios, produced less milk and had lower TE gains than when fed diets based on alfalfa silage (Casper *et al.*, 1993). More recently, a substantial body of data from lactating dairy cows have suggested that feeding grass silage as the sole forage source causes a large elevation of maintenance requirement compared to published values (Yan *et al.*, 1997).

Hypotheses

Solving the riddle of the basis for these differences in the efficiency of ME utilization between forages and concentrates and types of forages has been the 'Rubik's Cube' of ruminant nutrition, practically since the discovery that ruminants derive their ME primarily from absorbed VFA. Calorimetric studies suggested that the efficiency of utilisation of ME from acetate was lower than for propionate or butyrate (Armstrong *et al.*, 1957a and 1957b), suggesting that as feeding forages tends to increase ruminal acetate concentrations, that the ratio of absorbed acetate:propionate was responsible for the increase in HE with high-forage compared to high-concentrate diets. It was later suggested that reductions in the efficiency of ME use would be expected when molar acetate proportions in the rumen exceeded 70% of total VFA (Blaxter, 1962). Measurements of ruminal VFA concentration in the studies at Beltsville supported this concept, with a linear negative relationship observed between energetic efficiency and ruminal acetate concentration (Coppock *et al.*, 1964b), but numerous VFA infusion and feeding studies have not (eg. Ørskov *et al.*, 1969; Ørskov and Allen, 1966). One explanation for the disparity in the results obtained, first proposed by Armstrong (1965), is that the utilization of acetate for fat synthesis requires an

adequate supply of reducing power in the form of NADPH. The needed reducing equivalents will be more available if ample supplies of absorbed amino acids or glucose were present (Annison and Bryden, 1999). This concept was supported by the finding that the HE increment for acetate infused into the rumen was much lower in dry cows fed concentrate than those fed alfalfa hay alone (Tyrrell *et al.*, 1979).

In addition to variations in the relative proportions of acetate and glucose metabolized, other factors may contribute to differences in the efficiency of ME utilization. In the studies at Beltsville, growing steers fed grass silage had greater gut fill than steers fed alfalfa silage (Waldo *et al.*, 1990). In addition, relative to increments in DM intake steers had a much greater increment in oxygen consumption by the portal-drained viscera (PDV) with increasing intake of grass silage compared to the increment for alfalfa silage (Huntington *et al.*, 1988). This difference in incremental oxygen use by the PDV accounted for all the difference in incremental body oxygen consumption between the two forages.

In a comparison of high forage and high concentrate diets fed at 2 equalised ME intakes, heifers fed a 75% alfalfa diet had greater PDV blood flow and oxygen consumption at equal ME to the a 75% concentrate diet (Reynolds *et al.*, 1991a). This increase in PDV oxygen consumption accounted for 66% of the difference in body oxygen use between the 2 diets at an intake near maintenance, and 84% of the difference at an intake near twice maintenance requirements for energy. These studies suggest that a large portion of the difference in ME loss as HE between forages and concentrates and grasses and legumes is a consequence of increased oxidative metabolism by the PDV. This may be a result of changes in gut fill, the extent of rumination and the work of digestion. In addition, gut mass may be increased, especially the rumen, due to trophic effects of lipogenic VFA, physical abrasion of the epithelium or the work of digestion. Alterations in the profile of metabolites used may alter PDV oxygen consumption as well. In this regard, the PDV is a principle user of acetate, accounting for 50% of total acetate use in sheep fed alfalfa at maintenance (Bergman and Wolf, 1971) and as much as 25% of body fat. In the study of Reynolds *et al.* (1991a), feeding the high forage diet increased the ratio of acetate to glucose released by splanchnic tissues (PDV plus liver) two-fold compared to the high concentrate diet (Reynolds *et al.*, 1993).

Excess Dietary Protein

Many immature, heavily fertilised forages and legumes can be high in rumen degradable protein. Another consideration for the efficiency of utilisation of ME from forages is the negative effect of excess nitrogen on HE and amino acid availability. In a summarisation of early calorimetry studies at Beltsville, Tyrrell *et al.* (1970) found that excess protein consumption increased HE and decreased RE in lactating dairy cows. This reduction was equivalent to 30 MJ ME for each g of nitrogen consumed in excess of requirements, and this adjustment was included in the formula used for the calculation of NE_1 (Moe *et al.*, 1972). Alternatively, feeding lactating cows protein at a level below requirement reduced RE through effects on DM digestion, as opposed to metabolic effects (Moe and Tyrrell, 1972).

The effect of excess nitrogen intake on HE has been attributed to the energy cost of urea synthesis and excretion, which Martin and Blaxter (1965) estimated to be 3.8

kcal/g ammonia nitrogen in sheep. This was greater than the theoretical cost of 3.2 kcal, which they attributed to the recycling of urea to the gut and the relatively small cost of renal excretion. However, feeding growing heifers 75% alfalfa diets increased the amount of digestible nitrogen compared to a 75% concentrate diet providing equal ME, which markedly increased net PDV absorption of ammonia and liver urea release, but had no effect on liver oxygen consumption (Reynolds *et al.*, 1991b). In other work, feeding urea in alfalfa hay-based diets caused large (60%) increases in net PDV absorption of ammonia and liver urea release, with little change in the absorption of other nutrients, but had absolutely no effect on liver oxygen consumption (Maltby *et al.*, 1993). These observations may be due in part to the fact that although urea synthesis is described as a cyclic process, it is not isolated from other metabolic processes in the liver and the flow of metabolites through other metabolic pathways will be reduced when urea synthesis is increased. In addition, the cost of urea synthesis in terms of ATP is lower on a net basis when the generation of reducing equivalents from fumarate is considered (Reynolds, 1992). The real cost of urea synthesis in terms of ATP and oxygen use is much lower when the cycle is not considered in isolation.

In contrast to the studies just cited, feeding an increased level of soybean meal in a high-concentrate diet increased net PDV absorption of ammonia and liver urea release, as well as liver and body oxygen consumption in growing steers (Reynolds *et al.*, 1992). However, there was also an increase in PDV oxygen use, which was equal to the increase observed for the liver. Together, the PDV and liver accounted for all the increase in body oxygen use, and thus HE, when excess CP was fed. This suggests there may be specific effects of feeding excess protein, rather than nitrogen per se, and that the origin of the increase in HE may not be restricted solely to urea synthesis in the liver. In this study the increase in liver urea production with increased dietary CP level was associated with an increase in liver removal of methionine, tryptophan and lysine (Reynolds *et al.*, 1995). Effects of increased liver ammonia removal on the concomitant removal of amino acids has been suggested based on observed changes in α -amino nitrogen (Reynolds, 1992) or amino acid (Parker *et al.*, 1995) metabolism. However, studies in sheep using isotopic labelling of urea (Lobely *et al.*, 1995 and 1996) have not shown conclusive evidence that an increase in ammonia absorption requires an increase in the deamination of amino acids (other than glutamate) to provide the aspartate needed for urea synthesis. If there is an effect of excess ammonia absorption on liver amino acid removal, the response will likely be influenced by the energy and protein status of the animal.

As mentioned previously, abomasal infusions of protein or essential amino acids have improved milk yield and intake in cows fed forages high in rumen degradable protein (Oldham and Smith, 1980; Chamberlain *et al.*, 1989). However, these responses may reflect effects of excess rumen degradable protein on the efficiency of microbial protein synthesis in the rumen, rather than effects of excess ammonia absorption on liver removal of absorbed amino acids.

CONCLUDING REMARKS

Measurements of energy balance form the basis of most current rationing systems for energy in ruminants, thus are the standard used in judging the effects of forage chemical composition on energy value for production. In this regard, many laboratory

procedures for evaluating forage quality are used to predict the digestibility or ME value of forages *in vivo*. Measurements of energy balance are costly and time consuming to obtain, whilst the resources for the maintenance of a sustained program of calorimetry are at present limited. Thus the need for current, as well as new innovative approaches to the evaluation of forage quality and energy value for production.

Current rationing systems for energy and protein fail to adequately predict the response of the animal, both in terms of product composition and nutrient partitioning. However, the systems were never intended to be a replacement for practical wisdom and experience, but a guide and basis for 'rational' decision making. As discussed, the predictive limitations of current NE systems are in part due to the simplification of metabolism to a caloric basis, as well as the simplification of the effects of the animal's metabolism on the recovery of absorbed nutrients in a product to a series of efficiency 'constants'. If the 'nirvana' of a rationing system capable of predicting production response is to be attained, the need for more complex approaches is therefore suggested. This is the logic behind the development of models based on a prediction of the nutrients absorbed from the gut and their subsequent utilisation by specific tissues in the animal (AFRC, 1998). If predictive models incorporating the complexities of nutrient metabolism are capable of predicting response, the challenge will be for them to maintain a practical basis at the level of feed quality evaluation.

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Table 1. Tissue energy retention (RE) from supplemental ME in oxen fed fodder.

Supplement	RE/ME
Wheat Straw	17.4
Meadow Hay	41.4
Starch	61.5
'Extracted' Straw	63.0

Kellner and Kohler, 1900 (as cited by Armsby, 1903)