Meeting the protein requirements of ruminant livestock

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Ruminant animals acquire their amino acids from the small intestinal digestion of ruminally derived microbial protein and dietary protein which has escaped ruminal degradation. The UK metabolizable protein system provides a framework with which the net absorption of amino acids from the small intestine is computed in relation to the animal's requirements and is based largely upon a set of criteria by which feedstuffs are evaluated. While conceptually the system has many positive features, a number of serious weaknesses have been identified, particularly with respect to the techniques used to evaluate feedstuffs. Some of these issues are considered, particularly the over-reliance which is placed upon *in vitro* methodologies which have not been adequately validated against *in vivo* observations and have been shown to give unacceptable variation. Attention is also drawn to the inadequate representation of host tissue metabolism within such systems, for example, the importance of splanchnic metabolism with respect to overall nutrient utilization. It is concluded that improved representation of energy (i.e. carbohydrate) and protein interactions within the whole animal and not simply within the gastro-intestinal tract is urgently required; this inevitably will lead to a change in research direction. Equally, support for a mechanistic understanding rather than an empirical representation of protein metabolism in ruminant livestock is presented, given that the demands upon the ruminant industry, particularly with respect to predictability of animal response, is likely to increase as a consequence of increased consumer impact on the marketing of animal products.

Introduction

Much of the research effort into the nutrition of ruminant livestock over the last two decades has concentrated upon the processes of protein digestion in the rumen, the concurrent synthesis of microbial protein and measurement of the resultant supply of total amino acids to the small intestine, in relation to the amount and composition of dietary protein consumed. At the same time, the relative importance of the energy components of the diet, and in particular protein: energy interactions at both the rumen and host tissue levels, has been largely ignored.

The processes of protein nitrogen (N) utilization within the intestinal tract of ruminants have been known for over half a century. However, it is only recently that reliable techniques to permit quantification of the processes of microbial digestion, biomass synthesis and the intestinal absorption of amino acids have been developed. In turn this has led to the proposal of several schemes to permit estimation of the quantity of protein absorbed from the small intestine (AFRC, 1992; AFRC, 1984; CSIRO, 1990; Fox *et al.*, 1992; INRA, 1978; Madsen, 1985; NRC, 1985; Rohr, 1987), based on a knowledge of the quantity of diet consumed and appropriate analysis of the feed ingredients, in relation to the estimated amino acid requirements of the host animal. While most of these schemes appear to have national allegiance, they are broadly similar in concept. They are all empirical models designed to describe biological processes using data collected and analysed from both *in vitro* and *in vivo* experimentation, without necessarily providing any mechanisms of the processes involved.

In this article the scheme which has been recently proposed for adoption within the United Kingdom (AFRC, 1992) is discussed. By use of appropriate experimental data, it is demonstrated where these proposals are inadequate and it is suggested that, while the scheme has conceptual strengths, further improvements will be required before providing a significant improvement over previous protein rationing schemes. Finally it is proposed that none of the current schemes will ever be able to adequately predict all aspects of animal performance (e.g. product composition) until they explicitly represent protein and energy interactions at all levels of metabolism within the animal. Due consideration should be given to replacing empirical models with models which include the mechanisms involved plus representation of the important concept of time (i.e. dynamic mechanistic models).

Metabolizable protein — UK proposals

Calculation of metabolizable protein supply

The key element of the recent proposals by AFRC (1992) is the fractionation of dietary protein according to the scheme proposed by Ørskov & McDonald (1979), based on the concept that proteins can be classified with respect to their relative susceptibilities to the processes of ruminal digestion. One fraction is considered to be instantaneously degradable within the rumen (quickly degradable protein — QDP), a second fraction is considered to be slowly degradable (slowly degradable protein — SDP) while the final fraction is considered to be totally resistant to rumen degradation (undegradable protein — UDP) but capable of being significantly digested within the small intestine. Such values are routinely obtained using *in saccho* techniques, with the effective ruminally degraded protein (ERDP-p) component of the feed being estimated from the following equation:

$$p = 0.8a + (b \times c) / (c + r) \quad (1)$$

where

a = immediately soluble protein, assumed to be only 80% available for microbial synthesis,
b = non-soluble but potentially degradable protein,
c = the degradation rate constant for fraction b protein, and
r = the estimated fractional outflow rate of rumen digesta.

One major improvement in the scheme proposed by AFRC (1992) was recognition that the fractional outflow rate of rumen fluid is influenced by the level of dry-matter (DM) intake such that at increased feed intake the proportion of ERDP in a feed will decline while the amount of undegraded

dietary protein ([undegraded SDP] + UDP) flowing into the small intestine will increase (Beever & Cottrill, 1994). Initially it was suggested that outflow rates of 2, 5 and 8%/h should be applied at feeding levels approximating to one, two and three times maintenance ME requirements. Subsequently an equation was proposed to overcome the discontinuity associated with this approach, namely,

$$r = -0.024 + 0.179 \times (1 - e^{-0.278L}) \quad (2)$$

where

L = level of ME intake as a multiple of maintenance.

Subsequently the availability of ERDP is considered in relation to the availability of energy to support microbial protein synthesis. AFRC (1992) proposed the concept of fermentable metabolizable energy (FME), which was defined as total dietary ME intake less the energy contained in fermentation end-products of feeds such as silages, as well as the energy contained in dietary lipids, both of which were considered to be unavailable to support microbial synthesis. Subsequently ADAS (1991) proposed an equation based on the analysis of 171 grass silages of contrasting DM contents to predict the ratio of FMF/ME, namely,

$$FME/ME = 0.467 + 0.00136 \times ODM - 0.00000115 \times ODM^2 \quad (3)$$

where

ODM = oven dry matter content of the grass silage.

AFRC simplified this to assume that FME was equal to 0.9 and 0.95 × ME for grass silages and distillery by-products respectively.

The yield of microbial crude protein (MCP) is fixed at 9g/MJ FME at maintenance levels of feeding, increasing in response to higher feed intakes to 10 and 11 g/MJ for growing cattle and lactating dairy cows respectively, provided ERDP supply is not limiting. To avoid the use of fixed efficiencies of microbial protein synthesis, AFRC (1992) proposed the following equation to represent microbial protein synthesis in relation to feeding level and FME supply:

$$MCP\ (g/MJ\ FME) = 6.0 + 7.0\ [1 - e^{(-0.35L)}] \quad (4)$$

From the estimate of MCP yield, the proportion of microbial true protein (MTP) is assumed as 0.75, with the digestibility of MTP fixed at 0.85, such that the yield of digestible microbial true protein (DMTP) is calculated as:

$$DMTP = 0.75 \times 0.85 \times MCP = 0.6375 \times MCP\ (g/d) \quad (5)$$

To calculate the supply of digestible undegradable protein, the QDP plus the SDP traction degraded in the rumen are discounted from total protein intake. The undegraded SDP fraction [USDP] can be estimated as:

$$USDP = b(1 - c/[c + r]) \quad (6)$$

and thus the supply of undegraded dietary protein to the intestines is:

$$UDP = CP - QDP - SDP + USDP \quad (7)$$

with the yield of digestible undegradable protein (DUDP) calculated from the equation:

$$DUDP = 0.9 \times (UDP - (ADIN \times 6.25)) \quad (8)$$

which proposes that all UDP other than that associated with acid detergent-insoluble nitrogen (ADIN) is 0.9 digested in the small intestine, while all ADIN other than that associated with some distillery by-products is assumed to be completely indigestible.

Thus total metabolizable protein supply (MP) is calculated as:

$$MP(g/d) = DMTP + DUDP \quad (9)$$

from equations 5 and 8 respectively.

Estimation of protein requirements

In estimating the animal's protein requirements, it is necessary to consider the efficiencies with which absorbed protein is used for specific purposes. The concept of variable efficiencies is a major change from early proposals within the UK and, after considerable discussion, AFRC (1992) proposed the efficiency of utilization of an ideal amino acid mixture to be 1.00 for maintenance purposes, and 0.85 for all other synthetic processes. Thereafter, the relative values of absorbed amino acid mixtures, as opposed to an ideal mixture, were assumed to be 0.7 for growth, 0.8 for lactation, 1.0 for pregnancy and 0.3 for wool growth. Consequently, the values most frequently used in the new scheme range from 1.0 for maintenance, to 0.85 for pregnancy, 0.68 (0.85 × 0.8) for lactation, 0.59 for growth and 0.26 for wool growth.

Current experience with the new proposals

It is apparent that the initial characterization of the protein component in terms of its availability within the rumen is crucial to the success of the new science. *In saccho* techniques are used routinely by many laboratories and indeed remain the preferred method. However, attempts to standardize these procedures have been both limited and disappointing. The results of several intra-laboratory studies undertaken in the UK have been reported (AFRC, 1992). In the initial study, the laboratories were provided with standard samples of hay and soya but allowed to use their own *in saccho* technique. The extent of variation in the results was considerable, suggesting that greater specification was required with respect to the methodologies used. Consequently, the exercise was repeated but then the *in saccho* incubation methodology was standardized between laboratories. Even so, the extent of variation in the data was considerable, although admittedly less than had been noted earlier (Table 1).

Subsequently a European initiative involving 23 laboratories in 17 countries estimated the degradability of five identical concentrate feeds (cited in AFRC, 1992). With an assumed rumen outflow rate of 8%/h, average degradabilities (and SD) of 63% (11) soya; 51% (9) cottonseed meal; 47% (7) coconut meal; 23% (6) fishmeal; and 72% (7) barley were

Table 1 Between laboratory variation observed in the estimation of the protein degradability of standard samples of hay and soya

		Hay	Barley	Soya	Rape
Mean		44.0	75.4	60.8	64.0
Range	Low	39.0	60.0	56.0	64.0
	High	51.0	89.0	69.0	68.0

Source: Agricultural & Food Research Council (1992)

Table 2 Consequence of variation in the estimates (low v high) of protein degradability, determined using the *in saccho* procedure, on the supply of metabolizable protein from a barley:soya (80:20) concentrate.

	Estimate	
	Low	High
Protein degradability (g/100 g):		
Barley	58	85
Soya	34	79
ERDP* (g/kg DM)	93	162
DUP** (g/kg DM)	96	71
Metabolizable protein (g/kg DM):	155	174

* Effective rumen-degraded protein
** Digestible undegraded protein

obtained. The implications of this variation can be seen in Table 2 when the highest and lowest measured estimates of degradability for barley and soya were applied to a barley:soya concentrate (80:20).

The estimated metabolizable protein supply varied between 155 and 174 g/kg DM, an error in estimation equivalent to a difference in milk yield of 0.4 kg milk/kg concentrate fed, which is not acceptable. Nevertheless, some research workers have suggested that *in saccho* techniques to estimate protein degradability can be replaced by laboratory methods, thus obviating the use of experimental animals. Beever & Cottrill (1994) considered some of these options but concluded that until the *in vivo* data are more robust, any such moves must be treated with utmost caution. This applies particularly to the emerging science, or maybe art, of near infrared reflectance spectroscopy.

Some concern must also be expressed over the estimation of dietary FME contents. To date, no actual *in vivo* measurements of FME have been reported and it is likely that current estimates of FME as published by AFRC (1992) for a range of feedstuffs will have to be revised. Chamberlain *et al.* (1993) measured the non-FME components (i.e. fermentation products and oils) of 73 first-cut silages and compared FME estimates with those predicted from the equation given earlier. Overall agreement was poor which led the authors to conclude that further refinement of this important parameter was urgently required.

Beever & Cottrill (1994) considered the concept of FME in more detail and concluded that many of the values proposed by AFRC (1992) are not feasible. It is surprising that neither RDP or UOP are discounted from the estimation of FME, although the latter will make no contribution whatsoever to FME, while the former will supply at the most only modest amounts of energy. Consequently, the FME values for many protein concentrates appear high on theoretical grounds. For example, the FME content of fishmeal is given as 12.0 MJ/kg DM, equivalent to 0.85 of the ME content, yet in the same publication DUDP supply is estimated as 344g/kg DM, which amounts to 56% of the stated ME concentration. Equally for maize gluten, stated FME content is 0.94 of ME content yet stated DUDP supply is equivalent to 54% of ME.

Synchronization of energy and protein availability in the rumen

To optimize the efficiency of utilization of ruminally degraded N for microbial protein synthesis, it is important that a readily available source of energy is supplied at the same time in an amount commensurate with the microbial N requirement to sustain microbial growth. Beever (1993) drew attention to the fact that with most natural feedstuffs this situation is unlikely to prevail at all times throughout the feeding cycle. Considering that fresh grass consists of variable amounts of different carbohydrates, each of which will have different rates of digestion in the rumen, it follows that there may be occasions throughout the day when the ratio of available carbohydrate to protein is either greater or less than optimal microbial requirement. This point is exacerbated when grass silage is considered. During ensiling, most water soluble carbohydrate is fermented, leading to a significant reduction in readily available carbohydrate supply, with a greater proportion of the total carbohydrate being derived, albeit at a slower rate, from degraded hemicellulose and cellulose. At the same time, a substantial part of the forage protein will be degraded, due primarily to the action of plant proteases. This will increase the amount of non-protein N in the feed and the rate of availability of silage N in the rumen once the feed is consumed. Thus, the ratio of available carbohydrate to available N is likely to be impaired compared with that considered to be optimal for microbial growth. It must be accepted that this theory has never been adequately examined in animal experimentation, but studies by Beever *et al.* (1986) with fresh forage diets fed to beef cattle demonstrated that the ratio of available N to ruminally digested organic matter (RDOM) varied between 10 and 70 g degraded N/kg RDOM throughout the feeding cycle, compared with an optimal microbial requirement considered to fall within the range of 30–40 g N/kg RDOM.

Current feeding systems take no account of such aspects and therefore opportunities to improve both microbial protein yield and efficiency of utilization of degraded nutrients, especially N, in the rumen may be missed. Rooke *et al.* (1987) demonstrated the consequence of nutrient asynchrony with a grass silage diet fed to dairy cows. By intraruminal infusions of specific nutrients, they failed to demonstrate any response in net microbial synthesis when either urea or casein as sources of non-protein, or protein-N, was infused into the rumen. In contrast, infusion of glucose stimulated microbial protein synthesis, suggesting that readily available carbohydrate was a major limitation to microbial growth on grass silage. Furthermore, when glucose and casein were co-infused, the response in microbial protein synthesis was considerable. Growth efficiency increased to 38 g/kg RDOM compared with 22 g/kg RDOM on the unsupplemented silage and overall microbial protein yield was similarly increased.

Beever *et al.* (1987) attempted to improve the efficiency of utilization of degraded N from high-N containing white clover diets, using either monensin as a feed additive or by spraying the forage with formaldehyde prior to feeding. Monensin was considered due to claims that it will reduce rumen ammonia concentrations (Chalupa, 1980) and thus improve the overall efficiency of N utilization within the rumen.

Indeed, in the study with fresh clover, rumen ammonia concentrations were reduced substantially but there were no associated improvements in either the efficiency or net yield of microbial protein. In contrast, formaldehyde treatment and storage of the forage for six hours prior to feeding gave sizeable improvements in the flow of non-ammonia nitrogen (NAN) into the small intestine, and ruminal losses of dietary N were reduced accordingly. Of the increased NAN flow, over 75% was attributable to increased microbial protein synthesis, with only a small increase in the flow of undegraded dietary protein from the rumen.

Ammonia metabolism in diets containing high-N

On diets where ruminal N supply exceeds the capacity of the rumen microbes to synthesize microbial protein, rumen ammonia concentrations increase, resulting in increased absorption of ammonia from the rumen and a reduced supply of protein to the intestines. In a comparison of high-N ryegrass and white clover, Beever & Siddons (1986) estimated absorbed ammonia losses of between 23 and 30% of total dietary N (Table 3). Furthermore, the study of Siddons *et al.* (1985) indicated that ammonia absorption from the rumen is highly pH dependent, given that unionized ammonia (NH_3) is absorbed at a faster rate than the ammonium ion (NH_4^+). Consequently, the overall efficiency of ammonia utilization in the rumen to support microbial synthesis would appear to be related to both the rate of protein and carbohydrate digestion in the rumen.

The effect of increased ammonia absorption from the rumen on N utilization by the animal was considered by Wilton (1989). With beef cattle offered grass silage diets, there was a substantial increase in the net flow of ammonia into the portal vein following feeding. The response was observed within 30 minutes of commencement of the meal, and while all uneaten silage was removed after one hour, portal ammonia flow continued to increase for a further 60 minutes and did not return to pre-feeding levels for a further two hours. The increase in arterial ammonia concentration was however less pronounced, showing only a small increase from the baseline (0.1 mmol to 0.12 mmol) after four hours. This suggested that hepatic capacity to remove ammonia arriving in the portal vein was substantial and this was confirmed by considering hepatic outflow of ammonia, with net ammonia removal by the liver equal to net portal appearance of ammonia. However, hepatic urea-N output was in stoichiometric excess of ammonia-N removal by the liver, indicating that some amino acids may have been catabolized within the liver. This observation was supported by Maltby *et al.* (1992) who examined splanchnic metabolism of N in growing cattle fed maize silage supplemented with either urea or protected amino acids. On all treatments hepatic removal of ammonia was extensive while hepatic output of amino acids was considerably less than their portal appearance, this effect being most significant on the urea-supplemented diet. Part of this loss of amino acids may be apparent rather than real due to the synthesis of peptides or proteins prior to exportation from the liver. Equally, some amino acids may have undergone obligatory catabolism in the synthesis of glucose, while others may have been catabolized due to the possible regulatory role of the liver on the exportation of amino acids in relation to the requirements of peripheral tissues. However, there is evidence that at high ammonia loads, it may be expedient to remove ammonia by a pathway which involves the donation of an NH_2 group from amino acids which combines with one NH_2 group derived from ammonia. If this process is shown to occur when hepatic ammonia load is increased, the effect on peripheral amino acid supply on diets such as fresh grass and silages may be quite significant.

Table 3 Nitrogen digestion and utilization in the rumen of dairy cows fed fresh perennial ryegrass and white clover-based diets

Forage	Perennial ryegrass	Perennial ryegrass/ White clover	
Proportion: (PRG : WC)	100.0	75.25	50.50
Organic matter intake (kg/d):	11.75	14.05	16.62
Total N intake (g/d):	519	604	693
Duodenal NAN (g/d):	380	466	488
Duodenal NH_3(g/d):	55	51	58
Ruminally absorbed NH_3 (g/d):	84	87	147
Absorbed ammonia* (g/d):	139	138	205
(g/g N intake)	0.27	0.23	0.30

* Calculated as N intake less duodenal NAN; represents a minimal estimate attributable to the feed as no recycling of N was taken into account

PRG = Perennial ryegrass

WC = White clover

Opportunities to improve the utilization of dietary protein by ruminant livestock

To increase the efficiency of dietary protein utilization by ruminants, consideration can be given either to improving the composition of the food offered or modification of the processes of nutrient utilization known to occur within the animal.

Dietary tannins

Considerable interest has been shown in increasing the content of tannins in forage crops, especially legumes. As reviewed by Mangen (1982), several laboratories have demonstrated that tannins can confer substantial benefits upon the utilization of dietary protein through reduced rumen ammonia absorption and increased NAN flow to the small intestine. It is believed to be due to the formation of protein : tannin complexes which restrict the rate of protein degradation in the rumen. Barry & Manley (1984) demonstrated substantial and linear improvements in the small intestinal absorption of NAN (in relation to nitrogen intake) over a wide range of forage tannin contents. However in a parallel study, with low (49 g total tannin/kg DM) and high (120 g/kg) tannin containing *Lotus pedunculatus*, Barry & Duncan (1984) reported a significant depression in voluntary feed intake at the increased tannin content, attributable to a depression in the rate and thus extent of cellulose and hemicellulose digestion in the rumen and the whole tract. In a further study, Barry *et al.* (1986) offered white clover (no tannin) or Lotus (tannin containing) diets to growing lambs and examined fat metabolism in subcutaneous tissues taken at the time of slaughter using *in vitro* techniques. The results, illustrated in Table 4,

Table 4 Effect of low and high tannin-containing legumes on *in vitro* fat metabolism in subcutaneous tissue of growing lambs (Barry *et al.*, 1986) (units; nmol/g wet tissue/h)

	Clover	Lotus
Acetate incorporation	1906	1556
Glucose oxidation	118	94
Glycerol release	732	1238

indicated that factors associated with lipogenesis (acetate incorporation into fatty acids and glucose oxidation to produce NADPH) were reduced by approximately 20% on the Lotus diet compared with the values observed for the white clover, while lipolysis (glycerol release) was increased by almost 70%. Obviously these estimates are only a reflection of *in vivo* fat metabolism and refer to one specific adipose site. Consequently they cannot be used directly to quantitatively assess the effect of dietary tannins on net fat deposition, but they do suggest that the increased carcass protein:fat content often observed in animals fed such diets is not exclusively related to an increased absorption of amino acids (Thomson *et al.*, 1971).

Use of cereal supplements

Supplementation of forage diets with cereals increases ration energy density, and thus total intake of energy, in those situations where forage quality is likely to impair total feed intake and available energy levels. However, there is evidence that the ME derived from forage diets is less efficiently utilized compared with that from cereal-containing diets. Part of this effect may be related to an elevated oxygen consumption in splanchnic tissues which will lead to elevated heat production from such tissues (Reynolds *et al.*, 1991). In a comparison of high quality grass silage fed alone (H) with a low quality grass silage (as measured by apparent digestibility) fed alone (L) or with two levels of barley substitution (LCI, LC2) to growing cattle (Thomas *et al.*, 1988; Beever *et al.*, 1988), all four diets were characterized in terms of ME intakes and the supply of NAN to the small intestines, in addition to measurement of animal performance (carcass energy, fat and protein retention). With DM intake fixed across all diets, the respective ME intakes were 0.93 (H), 0.76 (L), 0.83 (LC1) and 0.87 (LC2) MJ/kg$^{0.75}$/d with absorbed NAN estimated as 1.47, 1.33, 1.17 and 1.23 g/MJ ME intake respectively. As expected, energy, protein and fat retention were reduced on diet L compared to H. However, at the highest level of barley inclusion (LC2), all indices of animal performance (retention of energy + 20%, protein + 33% and fat + 16%) were greater than those observed on diet H. This occurred despite ME intake, NAN supply and NAN supply/MJ ME being highest on diet H; therefore a full explanation of the improved efficiencies of nutrient utilization on cereal-containing diets is still required.

In a lactation study to examine the effect of increased concentrate supplementation of grass silage on energy utilization, Cammell *et al.* (1992) showed the milk energy response to be considerably greater at the first increment of concentrate (3 to 6 kg/d) than when concentrate allowance was further increased to 9 kg/d. This applied at all stages of lactation examined between weeks 5 and 29 of lactation. However, examination of energy partitioning, using open-circuit indirect calorimetry, revealed that a substantial part of the response at the lower concentrate increment was attributable to increased body energy mobilization, such that cows receiving 6 kg concentrates were at lower levels of body energy retention (or increased body energy mobilization) compared with all other cows. On average, they were three weeks later into lactation before positive body energy retention was achieved (week 11) compared to the other two treatments (week 8). It would appear that this repartitioning was regulated more by hormonal events than specific changes in nutrient supply, but changes in the endocrine status of the cows were not monitored in this study.

Use of forage alternatives

In his studies, Phipps (In press) examined several forage alternatives as part replacements for grass silage in dairy cow rations. These included fodder beet, urea-treated and fermented whole crop wheat silage, brewers grains and maize silage, at a 33% replacement for grass silage, and also maize silage at a 75% inclusion rate. The results, summarized in Table 5, indicated that, with grass silage as the sole forage, milk protein and fat contents averaged 30.8 and 41.5 g/kg respectively, and yields of protein and fat were 0.64 and 0.88 kg/d. All forage alternatives examined increased milk protein content (range 31.0–33.1 g/kg) while fat contents were reduced (range 40.4–37.9 g/kg) except with fodder beet where fat content was slightly increased (42.2 g/kg). In the most responsive situation (high maize silage inclusion) significant increases in both protein (0.86 kg/d) and fat (1.06 kg/d) yields were observed, in part due to an increased feed intake and a concomitant increase in milk volume, with the change

Table 5 Effect of including forage alternatives in the diet of dairy cows fed grass silage and concentrates (6 kg/d) upon total ration dry-matter intake, the yield of milk and milk constituents, and the composition of milk

Forage component	GS	GS/MS*	GS/FB*	GS/BG*	GS/MS**
Total dry-matter intake (kg/d)	16.30	17.80	19.00	18.30	19.20
Yields (kg/d)	20.90	24.00	24.20	27.00	27.40
Protein (kg/d)	0.64	0.75	0.80	0.83	0.86
Fat (kg/d)	0.88	0.98	0.99	1.02	1.06
Milk composition (g/kg)					
Protein	30.80	31.30	33.10	31.00	31.60
Fat	41.50	40.40	42.20	37.90	39.00
Protein: Fat	0.74	0.77	0.78	0.82	0.81

*(**) Indicates 33% (75%) inclusion in forage component
GS = Grass silage
MS = Maize silage
FB = Fodder beet
BG = Brewers grains

in protein to fat ratio (0.74–0.81 g/g) probably being of greatest financial importance. Such studies demonstrate that seemingly good quality grass silage, as determined by laboratory analysis, is often less than adequate as a feed for efficient milk production.

In support of this study, the potential of an adequate supply of readily available carbohydrate in the diet is illustrated by the data of Krohn *et al.* (1985) who examined three levels (160, 320 and 480 g/kg total DM) of molasses substitution on the performance of lactating dairy cows. At the first two levels of inclusion, milk yield increased, accompanied by increased milk protein yield as well as increased milk protein content. In contrast, fat contents and yields were unaffected. At the highest level of molasses inclusion, milk yield was compromised but milk protein content increased further so that milk protein output was unaffected. Similar results were noted by Roberts (1987) using fodder beet and Yan & Roberts (1993) using molasses, confirming that even modest inclusion of a readily available carbohydrate source can elicit substantial improvements in increased milk protein content.

Implication of body mobilization and repletion

In a study with 54 second- and third-parity cows, Gibb *et al.* (1992) quantified body tissue changes in relation to stage of lactation by serial slaughter between lactation weeks 2 and 29. At calving, mean body energy content of all cows was estimated at 6.3 GJ. As lactation progressed, this declined on average to 4.5 GJ (net loss of 1800 MJ) although the effect was dependent upon the level of ME intake achieved by the cows which received the three levels of concentrates referred to earlier (Cammell *et al.*, 1992). Of this energy loss, the amount accounted for as mobilized fat was considerably greater than mobilized protein. On average 37 kg fat were lost between calving and lactation week 8 and, in some cows, this value approached 60 kg. Assuming average efficiencies of conversion of mobilized fat energy into milk energy, this equates to over 300 litres of milk. In contrast, net protein mobilization was less than 6 kg, but this probably underestimates the considerable relocation of protein within the animal's body which occurs immediately after calving. Following parturition, liver and rumen-reticulum fresh weights were estimated to increase by 27 and 20% respectively, while the length of the small intestine increased by approximately 16%. These appear to be normal physiological events in all post-parturient cows and may in part explain the reduced voluntary feed intake which occurs at this time. Equally, the increased demand for protein to support tissue synthesis may be one cause of the reduction in milk protein content which generally occurs in early lactation.

Strategies to improve milk protein content

Experience gained from applied research in relation to increasing milk protein content, particularly the increased use of high carbohydrate-containing feedstuffs, has been confirmed more recently in practice. The use of minimally processed wheat (caustic soda treatment for five days prior to feeding) for dairy cows has increased dramatically over the last three years and on many farms is now being included in the ration at up to 20% of total DM intake. Milk protein content increases of over 2.5 g/kg have been observed, but as suggested earlier the mechanisms for this response have not been elucidated. Furthermore, it is recognized that the responses can be highly variable and therefore impossible to predict with any acceptable degree of accuracy.

To understand the processes of milk protein synthesis, particularly to increase milk protein content and improve the efficiency of utilization of dietary protein, studies have been initiated in conjunction with other UK scientists. Concentrating principally on metabolism in the mammary gland, Metcalf *et al.* (In press) demonstrated that fishmeal supplementation of a grass silage concentrate diet gave a predictable increase in duodenal NAN supply (0.69 g/g extra dietary N supplied), but the response in milk protein output was equivalent to only 19%, 12% and 8% of the increased small intestinal supply, duodenal flow or dietary intake of NAN (N) respectively. Furthermore, as seen in many other protein supplementation experiments, there were no discernible effects on milk protein content. Arterial supply of total amino acids to the mammary gland increased by only 2.5%, although the increase in essential amino acid supply was greater (+27%) and may have contributed significantly to the 29% increased uptake of amino acids by the gland. However, the response in milk protein output was less than would have been predicted on the basis of measured amino acid uptake. In a parallel study, which used protected soya to increase the small intestinal absorption of amino acids, this excess uptake of amino acids by the mammary gland in relation to amino acid output in milk was examined with respect to leucine. Using ^{13}C-labelled leucine, Bequette *et al.* (1994) demonstrated that with the protein-supplemented diet (+420 g dietary protein/d), milk protein yield increased by only 65 g/d (46 mmol leucine/d) despite an increased mammary uptake of leucine of more than 140 mmol/d. Of this increased leucine availability, a significant proportion was directed towards total mammary protein synthesis, but largely as non-milk proteins, while leucine oxidation within the gland was substantially increased. Findings such as these confirm that desirable animal responses cannot simply be achieved by a supply-driven system and, even when the uptake of specific nutrients by the target tissue is increased, there is no guarantee that this will result in the synthesis of extra products such as milk proteins.

Conclusions

The recently proposed metabolizable protein system as applied in the UK is now being rapidly implemented by the industry. While it is accepted as a major conceptual improvement, a number of weaknesses have been identified and discussed. In the short term it should be possible to improve these aspects to such an extent that the scheme does not fall into disuse because those who apply it are sceptical of its ability to predict animal performance, or at least to provide a closer match between the supply and requirements of amino acids. However, animal production in most parts of the developed world continues to become much more sophisticated. Demands to reduce the impact of intensive livestock production upon the environment are increasing as is the need to provide reliable predictions of the level of animal performance and the composition of the animal product. In most of Western Europe, the only opportunity which exists to increase the value of milk sales is to increase the protein content while maintaining or even reducing fat content. Technologies such

as the use of low ruminally degradable protein supplements or the dietary inclusion of ruminally protected amino acids such as lysine and methionine in the diet often give disappointing and variable results, suggesting that our understanding of protein metabolism within ruminants is inadequate. The study of Bequette *et al.* (1994) referred to earlier is an excellent example.

In future, it will be necessary to recognize the importance of nutrient interactions at all levels within the animal. The partition of effort between events occurring within the gut and the body of the animal has in the past been based largely on research convenience. With techniques such as modelling, we have a real opportunity of bringing all important processes together towards a better understanding of nutrient utilization. To achieve this, however, the desire and support to work in all areas of animal nutrition must exist.

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