Proc. Aust. Soc. Anim. Prod. 1996 Vol. 21

THE UNDERWOOD LECTURE FOR 1996

IMPROVING THE EFFICIENCY OF NUTRIENT UTILISATION AND THE PREDICTABILITY OF PRODUCT COMPOSITION IN THE LACTATING DAIRY COW

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INTRODUCTION

The UK dairy industry as part of the larger European market has experienced considerable change over the last decade or so and this situation is expected to continue. Following the introduction of quotas on milk production in 1984, a payment structure based on milk constituents was imposed with a price ratio of protein to fat of approximately 0.9:1. This differential in price now exceeds 3:2, reflecting oversupply of fat and an increased market demand for protein by milk processors. Consequently, all farmers are limited by a fat production quota, and the penalty on overproduction of milk, after correction to the fat base level, can substantially exceed the prevailing milk price (current penalty =1.2x milk price). Thus there are no incentives to overproduce milk, and farmers respond, either by the annual leasing or purchase of quota (current prices; approximately 50% and 300% of milk price), restricting output per cow by nutritional means or reducing the number of cows milked. In 1994, the Milk Marketing Board was disbanded, and replaced by a free market where individual dairies negotiate with farmers, offering incentives according to the quantity and composition of milk they require. Currently the market for milk is buoyant, although most predictions indicate this position will not be sustained and farmers anticipate lower returns in the longer term.

Feed costs still constitute a major part of the costs of milk production whilst feed composition can have a significant effect on milk composition. Thus there is renewed-interest in opportunities to improve the overall efficiency of nutrient utilisation by the cow, whilst increasing milk protein content and maintaining or possibly reducing milk fat content and yield. The introduction of feeder wagons on many farms has reduced the reliance on purchased concentrates, and increased on-farm use of commodity feeds (e.g. soya, wheat, maize gluten) with increased awareness of the importance of forage quality, principally grass and maize silage. If such changes were not sufficient, the UK industry is now at the centre of the Bovine Spongiform Encephalopathy (BSE) issue, and it is premature to predict the implications of such on the UK dairy and beef industries. This paper will consider the implications of some of these changes and attempt to relate current research effort to the practical feeding of dairy cows for quality milk production.

Nutrient intake

Given that a significant proportion of UK milk is produced from conserved forage, the importance of optimising silage intake is obvious. Grass silage remains the principal source of conserved forage, with most of that fed to dairy cows being produced from heavily fertilised grass swards cut as primary growths in early May. Most of this silage will be clamped, with increased attention being paid to ensiling conditions as demonstrated by Aston *et al.* (1994) who, in comparing four silages fed to dairy cows, concluded that the ensiling process was considered to have a greater effect on silage intake than a reduction in grass quality, as influenced by factors such as inclement weather at the time of harvesting. However, despite a comprehensive characterisation of the silages, Aston *et al.* (1994) were unable to identify those factors responsible for the large differences in dry matter (DM) intake noted when the silages were fed without supplement to lactating dairy cows. Thus, prediction of silage intake remains a research goal, and it may now be opportune to abandon the empirical approach to feed intake regulation and establish the importance of the mechanisms involved.

At the same time, feeding maize silage to dairy cows has increased dramatically. In 1990, 30,000ha of maize were grown for ensiling; by 1995 this had increased to over 110,000ha and with the introduction of early maturing varieties plus improved knowledge on the agronomy of maize, the production of maize silage has spread to more northerly latitudes of Britain. In studies at CEDAR, the effect of replacing 33% of the grass silage component of the diet with maize silage on increased forage dry matter (DM) intake and improved milk output was established, and more recently Phipps *et al.* (1995) found that this response was maintained as the proportion of maize silage in the forage component of the ration was increased to 75% (Table 1). Consequently, many farmers include maize silage in excess of *60%* of the forage component of the ration. Also, Phipps *et al.* (1995) examined other potential replacements for grass silage, and established that 'forage' DM intake was stimulated in every case as grass silage was partially replaced within the diet (Table 1). In most instances, these changes were accompanied by improvements in milk yield and alterations in milk composition, the reduction in milk fat content associated with brewers grains inclusion being particularly interesting. A similar effect was observed by Smoler *et al.* (1995) when barley dark grains were included in the diet and the mechanisms of this effect are currently being investigated.

Table 1. The effect of replacing part of the grass silage component of the ration of lactating dairy cows with 'alternative forage' sources on forage intake, milk yield and milk composition. FW, UW, BG, FB, MS refer to fermented whole crop wheat silage, urea treated whole crop wheat silage, brewers grains, fodder beet and maize silage respectively, all at 330g/kg total forage DM, and MSH refers to maize silage inclusion at 750g/kg total forage DM, with grass silage (GS) comprising the remainder of the forage component in each diet (i.e. 670 or 250g/kg total forage DM respectively)

Forage type	GS	+FW	+UW	+BG	+FB	+MS	+MSH
Forage intake(kg/d):	9.3	10.6	10.2	10.3	11.5	10.6	12.5
Milk yield(kg/d):	23.0	24.2	24.0	26.7	25.9	26.4	27.6
Milk composition(g/kg):							
Fat	41.7	41.7	42.1	40.1	42.9	41.8	40.6
Protein	29.9	30.8	30.8	30.8	32.1	31.2	31.9
Total fat+protein yield(kg/d):	1.62	1.73	1.73	1.87	1.96	1.93	2.00

Despite such opportunities with forage alternatives, grass silage will remain the principal forage fed to housed dairy cows. However, in response to impaired feed intakes often recorded on farm, and a realisation that the nutritional value of grass silage appeared to be higher in Holland where grass is extensively wilted prior to ensiling, UK farmers are abandoning the direct ensiling of low DM grass. The wilting of cut grass prior to ensiling is increasing and many farmers are investing in wide rakes to spread the grass in order to increase the rate of moisture removal. Undoubtedly, such practices are leading to increased silage intakes, but much remains to be understood about the ensiling process if the ultimate predictability of silage quality is to be achieved. There are over 100 silage additives on the UK market, but farmers have difficulty in establishing which of the manufacturers claims are likely to be of financial benefit to their businesses. However, until greater attention is paid to the chemical composition of the crop at harvesting and ensiling, it is unlikely that sustained advances in silage feeding value will be achieved.

Nutrient digestion and absorption

Introduction of the UK metabolisable protein (MP) scheme in 1992 was the culmination of many years research effort into the factors influencing protein utilisation by ruminants, albeit heavily biased towards events within the gastro-intestinal tract, with scant regard to post absorptive processes. Such changes have increased awareness of variation in the nutritional value of different protein sources, in terms of their relative abilities to support microbial protein synthesis or augment small intestinal protein supply. The proposals were published for practical use by Alderman and Cottrill (1993), as other countries in Europe and the USA were presenting their own recommendations. Whilst all systems are conceptually similar, they vary in detail and some of the approaches adopted. This was inevitable and the lack of a standardised procedure, at least within Europe, is regrettable. Consequently, where the UK system was found to be inadequate, other systems have been considered. Currently, the Cornell Net Carbohydrate and Protein System (CNCPS) is gaining some popularity within the UK, despite the feed database having little relevance to UK feeds. There is no proof, however, other than anecdotal evidence, that CNCPS is superior to other models in predicting animal performance.

One major development within the UK system was recognition of the importance of energy:protein interactions, albeit only with regard to ruminal metabolism. Fermentable metabolisable energy (FME), defined as the energy available within the rumen to support microbial metabolism, is assumed to be dietary ME intake less the energy content of dietary lipids and fermentation end products (e.g. as in ensiled feeds), both being considered to be unavailable for microbial metabolism. In principle this definition is acceptable but the values derived will be influenced by the value ascribed to the ME content of the feed. In the study of Beever *et al.* (1996), predictions of the ME content of 2 maize silages by 8 independent laboratories showed a 2 MJ/kg DM range, and few of the estimates bore similarity with those obtained when the same diets were fed to lactating dairy cows, and corrected for level of feeding. All laboratory estimates indicated higher ME values for the later harvested maize silage when, in fact, the *in vivo* estimates for this diet were lower, despite a higher starch content, due to the lower gross energy content associated with a lesser extensively fermented crop. As to the deductions associated with the contents of lipids and fermentation products, in theory this should be relatively straightforward. However, such nutritional entities require extensive laboratory analysis, and thus current practice is to predict them from other feed parameters, as suggested by the equation based on the oven DM content of silage proposed by ADAS (1992). To date no *in vivo* estimates of FME are available and not until such are available, will progress be made towards reliable predictions of FME values on a routine basis. One further point relates to the failure to discount dietary proteins which are unavailable for degradation in the rumen. On many diets, this omission will be inconsequential, but on those containing significant amounts of feeds such as fish meal and protected soya to specifically augment small intestinal amino acid supply, the effect on FME estimates may be considerable. For fishmeal, the quoted FME content is 12.1 MJ/kg DM, yet with an agreed digestible undegradable protein (DUP) content of 344g/kg DM, it is not possible for FME content to exceed 4.1 MJ/kg DM.

In support of the MP system, feedstuff analyses now include estimates of the respective contents of effectively rumen degradable protein (ERDP), and DUP. Both are important in rationing protein for ruminants, but are routinely derived from relationships which were developed from studies where the *in sacco* digestion procedure was used to estimate the relative proportions of the different protein fractions. As indicated by Beever and Cottrill (1993), intra laboratory variation in such procedures can be considerable, even when standardised procedures are used, and current experience is that the technique is not sufficiently sensitive to detect differences which may have considerable biological importance. Once again, the *in vivo* data base, especially with respect to high producing dairy cows, is inadequate and must be improved before robust predictive equations can be established for routine laboratory use. Unfortunately, many laboratories ignored this concern and continue to report data that often serves to confuse rather than clarify.

Unfortunately there has been little concerted effort to assess the degradation characteristics of the carbohydrate components of feedstuffs, despite recognition of the importance of readily fermentable carbohydrate (sugars and starches) in the diet, or the fact that different starch sources, especially those which have been processed, will have different rates and extents of digestion in the rumen. There is some interest by commercial companies in assessing the digestion characteristics of the starch component of maize silage, and results have indicated that they are influenced by stage of harvest and subsequent ensiling conditions. Knowledge of the in vivo ruminal digestion of starch, and the level of dietary starch likely to escape rumen degradation in dairy cows, remains limited, although this does not prevent laboratories and consultants indicating the relative proportions of ruminally-available and -resistant starch.

The importance of energy and protein synchronisation in the rumen was elegantly demonstrated by Rooke *et al.* (1987), where despite modest levels of grass silage fed to non lactating cows, the consequences of nutrient losses during the ensiling process were quantified. The results (Table 2) show that on the control diet, rumen ammonia levels were relatively high and both yield and efficiency of microbial protein synthesis were low. Ruminal supplements of casein or urea (by infusion) had no discernible effects on microbial yield, whereas infusion of glucose significantly increased microbial protein synthesis, and this accounted for the increased flow of non ammonia nitrogen to the small intestine, whilst rumen ammonia concentrations were significantly reduced. However, the largest response occurred when glucose and casein were co-infused, with a 50% improvement in microbial protein synthesis compared with the unsupplemented silage. Such data permit quantification of the consequence of ensiling in terms of reduced nutrient availability and establish the need to restrict this loss by improved ensiling methods or to minimise the effect on the animal by the use of appropriate supplements.

One other area of concern is the inability to predict the outcome of rumen fermentation in terms of total volatile fatty acid (VFA) yield and composition. Given propionate is the primary substrate for glucose in the ruminant, and that the dairy cow yielding 35 kg milk/d has a minimal glucose requirement of 2.5 kg/d (MacRae *et al.* 1988), the need to establish how much of this demand can be met from propionate or small intestinally derived glucose, with recourse to the use of gluconeogenic amino acids as necessary, is self evident. Equally, acetate and butyrate are important precursors for the synthesis of milk fat, supported in early lactation by fatty acids derived from mobilised body fat. The need to control milk fat synthesis has been discussed, whilst the ability to manipulate the relative proportions of unsaturated and saturated fatty acids in milk is likely to become more important. Consequently, the need to predict the relative quantities of lipogenic VFA arising from rumen fermentation can not be ignored. Furthermore, partition of hexose disposal within the rumen between that used directly to support microbial growth, that which is fermented to supply essential ATP to support microbial maintenance and that considered to be in excess and thus either fermented or incorporated into microbial polysaccharide, will have a major effect on the relative yields of individual VFA (Beever 1993).

Table 2. The effect of intraruminal infusions of nutrients on nitrogen metabolism in the rumen of cattle receiving grass silage. Cas. and Glu. refer to casein and glucose infusions (OMADR = organic matter apparently digested in the rumen)

Treatments	Control	Urea	Cas.	Glu.	Glu/Cas
Dietary N intake (g/d):	94	119	116	86	103
Rumen ammonia (mgN/l):	51	82	98	28	39
Duodenal supply (g/d):					
Non ammonia N	89	91	94	106	139
Amino acid N	61	63	68	75	94
Microbial total N	63	68	75	81	109
Efficiency of microbial total N synthesis (g/kg OMADR):	22	25	25	27	38

Despite considerable interest in the manipulation of rumen VFA proportions some 15 to 20 years ago, using ionophores (Chalupa 1979) or buffer salts (to increase rumen dilution rate, Harrison and McAllan 1979), there is little evidence of such technologies being applied in the European dairy industry. The ionophore monensin, which has been successfully used within the beef industry throughout the world, has been undergoing dairy efficacy trials within Europe and the USA. The aim of this co-ordinated study was to consider its effects on reducing milk fat content, whilst possibly increasing milk protein content, and the consequence of such changes on overall efficiency of nutrient utilisation; all being considered as possible consequences of alterations in the glucogenic:lipogenic VFA ratio. Limited results are available from this study, and the future of further research is highly dependent on a possible European directive to ban the use of all feed additives, including ionophores.

Nutrient supply and metabolism

Following absorption, rumen derived VFA enter the ruminal vein and are transported via the portal vein to the liver. The rumen wall is metabolically active, and whilst acetate is absorbed unchanged, both propionate and butyrate may be extensively metabolised to lactate and ß-OH butyrate respectively, during absorption. Within the portal vein, rumen VFA are associated with amino acids and glucose (if any) absorbed from the small intestine, plus small quantities of VFA derived from hind gut fermentation of potentially degradable carbohydrates which escaped ruminal digestion. Studies by Reynolds *et al.* (1995) and others indicate that amino acid metabolism within the portal drained viscera may be significant in response to the extent of protein turnover which occurs in such tissues, and will reduce amino acid supply to the liver compared with the quantity absorbed from the intestines. Amino acid catabolism may also be extensive within the liver. From nutrient balance studies across the liver, it would appear that the quantity of individual amino acids, leaving the liver in the free form, with the possible exception of the branched chain amino acids may be substantially less than the quantity entering the liver. This may be related to the synthesis and subsequent export of serum proteins or peptides from the liver, or to homeostatic mechanisms operating within the liver to regulate amino acid output to peripheral tissues. Additionally, part of this loss may be associated with the role of the liver to remove ammonia, by conversion to urea. Ammonia entering the liver will be principally of ruminal origin, under conditions where nitrogen availability exceeds microbial demands. In normal feeding conditions, hepatic ammonia load will not be excessive and unlikely to fluctuate widely with respect to feeding pattern, and it would appear that the liver is capable of quantitatively removing ammonia as urea, with ammonia-N removal and urea-N appearance being in stoichiometric balance. However, when ammonia loading increases, and especially when the pattern of ammonia supply fluctuates, as illustrated by Wilton (1989) in growing cattle meal fed on grass silage, urea-N output often exceeds ammonia-N removal, suggesting the involvement of an alternative source of nitrogen which donates one NH group to combine with one ammonia molecule. This phenomenon was reported by Maltby *et al.* (1991), and using N-l 5 labelled ammonia, Lobley *et al.* (1995), demonstrated that a substantial part of the urea synthesised in the liver was derived from non-ammonia (i.e. non N-15 labelled) sources. The extent to which this occurs in normal feeding practice is difficult to quantify, but it is possible that it could occur in animals receiving significant quantities of grazed or conserved grass. The implications of such on peripheral amino acid supply are obvious, and may, in part, explain the impaired utilisation of protein often recorded on grass based diets fed to lactating or growing ruminants.

One further area of importance with respect to liver metabolism is the provision of glucose to peripheral tissues. Gut tissue is a net utiliser of glucose, albeit a significant part of this may be derived from arterial supply. Nonetheless, under most feeding conditions, the gut makes no net contribution of glucose to portal supply, and the animal relies almost exclusively on the hepatic conversion of ruminally derived propionate to glucose which is then partitioned to the productive tissues of the body. At all times, the animal needs to maintain circulating glucose levels within reasonable limits, and if required, gluconeogenic amino acids will be catabolised within the liver. As to the quantitative extent of such processes, it is difficult to provide definitive data, but with average yield of milk continuing to increase and some cows now producing in excess of 60 litres/d at peak, glucose supply becomes critical. Based on the estimate provided by MacRae *et al.* (1988), that one litre of milk requires a minimum of 70g glucose, this equates to an overall glucose requirement in excess of 4 kg/d. With an estimated maximum digestible organic matter intake of 17-18 kg/d, this suggests, after due allowance for energy lost as heat and methane during the processes of ruminal digestion, that almost 30% of the energy absorbed from the gastro-intestinal tract of a dairy cow must ultimately be supplied to peripheral tissues as glucose. Given that most of this will be derived from propionate, the need to optimise ruminal fermentation is apparent, as are the possible benefits which could be achieved either by feeding diets which promote propionate fermentations or the use of appropriate rumen manipulants.

As research attempts to refine dairy cow feeding in order to increase the efficiency of conversion of dietary nutrients into milk constituents and improve the predictability of milk composition, the importance of a better knowledge of metabolism in both the portal drained viscera and the liver will be realised. Suffice to conclude, at this stage, that the techniques for such studies are only now sufficiently robust that reliable arterio-venous differences of metabolites including individual amino acids can be obtained. Estimates of oxygen consumption across the portal drained viscera and the liver indicate both tissues can each account for 25% of whole body oxygen consumption, and when combined with a further 25% associated with mammary metabolism, the overall importance of such tissues to nutrient utilisation in the lactating dairy cow is apparent.

Whole body metabolism

The UK metabolisable energy (ME) system will predict overall energy utilisation, albeit for long term (i.e. substantial parts of the lactation) rather than short term situations. It does not however predict milk composition and how this may be affected by the composition of metabolites derived from the degradation of ingested feedstuffs. In this regard, the study of Thomas *et al.* (1987) provided an excellent example where increasing digestible energy intake by increasing concentrate:forage ratio in the diet gave milk energy outputs which failed to meet those predicted by the ME system (for details, see MacRae *et al.* 1988). In response to extra concentrates, milk yield increased but reduced milk fat content and hence yield, attributable to the changed nature of the diet, were responsible for the impaired milk energy output. Equally, Sutton *et al.* (1985) demonstrated that feeding the same diet in 2 or 6 meals per day markedly influenced milk solids yield. With 2x per day feeding (Table 3), increasing concentrate:forage ratio caused major reductions in both milk fat content and yield (-45% and -34% respectively of the values observed on the higher forage diet). In contrast, when the same diets were fed 6x per day, the reductions noted on the high concentrate diet were considerably less (content, -24%, yield, -22%), an effect which the authors attributed to changes in the pattern of insulin release and resultant circulating concentrations. Feeding 2x per day induced large pulsatile increases in insulin concentrations, which were considered to partition more lipogenic precursor towards body tissue synthesis, whilst insulin levels were more attenuated in the 6x per day feeding regime, and the drive towards body tissue synthesis was less ‘pronounced.

Further evidence of the failure of the ME system to accurately partition dietary ME to milk energy is provided by the calorimetry study of Cammell *et al.* (1992), which considered the effect of 3 levels of concentrate supplementation on energy utilisation throughout the first 29 weeks of lactation. In early lactation, all cows lost body energy (Figure l), but this was greatest on the medium concentrate fed animals. This effect was maintained as lactation progressed with. cows on low and high concentrates achieving positive energy balance before those on the medium level. These responses can be reconciled by examination of differences in the respective milk energy outputs which were greater between low and medium concentrate than between medium and high levels. Thus, although medium concentrate provided more ME than the low level, cows mobilised more tissue and thus supported increased milk energy output. The mechanisms involved can not be readily identified, but it is likely that significant changes in the nature of the end products of digestion occurred as a consequence of the increased level of concentrate inclusion. Whether the observed responses were a direct manifestation of these changes or indirectly associated with changes in the endocrine status of the cows due to changed nutrient supply, it is not possible to establish from the study cited.

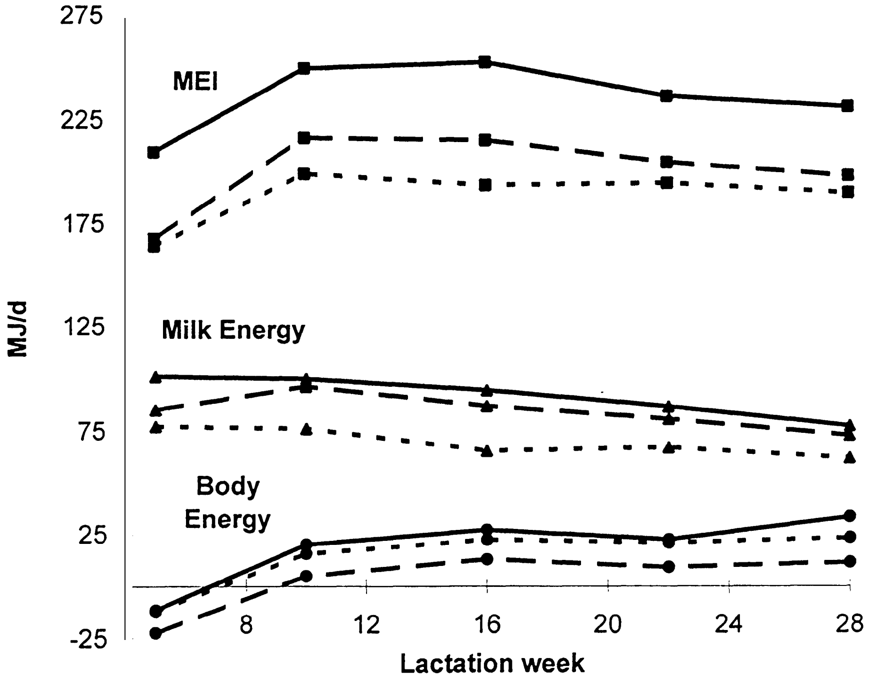

Figure 1. The effect of supplying 3 (--------), 6 (– – – –) or 9 (————) kg DM/d concentrate on energy utilisation in lactating dairy cows offered *ad libitum* grass silage

Table 3. The effect of feeding frequency on the lactational performance of dairy cows

Concentrate/forage	70/30		90/10	
Meals/d	2	6	2	6
Milk yield (kg/d)	19.7	20.2	23.0	21.4
Milk composition (g/kg)				
Fat	32.6	39.2	17.9	29.7
Protein	33.2	34.1	32.0	33.2
Lactose	47.3	46.3	48.0	47.1
Component yield (kg/d)				
Fat	0.64	0.79	0.42	0.62
Protein	0.66	0.68	0.73	0.71
Milk energy output (MJ/d)	55.8	62.1	51.7	57.3

One other issue concerns the effect of body composition on nutrient utilisation by the cow. In a study involving 54 multiparous cows receiving the diets used by Cammell *et al.* (1992), serial slaughtering from immediately post-calving until lactation week 29 allowed changes in body composition to be quantified. From this Gibb *et al.* (1992) found that in post-calved cows, fat accounted for 69% of empty-body energy, with 60% attributable to the carcass, 20% as visceral and omental fat and 11% associated with kidney, perinephric and mammary tissues. Total body protein on the other hand was located principally in the carcass (65%), along with head, hide and feet (16%) and blood and intestinal tissues (5% each). This study also demonstrated that by lactation week 8, body energy mobilisation averaged 1.6 GJ for all cows, compared with a post calving assessment of body energy of 6.3 GJ, indicating 25% of initial body energy had been mobilised. Furthermore, 90% of this loss was attributable to body fat, with mobilised protein making only a small contribution. Assuming an average efficiency of utilisation of 0.84 for mobilised tissue (Alderman and Cottrill 1993), equates to an increased availability of net energy of 1.35 GJ, representing an additional 480 litres of milk of average composition. All cows in the study lost similar amounts of body fat by week 8-l 1 of lactation, but thereafter, body fat as well as protein were repleted more rapidly with the high concentrate cows. In contrast, the low concentrate cows showed only marginally increased levels of body fat and energy by week 29. Examination of lipogenesis and lipolysis in adipose tissue taken at the time of slaughter confirmed these effects (Walsh *et al.* 1992). On medium and high levels of concentrates, there was a virtual cessation of lipogenesis in both subcutaneous and omental tissue until lactation week 11, whilst initiation of this process was delayed 3 more weeks on the low concentrate diet. At the same time, tissues from all cows showed accelerated lipolytic rates, and these were maintained even when lipogenesis had recommenced.

Compared with major changes in fat metabolism, it is interesting to speculate on the possible metabolic fate of body protein in the postpartum cow. The data of Gibb *et al.* (1992) as well as that of Sutter *et al.* (1994), which specifically examined energy and protein. metabolism in the first 8 weeks of lactation of cows receiving adequate or suboptimal levels of dietary protein, suggest that net protein catabolism is neither extensive nor extended in such animals. Sutter *et al.* (1994) found all cows approached net nitrogen balance by lactation week 3, and thereafter small net nitrogen balances were observed, whilst Gibb *et al.* (1992) reported significant increases in the weight of specific tissues such as liver, stomach and intestines, all of which have relatively high protein contents. Thus it is suggested that during early lactation, redistribution of protein within the body is of greater significance than protein catabolism to supply energy or glucose to support milk synthesis. Consequently, it may be appropriate to consider the immediately post-partum cow as having both lactational and growth demands, and this conflict of interests may be the underlying cause of the substantial reductions in milk protein content which occur at this time, and appear to be largely unavoidable. Currently, there is interest within the UK in feeding ruminally-protected protein prior to calving and its possible beneficial effect on milk protein content in the early stages of the subsequent lactation. Unfortunately, the results are equivocal and will remain so until it is accepted that the natural decline in milk protein content after calving may have both nutritional and endocrinological implications.

Feeding the high yielding cow

Both improved genetic and nutritional knowledge have contributed to the significant improvements in milk yield being achieved in many cows within the UK national herd. The current average of 5500 litres for all cows and heifers represents an increase of over 1000 litres in the last decade or so, yet an increasing number of cows are yielding in excess of 10,000 litres over a 305d lactation, and where farmers are attempting to dry off cows yielding 30+ litres/d prior to calving, the possibility of moving towards extended lactations is being seriously considered. In a recent review, Reynolds and Beever (1995) assessed the implications of feeding cows to achieve high yields of milk with acceptable levels of protein and fat. Taking into account the likely contribution from mobilised tissue, as discussed earlier, as well as the fact that peak intake is not usually achieved until some 3-4 weeks after attainment of peak milk yield, they concluded that many cows could be nutritionally compromised if total ration ME fell below 13.0 MJ/kg DM. This suggested that opportunities for including significant amounts of forage in the diet could be severely restricted, which would have major implications in relation to the integration of dairy farming into the wider aspects of UK agriculture. Furthermore, it emphasises the need for first class nutritional management, with the implications of any errors being potentially disastrous in terms of cow performance, longevity and profitability. Based on cows with milk yields of 60 litres/d, and fat and protein contents of 39.4 and 31.9g/kg respectively (current UK national averages) whilst losing 1.5 kg body weight/d, Reynolds and Beever (1995) estimated a minimum total dietary DM intake of 25.0 kg/d would be required, with 80% of this derived from concentrates to provide a total ration ME density of 13.1 MJ/kg DM. If a reduction in ME density to 12.5 MJ/kg DM is unavoidable, this would necessitate an increased feed intake of 26.2 kg DM /d, whilst failure to achieve this would lead to either increased tissue mobilisation or impaired lactational performance. Based on experience within the industry, but in part supported by nutritional studies being undertaken in high yielding cows at CEDAR, it would appear that the response of high yielding cows facing an increasing energy deficit is to compromise milk composition, with little evidence that lactational drive, defined as the requirement to secrete milk, is compromised.

Given that most farmers are now financially rewarded for the yield of milk solids, it is interesting to consider that where milk composition has been compromised in high yielding cows, without any concomitant reduction in milk yield, the same yield of milk solids could be readily achieved with more modest milk yields where milk composition was not affected. This could have important implications with respect to cow longevity and associated issues concerned with animal welfare. Furthermore, the trend towards reducing the proportion of forage in the diet of high yielding cows is of concern with respect to the possibility of increased digestive or metabolic disorders.

Role of addedfats in the diet of dairy cows

One means of increasing energy density of the diet is the inclusion of fat supplements. This has been the trend within the USA for the last decade or so, and there is now considerable interest in such products within the UK. Provided the fat source is digestible, the cow can utilise the resultant absorbed energy, and recently Andrew *et al.* (199 1) established that optimal efficiency of dietary ME utilisation was achieved when dietary fat supplied 16% of total ME intake. This study also demonstrated reduced production of methane and an improved partition of ME towards milk energy. Given the higher calorific value of fat compared with carbohydrate, the level of fat inclusion suggested by Andrew *et al.* (199 1) equates to between 5 and 8% on a DM basis. However, the method of fat inclusion is critical for, dependent upon source and composition of the added fat, high fat levels can have adverse effects upon total intake, ruminal digestion of fibre and microbial protein synthesis, all of which may cause milk composition to be impaired. Soluble fat sources, including unsaturated vegetable oils, may be most deleterious to ruminal fibre digestion, and thus many commercial fat sources are supplied as calcium salts in order to render them ruminally inert. Unprotected fat sources may react with calcium or magnesium in the rumen, and whilst this will render them less reactive within the rumen, the reduced availability of such minerals may be important to the early lactation cow, especially spring calvers reliant upon grazed pasture.

To overcome some of the possible adverse effects of added fats on whole animal performance, it may be advisable to feed the diet as a total mixed ration, thus ensuring frequent meals of a balanced mixture of all ingredients. Feeding whole oil seeds (e.g. sunflower, soya bean or cotton) may be one way of increasing dietary fat levels, and experience with such feeds suggests that adverse effects on rumen digestion and feed intake are minimised. However, when dietary fat levels are increased, the expected increase in milk yield is generally associated with a reduced milk protein content, whilst milk fat content and yield response is dependent on fat type, stage of lactation and current milk yield. Coppock and Wilks (199 1) reported mean responses of +2.4 kg milk/d, and +0.5 and -0.6g/kg in milk fat and protein respectively to a fat supplement of *0.45* kg/d, based on an extensive review of the literature.

Table 4. The effect of dietary fat supplementation and abomasally infused casein on milk yield and composition in lactating dairy cows

Treatments	Control	+Fat	+Casein	+Fat and casein
Milk yield (kg/d)	24.8	26.6	25.4	27.2
Milk composition (g/kg)				
Fat	36.5	38.2	36.0	38.2
Protein	32.9	30.9	33.4	32.2
Total fat + protein yield (kg/d)	1.72	1.84	1.76	1.91

The reduction in milk protein content may be related to impaired fibre digestion in the rumen with an associated reduction in microbial protein synthesis due to the reduced availability of energy available within the rumen. In reality however, much of the reduction is due to an increased yield of milk with little or no associated increase in the yield of milk protein. This suggests that despite increased energy availability within the tissues, there may be some limitation within the cow to synthesise extra protein. In this respect the data of Cant *et al.* (1993) is interesting (Table 4), where protein content reduction on the fat supplemented diet was alleviated only when protected (abomasally infused) casein was supplied in conjunction with the extra fat. Equally, the effect may be mediated through metabolic events as indicated by DePeters and Cant (1992), who proposed that an increased level of circulating free fatty acids may significantly alter the endocrine regulation of mammary protein synthesis.

Recently, Gaynor *et al.* (1994) examined the effect of different fatty acid supplements on milk composition, specifically in relation to those with double bonds in the cis-configuration, which occur extensively in nature, and those with trans double bonds which occur in microbial lipids and products based on the commercial hydrogenation of unsaturated fatty acids. By infusing equal amounts of the fatty acids into the small intestine of lactating cows, Gaynor *et al.* (1994) found only small effects attributable to the cis-fatty acids compared with a substantial reduction in milk fat content with the trans-fatty acids. It is suggested that these effects are related to changes in lipid metabolism within the udder, and may in part be similar to those observed when brewers' or distillers' grains are included in the diet (Phipps *et al.* 1995; Smoler *et al.* 1995). Equally such responses may be accompanied by changes in milk fatty acid composition. In this respect, there has been concern that the method used to routinely estimate milk fat content, based on mid infra red reflectance spectroscopy, may be underestimating fat content if fatty acid configuration has been significantly altered. However, recent studies using more conventional methods of fat analysis have confirmed that the reduced fat contents are real, and not an artefact of the analytical method used.

Amino acid supplementation

There is considerable interest within UK and Europe in feeding ruminally protected amino acids, principally methionine and lysine to dairy cows. Products based on protected methionine and/or lysine are being extensively marketed in France, whilst there is a limited market within the UK. To 'date however, animal response in terms of increased milk yield and protein content remains equivocal, and when the data of Rulquin and Verite (1993) are considered in more detail, it would appear that the magnitude of many of the responses is marginal, especially when assessed against the costs involved. From this it must be concluded that methionine and lysine are not always the first limiting amino acids, and serious consideration should be given to the wider issues associated with amino acid supplementation for dairy cows.

In a long term study being undertaken in this laboratory in conjunction with the Rowett Research Institute, Aberdeen, the metabolic role of the mammary gland as well as that of the gut and the liver is being systematically examined in high yielding cows. In a recent study Metcalf *et al.* (1996) perturbed the supply of amino acids to the animal by the use of formaldehyde-soya and established that the supply of essential amino acids to the mammary gland increased in a linear manner to the two levels of treated soya in the diet. However, examination of amino acid arterio-venous differences across the mammary gland, in conjunction with estimates of blood flow, revealed that increased uptake of essential amino acids by the gland was less than 10% of the increased supply, and the increased output of protein in milk was further reduced. Such data indicate that the regulation of amino acid uptake and utilisation by the mammary gland is complex, and can not be stimulated simply by increasing amino acid supply. In a subsequent experiment, Bequette *et al.* (1996) used a stable isotope of leucine to estimate the metabolic fate of increased leucine uptake by the gland, and established a significant increase in leucine oxidation by the gland.

In further studies on liver and mammary metabolism an alternative approach has been adopted whereby mixtures of amino acids are supplied by infusion either into the jugular or the mesenteric vein, thus removing the possibility of any gut mediated events. In the first study (Metcalf *et al.* 1995) supplying the essential amino acids which are principally found in 400g of milk protein by jugular infusion to mid lactation cows receiving a diet with sufficient protein to meet estimated requirements, increased milk protein content from 32.5 to 36.9g/kg, whilst supplying the same quantity of essential amino acids but with the corresponding quantity of non essential amino acids found in milk protein, gave a smaller (+2.6g/kg) response. Furthermore, Metcalf *et al.* (1995) established that the response to essential amino acid supplementation was both rapid (i.e. within 12h of commencement of the infusion) and sustained (<7 days). Subsequently, Reynolds *et al.* (1996) examined mesenteric infusions of the total, essential and non essential amino acids equivalent to 600g of milk protein, in mid lactation cows receiving a similar diet to that used by Metcalf *et al.* (1995). The milk protein responses took longer to become established, possibly related to metabolic adaptation within the splanchnic tissues, and this phenomenon has been confirmed when amino acids were infused directly into the lumen of the small intestine. However, essential amino acids gave an overall response in milk protein content of +4.5g/kg, whilst total amino acids supported an increase of 3.5g/kg, which was greater than that observed by Metcalf *et al.* (1995). At the same time, significant depressions in milk lactose content (approx. -2g/kg) were observed, and milk yield was stimulated only on the total amino acid infusion. In contrast, supplying the non essential amino acids of milk protein led to small but consistent reductions in milk protein content and milk yield, suggesting significant negative effects when non essential amino acids are supplied in excess of essential amino acid supply.

Subsequent studies are in progress to establish the magnitude of such responses when amino acid mixtures are supplied to higher yielding cows in early lactation, supported by experimentation to identify why the intravascular route of administration appears to be much more successful in stimulating milk protein synthesis compared with administration by means of the lumen of the alimentary tract. Further studies are also in progress to refine the mixture of essential amino acids required to optimise the milk protein content response. However, progress to date suggests that milk protein synthesis can be stimulated without a concomitant increase in milk lactose yield, such that milk yield is largely unaffected and the extra yield of milk protein is manifested in an increased concentration of milk protein.

CONCLUSIONS

Through improved knowledge on the processes of ruminal and intestinal digestion in lactating dairy cows, it is now possible to improve the precision with which the end products of digestion, especially protein, can be quantitatively predicted. It is at this stage that these then should be compared with the estimated requirements of the animal to provide the level of performance sought by the dairy farmer. However, it is in the area relating to the metabolism of nutrients by the animal that information is still inadequate. Thus the last decade or so has seen a number of models developed to predict the end products of digestion, but the metabolism component of those models which purport to represent nutrient utilisation are often lacking in both detail and accuracy. Greater attention needs to be focused towards the interrelationships of specific nutrients to support maintenance of the animals' essential functions as well as the production of animal products of predetermined composition (e.g. high protein, low fat milk; lean meat in beef cattle) if the ultimate objectives of the livestock industry are to be achieved. In this respect, improvements in feed characterisation must be maintained, real attempts made to provide objective and quantitative assessments of the body composition of the animal, and opportunities to manipulate those processes involved in the synthesis of milk (and meat) components must be identified if the industry is to retain its financial viability, and retain an integral part within modern society, where environmental pollution and compromised animal welfare will no longer be tolerated.

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