THE USEFULNESS TO THE ANIMAL PRODUCER OF RESEARCH FINDINGS ON NUTRITIONAL FACTORS WHICH INFLUENCE THE YIELD AND COMPOSITION OF MILK

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The substantial increases in the average milk yields of ‘dairy cows in developed countries achieved over the past 3-4 decades stem largely from improved feeding standards, with significant inputs from animal breeding, and from more effective disease control. During this period the main features of ruminant digestion and metabolism have emerged, and the impact of this knowledge on the nutrition of the dairy cow will be discussed in this paper.

The main determinants of animal production in ruminants are the amounts of energy-yielding nutrients and essential amino-acids which become available to the tissues, and both of these aspects of nutrient supply are influenced by the extensive microbial fermentation of ingested food in the rumen. Although the essential amino acid requirements of ruminant tissues are similar to those of non-ruminants, for example, their supply is dependent on the amount, amino-acid composition and digestibility of both the dietary protein that escapes ruminal degradation, and of the microbial protein synthesised in the rumen. The energy required for microbial cell growth is largely supplied by the fermentation of dietary carbohydrate, and the end-products of fermentation the volatile fatty acids (VFA) acetate, propionate and butyrate, are absorbed from the rumen and constitute the major energy sources supplied to ruminant tissues. Only small amounts of glucose are absorbed from the alimentary tract, and gluconeogenesis is a major metabolic activity since the extent of glucose utilization in ruminants appears to approach that of non-ruminants (see Ballard, Hanson and Kronfeld 1969). In the lactating animal the glucose requirement for lactose synthesis may dwarf the normal requirement (see Annison 1971). The major precursors of glucose are propionate and amino acids. Lipogenesis also shows marked differences in ruminant tissues; whereas in most non-ruminants glucose is the major precursor of long-chain fatty acids, in ruminants this role is largely taken over by acetate (see Ballard et al. 1969).

Lactation greatly increases the requirements for dietary energy and protein. Cows yielding 30 kg milk/day for example, usually require a 3-4 fold increase in food intake above the maintenance requirement. In order to sustain high milk yields, the digestibility of the rations must be reasonably high. The extensive studies of Conrad, Pratt and Hibbs (1964) suggested that lactating cows compensated for the dilution of digestible energy (DE) of the ration by increased feed intake only if the digestibility was above about 67% for cows yielding about 17 kg fat corrected milk (FCM)/day, or above 70-71% for higher yielding animals (28 kg FCM/day). These data are in line with current views on

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the factors which control food intake in ruminants, namely, that gut fill is the first limiting factor on high roughage diets, but that on diets of higher digestibility, food intake is regulated by energy requirement (see Baile and Forbes 1974). It must be emphasised that these responses will only be obtained when dietary protein is not limiting. The now classical work of Egan and Moir (1965) elegantly demonstrated that the intake of low protein roughage could be dramatically increased by supplying protein postruminally.

**Nutritional factors influencing milk yield**

(a) **Protein requirements**

The considerable information on protein requirements obtained in feeding trials in which protein intake was varied in lactating cows receiving adequate energy intake has been perceptively reviewed by Broster (1972) who concluded that the milk production response to level of protein intake is curvilinear, with declining responses as the basal level of intake increases. The mean value from 16 estimates of the optimum level of intake was 56.12 ± 1.82gDCP/kg milk, with 95% confidence limit of 52.26 and 59.98gDCP/kg milk. As pointed out by Broster (1972), the values derived by many other workers, including the Agricultural Research Council (1965) and the National Research Council (1966), all fall within this range.

Balch (1967) pointed out that since in most circumstances the energy-yielding component of the diet is the major factor limiting milk output, it is highly desirable to calibrate nitrogen requirements in terms of energy needs. The point of inflection of the response curve to protein is highly significant, and may justify the concept of a protein requirement (Broster 1972).

The consistency of response to dietary protein seen in the trials discussed above is difficult to reconcile with several recent observations on the production responses to casein infused postruminally in cows fed to normal feeding standards (see Clark 1974). Increases in milk production of 1-4 kg/day have been reported, and the largest responses were seen in cows with milk yields in excess of 20 kg/day. The optimum rate of infusion of casein appears to be about 500 g/day (see Clark 1974). These data suggest that in the cows responding to postruminal casein the supply of amino acids to the udder during normal feeding was inadequate, but the role of protein as an energy source must not be overlooked. Recent studies at this laboratory on lactating goats fed to normal feeding standards have shown significant production responses to casein infused into the abomasum but the infusion of an equivalent amount of energy as glucose had no effect on milk yield (R.C. Kellaway and S.S.E. Ranawana, unpublished observations).

In all experiments involving treatments which result in raised circulating levels of amino acids, the role of amino acids as triggers for the release of hormones involved in lactation must be borne in mind. Increases in circulating growth hormone, for example, have been observed in response to intravenous infusions of arginine in ruminants (Hertelendy et al. 1970; McAtee and Trenkle 1971; Davis 1972). The significance of growth hormone in lactation was clearly demonstrated by Machlin (1972), who showed that the injection of highly purified growth hormone into lactating cows resulted in a sustained increase in milk yield.
Energy requirements

Dietary energy is the most important determinant of animal product ion, and a vast amount of effort has been spent in devising feeding standards which relate the energy requirements of the dairy cow to the energy value of feed ingredients (see Flatt et al. 1972). Controversy still exists concerning the merits of feeding systems based on net energy (NE) or on metabolisable energy (ME), but the latter approach developed so elegantly by Blaxter (1974) has the advantage that the characteristics of the feed are separated from the biological responses of the animal.

The most comprehensive studies on the energy requirements of dairy cows have been those of Drs. Flatt and Moe, and their colleagues at Beltsville, U.S.A., who have carried out total energy balance studies based on indirect calorimetry on relatively large numbers of individual cows (Flatt et al. 1972). The data have been used within the framework of a net energy system (Moe, Flatt and Tyrrell, 1972) in which the net energy required for milk production (NE milk) is defined as the amount of energy contained in the milk produced as measured by bomb calorimetry. Regression analysis of the relationship between energy intake and milk production on a range of diets established that the amount of energy apparently required at zero milk production was equivalent to 73 kcal/kg^0.75 of live body weight (Moe et al. 1972). The total requirement of the dairy cow may be calculated from the total milk energy plus 73 kcal^0.75 k cal NE milk. The same unit is used to describe the energy value of feedstuffs.

Broster (1970) discussed the need to consider dairy cow feeding over the whole lactation cycle, and during the period before calving. A number of feeding trials were carried out to assess the value of feeding concentrates before calving (steaming up), and the long term effects of feeding different levels of energy intake during each stage of the lactation cycle were examined. When pregnant animals had adequate body reserves, additional feeding before calving had no effect on milk yield either immediately after calving, or during the whole lactation provided that the level of feeding post-calving was adequate. Further work showed that the effects on milk production of levels of feeding pre-calving and post-calving were closely related. A high level of feeding post-calving compensated for inadequate body reserves, and conversely, good body reserves ensured a high milk yield even if only small amounts of concentrates were fed after calving (Broster, Tuck and Balch 1964; Broster and Tuck 1967). In early lactation, as in late pregnancy, voluntary food intake is low (Broster et al. 1964). The level of feeding before calving must therefore be such that after calving the food requirement is not in excess of the intake capacity of the animal. Inevitably, in high yielding cows, the energy demands of lactation cannot be entirely met by feed intake, and body reserves are mobilised. Some guidance on the optimum size of body reserves before calving has been provided by Broster (1970), who has suggested that the liveweight gain in late pregnancy should exceed 0.5 kg/day.

The responses to differing levels of dietary energy during lactation depend on the genetic potential of the animal. Energy is used firstly to meet maintenance requirements, and the remainder is partitioned between milk and body reserves. High yielding cows
divert dietary energy to milk production at the expense of body reserves, as discussed by Broster (1970). Total energy balance studies based on calorimetry have shown that the total efficiency of food conversion is roughly constant during the lactation cycle (see Flatt et al. 1972) irrespective of whether dietary energy is used for the synthesis of milk or body tissue.

**Nutritional factors influencing milk composition**

The protein and lactose content of milk is reasonably constant, and in general, the percentage of solids-not-fat (SNF) closely follows milk yield. Milk fat is more variable, however, and shows considerable variations between breeds. Problems of low SNF usually reflect inadequate dietary energy. Since the lactose content remains constant unless energy is severely restricted, observed changes in SNF largely reflect changes in milk protein.

(a) **Milk protein**

A rise in the plane of nutrition of the cow increases the protein content of milk (Rook and Line 1961). Recent studies have shown that lactating cows fed to accepted feeding standards may respond to supplementary casein infused post ruminally by an increase in the level of milk protein and the milk yield (see Clark 1974). Other work demonstrating similar responses to certain essential amino acids supplied post ruminally (see Clark 1974) would suggest that these metabolites may be limiting for milk production in some circumstances unless their effects are mediated via a hormonal response, as discussed earlier.

(b) **Milk fat**

The short-chain and medium-chain fatty acids (C4 - C14) and about half of the C16 fatty acid (palmitate) in milk fat arise by de novo synthesis from acetate and \( \beta \)-hydroxybutyrate extracted from blood. The remainder of the palmitate and all of the C18 fatty acids are derived from plasma triglycerides (see Linzell 1968). Dietary fat contributes to some of the fatty acids of plasma triglycerides, but the greater part is synthesised in the tissues from acetate. Glucose, although providing much of the reducing equivalents for fat synthesis, is not a precursor of fatty acids in ruminants (see Ballard et al. 1969).

The contribution of dietary fat to milk fat is limited by the relatively small amounts of fat (7-8%) that can be fed without reducing cellulose digestion in the rumen (see Scott and Cook, 1976). Even at low levels, however, the energy content of the fat must be considered. The impact of dietary fat on the fatty acid composition of adipose tissue and milk fat is considerably lessened by the extensive hydrogenation of unsaturated fatty acids in the rumen. As much as 90% of the linoleic and linolenic acids in ruminant diets may be hydrogenated to stearic acid (Bickerstaffe, Noakes and Annison 1972). Nevertheless, the chain length, if not the degree of saturation of fatty acids in milk fat may be influenced by the composition of the dietary fat (Storry, Rook and Hall 1967), and modest increases in milk fat levels may be achieved. The successful protection of dietary fat from ruminal attack by Scott et al. (1970) has removed many of the constraints associated with the use of dietary fats, since the micro-organisms in...
the rumen are protected from the adverse effects of the fat. Supplementary fat may be used as an energy source, but its most striking use has been to introduce unsaturated fatty acids into adipose tissue and milk fat. For example, feeding protected linseed oil increased the proportion of linolenic acid in goat milk fat from 1-2% to 20-25%, and of linoleic acid from 2-3% to 9-11%, with corresponding falls in the proportions of myristic, palmitic and oleic acids (Scott, Cook and Mills 1971). Changes in the fatty acid composition of milk fat were observed within 48 h of feeding protected fat.

Quantitative data on the effects of supplying increased amounts of intact fats may be obtained by infusing emulsified fat directly into the duodenum. When increasing amounts of sunflower oil were infused intraduodenally into a lactating cow, milk yield (22 l/day) remained unchanged, but milk fat output increased from 750 g to 1050 g/day, and the linoleic acid content of the milk fat rose from 3.0-7.0 moles/100 moles (see Annison, 1972). These results could be duplicated by feeding appropriate levels of "protected" sunflower oil.

Milk fat production in dairy cows may fall if the ratio of digestible carbohydrate to roughage in the diet is high, or when the roughage component of the diet is finely ground (see Davis and Brown 1970). Diets of these types result in a decrease in the molar ratio of acetate to propionate in the rumen. Armstrong and Prescott (1971) collated available data relating the molar proportions of rumen VFA to milk fat percentage, and demonstrated a highly significant relationship between proportion of propionate and the fall in milk fat percentage.

The changes which occur in response to low roughage diets were examined in four cows surgically prepared for the simultaneous study of rumen and udder metabolism and the whole body turnover of milk precursors (Annison, Bickerstaffe and Linzell 1974). The comprehensive data obtained provided an explanation of the syndrome much in line with the postulates of earlier workers. The important feature was the changed pattern of rumen fermentation in response to the high concentrate diets. Acetate concentrations were largely unchanged but propionate concentrations showed a marked rise. This resulted in a 50% increase in glucose entry rate when cows were switched from a high to a low roughage diet, and evidence was obtained that the increased availability of glucose was responsible for the lowered milk fat synthesis, as suggested by McClymont and Vallance (1962). On the low roughage ration, circulating levels of acetate were reduced, and acetate entry rates fell. Part of the fall in acetate supply appeared to be due to a reduced endogenous acetate product ion, if the lowered acetate release by the udder was typical of all tissues. Circulating plasma triglycerides were somewhat lower on the low roughage ration but for this substrate, but not acetate, there was a lowered extraction rate by the udder. The net result was that the mammary uptakes of the two main precursors of milk fat, acetate and plasma triglyceride, were both markedly reduced for cows in which levels of milk fat were reduced.

The reason for the lowered availability of acetate and plasma triglyceride stems from the increased supply of glucose. This appears to stimulate insulin release (Walker and Elliot, 1972) which promotes lipogenesis in adipose tissue, and reduces triglyceride mobilisation as plasma FFA. In the above work, although plasma FFA levels were largely
unaffected by the change in diet, the entry rate of plasma palmitate, a typical plasma FFA, was reduced to a third of its original value when cows were transferred to the low roughage diet. This lowered availability of plasma FFA probably reduced lipoprotein synthesis in the liver, which would account for the lowered plasma lipoprotein levels (Annison et al. 1974).

Concluding comments

Research has provided the dairy farmer with feeding standards for the cow in pregnancy and lactation. Indeed, when diets of known energy value are fed, milk production can be adjusted to the economically optimum level. Milk composition is not a problem if adequate energy is fed to maintain SNF, and if sufficient long roughage is included in the diet to prevent the low milk fat syndrome. The level of milk fat, and its composition, can be changed by feeding protected fat.

This discussion on the usefulness of nutritional research to the producer might suggest that no major problems remain. Unfortunately, the extensive systems of dairy cow feeding practised in many parts of Australia often means that the only guides to the adequacy of the feed is the milk output, and the condition and fertility of the herd. Although procedures exist for assessing feed intakes of animals at pasture, and for measuring the energy value of the herbage, these are not generally available. Furthermore, when a decision is made to supplement pasture feeding with feeds of higher energy density (grains or concentrates), the increases in milk yield or improvements in live-weight which result are often much lower than would be anticipated from the energy provided by the supplements. Clearly, in these instances, the animals have reduced their intake of pasture.

Current research is tackling this problem from several directions. Attempts are being made to assess the nutritional status of herds by the analysis of blood from selected individuals using the metabolic profile technique (Payne, Manston and Dew 1972). This procedure may reveal mineral imbalances and trace element deficiencies in addition to providing a guide to the nitrogen and energy status of herds. Exciting work is being carried out to improve the voluntary feed intake of animals on low nitrogen pasture by providing supplementary protected protein, since, as discussed earlier, the supply of essential amino acids to the tissues may be rate limiting for feed intake. Finally, much work is being done on the factors which influence rumen metabolism, with the object of obtaining data which will make it possible to design feed supplements which complement herbage without inhibiting its intake.

REFERENCES


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