

## BALANCING NUTRIENTS FOR EFFICIENT MILK PRODUCTION IN DAIRY COWS

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## SUMMARY

In the high-yielding dairy cow, prodigious amounts of nutrients must be supplied to the mammary gland to meet the needs for milk secretion. The principal nutrients are: glucose and amino acids (precursors of lactose and protein) and acetate,  **$\beta$ -hydroxy-butyrate**, triglycerides and lipoproteins (supplying energy and as precursors of fatty acids). Dietary nutrients and products of ruminal fermentation (VFA and digestible microbial components) enter the blood plasma pools after absorption from the alimentary tract, or upon mobilization of body tissues. These nutrients are partitioned towards milk constituents or body reserves according to the cow's current physiological requirements which depend on factors such as breed and stage of lactation. Partitioning appears to be affected by plasma levels of growth hormone, insulin-glucagon and probably various gut hormones.

Milk yield is affected principally by breed and availability of dietary energy but also higher yields generally occur with higher concentrations of crude protein in the diet (although excess protein may impair fertility). Diet also affects milk composition. A lower ratio of fibrous material: readily fermentable carbohydrate can result in a lowered milk fat content without major effects in the short-term on solids-not-fat (SNF). SNF may be reduced by underfeeding, but may be higher on low-roughage diets, especially when maize is a major component.

## INTRODUCTION

The milk yield per cow in Australian dairy herds is generally lower than that in similar herds in European countries, where cows often yield more than 6000 litres/lactation. This lower production is probably largely a result of poorer nutrition, particularly where pasture makes up a significant part of the diet. When production per cow is increased, the fraction of the total feed inputs used for maintenance is reduced; fixed and **labour** costs per unit production are also reduced and economic returns may be improved.

In the future the economic incentives which currently determine the nutritional management of milking herds will differ from those that exist at present. Producers are presently paid for milk on the basis of total solids, fat content or solids-not-fat (or combinations of these); protein concentration per se is not usually considered. In the future, the emphasis may change towards production of milk with higher ratios of protein and lactose to fat (see Van Es and Van der Honing 1979), because of changing attitudes in society to milk and milk products with respect to protein nutrition, and obesity and cardio-vascular disease. The development of management strategies that will lead to higher efficiencies of milk production with an appropriate balance of fat and protein will depend, ultimately on a basic understanding of the processes involved in milk synthesis and excretion.

This paper provides a general overview of our current knowledge of the digestive and metabolic processes that affect milk yield and composition.

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## MILK SECRETION

The alveolus is the main organ involved in milk secretion and is a small, hollow, spherically-shaped structure lined internally by a **single** layer of secretory epithelial cells. In the mammary gland the alveoli are linked by a system of branching ducts that enable milk to collect and eventually pass out of the udder. The alveoli are richly endowed with **capillary** blood vessels that provide nutrients, and chemical messengers, and remove end-products of metabolism. The alveoli are also bathed by lymph fluids. During pregnancy adipose tissue is mobilized and replaced by **mammary** parenchyma; the alveoli develop and there is a marked branching of the duct system (Mepham 1976). The specific secretory capacity develops towards the end of gestation with lactogen from the placenta probably being **involved** (Forsyth and Hayden 1977). Proliferation of epithelial cells apparently continues after parturition in some mammalian species including rats, rabbits, pigs (Anderson 1974); however, this is thought to occur to only a minor degree in the cow (Baldwin 1966), which Swan (1979) points out is surprising, as peak lactation does not occur until 2-6 weeks after calving. The increase in yield in early lactation is therefore, presumably due to an increased rate of secretion per cell induced by increased supply of nutrients. Milk yield per lactation depends on the rate of secretion per cell, and the longevity of lactating cells, both of which are affected primarily by nutrient availability (Swan 1979), but also by the extent and frequency of milk withdrawal from the udder.

## SECRETION RATE AND COMPOSITION

The rate of milk secretion is linearly related to blood flow rate through the mammary gland (Linzell 1971) as well as the concentrations of nutrients in the blood and their rates of transfer into secretory cells.

The major constituents of milk from dairy cows are: water (**86-88%**), fats (**3.7-5.1%**); lactose (**4.5-4.7%**) and proteins (**3.1-3.8%**). Lactose and protein are the main constituents of the solids-not-fat in milk; lactose is the major osmotically-active solute apparently affecting yield of milk (which is isotonic with the blood) by its effect on net water movement into the secretory cells (Rook 1976). Changes in milk composition are therefore largely affected by rates of secretion of proteins and fats relative to lactose. A reduction in milk fat content can be induced either by an increase in milk yield which is brought about by increased production of lactose and/or by decreased secretion of fat. A wide range of ratios of fat: lactose can be induced experimentally indicating that secretion of these components can proceed largely independently, whereas the smaller range in ratios of protein: lactose indicates that secretion of these components may be more closely linked (Sutton 1981).

Milk composition differs between breeds (See Table 1 in **Oldham** and Sutton 1979) and amongst individuals within a breed. It also changes as lactation advances. Colostrum contains a high content of protein and total solids may exceed 25%. In the first few days after calving, protein content falls rapidly. Thereafter protein, fat and total solids concentrations continue to decline, while lactose content rises, and milk yield rises to maximum usually **6-12** weeks after calving. Later, protein and fat contents increase while lactose content and yield decline slowly; protein content may rise noticeably in pregnant cows in the last 3-4 weeks of lactation (Rook and **Campling** 1965). Thus the concentration of total solids is generally inversely related to milk yield **whether** yield is affected by breeding or

feeding or stage of lactation (Oldham and Sutton 1980). Selection within a breed for higher milk yield results in a reduction of fat and protein content. Nevertheless, the total yield of solids generally increases with increasing yield (Touchberry 1974).

#### NUTRIENTS UTILIZED BY OR SYNTHESISED IN THE MAMMARY GLAND

The major substrates extracted from the blood by the mammary gland are glucose, acetate, amino acids, lipoprotein triglycerides and  $\beta$ -hydroxybutyrate. Much of our quantitative knowledge of the uptake of these nutrients has been obtained either by a measurement of arteriovenous concentration differences across the mammary gland combined with estimates of blood flow, or by using the isolated perfused udder (see Linzell 1971). Some of these substrates are discussed below.

#### Glucose and lactose metabolism

In the high-yielding dairy cow 70-90% of the glucose entering blood plasma can be extracted by the mammary gland (Annison and Linzell 1964; Kuhn 1978), even though its tissues constitute only 5% of the cow's live weight, and 40-60% of this glucose is used in the synthesis of lactose. Glucose is essential for milk production and Linzell (1967) concluded that its availability may limit milk secretion. Hardwick et al. (1961) studied the isolated, perfused mammary gland of the goat and found it continued to produce milk (of decreasing fat content) when acetate concentration was reduced in the perfusate; however, when glucose concentration was reduced below 200 mg/litre, milk secretion ceased abruptly. Later studies (Hardwick et al. 1963) with (U -  $^{14}\text{C}$ ) glucose showed that 77% of the lactose -C, 23% of the milk triglyceride glycerol -C, 41% of milk citrate -C, and 39% of the  $\text{CO}_2$ -C output by the perfused gland was derived from glucose. Glucose contributes approximately 5% of the C in total milk fat and 5% of the C in milk casein.

Thus blood glucose is the main precursor of lactose in milk. It is also a major precursor of triglyceride glycerol and a source of energy for metabolic processes, in particular the reduced NADP required for lipogenesis; 30% of the glucose extracted by the mammary gland entered the pentose phosphate pathway (Kuhn 1978) and flux of glucose 6-phosphate through the pathway was sufficient to account for 34% of the NADPH required for fatty acid synthesis and for all the  $\text{CO}_2$  produced from glucose in the mammary gland of the fed, lactating goat (Chaiyabutr et al. 1980). Glucose requirements of high yielding cows are therefore necessarily high. For example, Armstrong and Prescott (1971) have calculated that a 590 kg cow yielding 20 kg milk (4% fat: 4.7% lactose) would require at least 1.5 kg glucose.

A number of workers have made estimates of glucose turnover rates in lactating cows using tracer dilution methods (see Leng 1970). The results give an indication of whether glucose supply to the mammary gland (from absorption and gluconeogenesis) is likely to be a primary limitation to milk yield. For example, Bruckental et al. (1980) made estimates of glucose kinetics in cows of 590 kg live weight producing 25-33 kg/day milk by means of single injections of [6- $^3\text{H}$ ]-glucose in weeks 2-9 of lactation. Using Armstrong and Prescott (1971) as the basis of calculation these cows might have been expected to require 1.8-2.2 kg glucose/day. The actual estimates of irreversible loss of glucose were 2-3 kg/day indicating that these cows were able to meet their theoretical minimum requirements, and therefore that

glucose per se was probably not a primary limitation to milk yield. Nevertheless, there is generally a close correlation between glucose irreversible loss and milk yield, and between mammary uptake of glucose and milk yield (Patterson and Linzell 1974). The glucose irreversible loss rates of **Bruckentall et al. (1980)**, expressed in metabolic live weight terms were 14-22 mg/min per  $W^{0.75}$ . In comparison, estimates made recently by G.J. Lee, D.W. Hennessy, T.J. **Kempton**, J.V. Nolan and R.A. Leng, in Hereford cows at the same stage of lactation were only **3.5-5.3 mg/min per  $W^{0.75}$** .

Rates of irreversible loss of glucose in non-lactating ruminants are linearly related to digestible or metabolizable energy intake (Judson and Leng 1972). In general, a similar relationship occurs in lactating cows, although a curvi-linear relationship may give a better fit to the available results (see Fig. 1). Curvi-linearity may occur at higher ME intakes which are usually achieved using concentrate diets that provide by-pass starch and may give rise to absorbed glucose that complements **gluconeogenesis**. Similar relationships from a variety of species in different physiological states are given by **McEwan et al. 1976**.

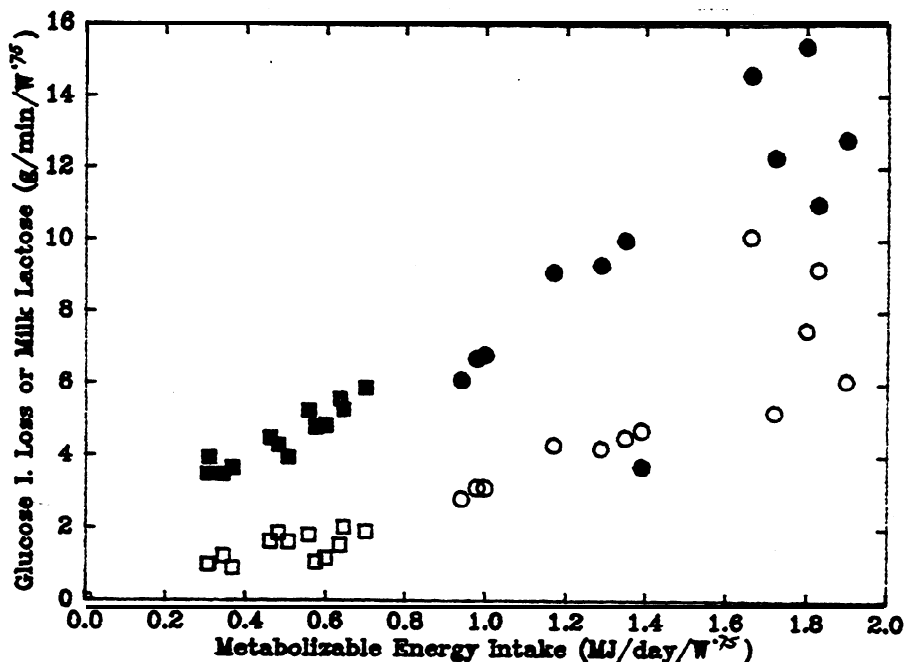


Figure 1: The relationship for lactating cows between the rate of irreversible loss of plasma glucose (filled symbols) or rate of secretion of milk lactose (unfilled symbols) and metabolizable energy intake. ○, ● data of Horsfield et al. 1974; □, ■ data of G.J. Lee et al. (in preparation).

Despite the relatively high requirement for glucose in high yielding cows, milk yield responses to abomasal infusions of glucose usually have not occurred (e.g. Tyrrell et al. 1972; Ørskov and Grubb 1977; Rogers et al. 1979), although yield was raised in one experiment with goats on normal diets when injected with glucose (Linzell 1967).

The information currently available suggests that availability of glucose to the mammary gland is seldom a primary limitation to milk secretion in high yielding cows given conventional concentrate diets but, this conclusion may not hold when lactating cows are fed predominantly low quality forages.

## Amino Acid Metabolism

In milk there are two major groups of proteins, the **casein** and **non-casein** or whey proteins. Most of the milk protein is synthesized in the mammary gland where there is extensive intracellular metabolism of **amino acids** prior to protein synthesis. Plasma proteins make only a very small direct contribution to milk **proteins**. The extraction of non-essential amino acids from blood plasma is highly variable and it is therefore probable that synthesis and metabolism of these acids is also variable. Non-essential amino acids are synthesized using carbon from a variety of carbohydrates, fatty acids and amino acids. In the goat (and probably other species) relatively large amounts of arginine and ornithine are extracted from blood plasma and metabolized in the udder and, interestingly, in the perfused mammary gland of the goat, (but not of cows) urea is produced (see Mepham 1971). Glutamate and other amino acids appear to be oxidized to provide energy. The essential amino acids appear to be obtained almost entirely by extraction from blood plasma, in amounts generally slightly in excess of requirements for the milk proteins secreted (see Mepham 1971). There is some evidence that availability of essential amino acids to the mammary gland may at times limit rates of milk secretion. No one amino acid stands out as being clearly limiting in the high-yielding cow, but there appears **to** be a reasonable case for considering methionine and phenylalanine as likely to be first limiting with, under some conditions, threonine and lysine being co-limiting (Mepham 1982).

## Lipid metabolism

In non-ruminants glucose is a precursor of fatty acids in milk whereas, in ruminants the virtual absence of ATP: citrate lysase may prevent its use for this purpose (Hardwick 1966) and acetate and  **$\beta$ -hydroxy-butyrate** are used instead. Other workers have found higher levels of this enzyme; they suggest that the enzyme is inhibited by higher levels of **acetyl-CoA** and that it is induced when appreciable amounts of glucose are absorbed from the alimentary tract. Differences in glucose metabolism between ruminants and non-ruminants may therefore occur because of effects of different levels of **acetyl-CoA** or glucose **on the** respective enzyme activities (see Rook 1971).

The pathways of milk fat synthesis in ruminants have been reviewed comprehensively elsewhere (see for example, Smith 1980). Briefly, fatty acids with **4-10** carbon atoms representing approximately 26% of the fatty acids excreted in milk (Chaiyabutr et al. 1980) are derived mainly from acetate but also  **$\beta$ -hydroxy-butyrate**; those with 18 carbon atoms (37% of milk fatty acids) are derived from blood plasma triglycerides and low density lipoproteins; and those of intermediate chain length from any of these sources. Acetate absorbed from the **rumen** is a major source of milk fat. Where this is limiting, particularly in early lactation, there is uptake by the mammary gland of triglyceride fatty acids from **chylomicrons** and blood lipoproteins that are derived mainly from adipose tissue. Fatty acids are released from fat cells into the blood where they are bound to albumin and transported **to** the mammary gland (and other tissues) and used **as** energy sources.

The composition of milk fat changes as lactation proceeds and the ratio of **C<sub>16</sub>-C<sub>18</sub>:C<sub>6</sub>-C<sub>14</sub>** fatty acids decreases because the contribution of body reserves to milk lipids also decreases throughout the lactation cycle. In early lactation, the cow may draw heavily on body reserves and lose weight; this results in higher concentrations of plasma non-esterified fatty acids which are positively correlated with the yield of milk fat during this period (Morris and Swan 1975). Plasma triglyceride fatty acids are hydrolyzed by

lipoprotein lipase located in the **capillary** endothelium of the mammary gland, and the acids released, plus those synthesized in the alveolar cells, are esterified by the phosphatidic and diglyceride pathways into triglycerides and incorporated into the milk fat globule. The necessary phosphatidic acid is obtained from free glycerol or glucose (see Storry 1981).

The composition of milk fat depends to some extent on the fat in the diet, but more specifically on the nature of the fat absorbed from the small intestine. Dietary fat is extensively metabolized in the **rumen** unless it has been "protected", for example, by encapsulation in **formaldehyde-treated casein** (Scott et al. 1970). The lactating cow can absorb, transport and metabolize large quantities of fatty acids (1.2 - 2.1 kg fat/day in **Friesian** cows) without metabolic stress (see Storry 1981).

Although lipids are major precursors of milk fat, they are also major sources of energy in the mammary gland of the ruminant which has a need to conserve glucose (Smith and Taylor 1977).

#### EFFECT OF SUPPLYING PROTEIN VERSUS GLUCOSE

Increases in milk yield occur in high yielding dairy cows when **casein** is infused intravenously or into the abomasum (for review, see Clark 1975). An important question is whether the availability of protein per se, that is of essential amino acids, can be a primary limitation to synthesis of milk proteins and thereby milk yield. **Ørskov** et al. (1977) fed four potentially high-yielding **Friesian** cows on a ration calculated to provide sufficient nutrients for maintenance and 10 kg/day of fat-corrected milk and infused variable amounts of **casein** and glucose into the abomasum for periods of 12 days in a Latin-Square design. As glucose was replaced by **casein**, milk yield and fat and protein content increased and energy balance became more negative. They concluded that, in early lactation, protein availability may restrict milk yield, apparently through an effect on mobilization of body reserves. In goats fed a diet adequate in energy but low in protein, **Farhan** and Thomas (1977) found that an abomasal infusion of **casein** produced a 29-31% improvement in yield of milk and milk lactose whereas an **iso-energetic** infusion of glucose produced only 6-8% improvement in milk and lactose output. They concluded that the availability of amino acids increased lactose synthesis in the mammary gland and milk yield, not by amino acids acting as direct precursors of glucose, but by some independent mechanism.

In similar types of experiments (Rogers et al. 1979), lower-yielding cows (10 kg milk/day) were offered constant amounts of unwilted pasture silage (29 g N/kg DM). The milk yield and milk protein concentrations were increased by abomasal infusions of **casein** in all experiments but not by **iso-energetic** amounts of glucose. Infusions of **casein** (300 g/d) or methionine (12 g/d) gave similar responses suggesting that methionine was the first limiting amino acid. It appeared to be markedly deficient, i.e. milk yield increased by 1.1 kg/d and milk protein content by 0.19%. Smaller responses to **casein** infusion were obtained in cows given similar amounts of pasture (24 g N/kg DM). The results indicate that milk production of cows on these diets was limited by supply of amino acids per se (**rather** than energy), and specifically methionine, to the small intestine. However, in other studies infusion of methionine into the abomasum, or intravenously, has given responses that were small or non-existent (see **Oldham** 1980).

One point should be noted here. McCarthy et al. (1968) hypothesized that methionine may have specific effects on lipoprotein metabolism in the liver. A deficiency might limit synthesis of lipoproteins and reduce lipid

transport from the liver and thereby alter the partitioning of fat between body tissues and milk.

#### PARTITION OF ENERGY INTO MILK OR BODY TISSUES - HORMONAL EFFECTS

Differences between and within breeds in the relative amounts of energy substrates directed towards the mammary gland or body tissues are clearly genetic in origin. For example, Bines and Hart (1978) provide comparative information on milk yield and live weight change from 0-12 weeks of lactation that exemplify the differences between **Hereford cross** cattle (total milk yield, 518 kg; weight change, +44 kg) and **Friesian** cows of similar weight at calving (1673 kg milk; - 45 kg).

In non-ruminants insulin, glucagon, growth hormone (GH) and various gut hormones are all responsive to increased amino acid availability but there is less information for ruminants (see **Oldham** 1980).

Mammary gland development is essentially complete at calving by which time the maximum yield potential is already decided; the realized yield therefore depends on the subsequent adequacy of supply of nutrients to the gland from the diet and from mobilization of tissue reserves. Highly purified **GH** promotes mobilization of body fat and thus diverts absorbed energy away from tissue synthesis (Bines and Hart 1978). Administration of **GH** to heifers after calving increased milk yield throughout lactation (Shaw 1955) and daily subcutaneous injections of GH in cows, already producing in excess of 30 litres milk per day, increased yield. In beef cows **GH** levels were relatively low throughout lactation whereas, in high yielding cows, **GH** levels were much higher; also they were highest at the time of peak lactation and declined as lactation continued (Hart et al. 1978).

**Oldham** and co-workers infused **casein** via the abomasum in lactating goats and beef cattle and obtained increased in total yield, and in fat and protein content of milk, and also raised plasma GH levels. In subsequent experiments, they found that **GH** levels were increased by feeding protected **casein** to lactating dairy cows (see **Oldham** 1980). Bassett (1975) has suggested that the amount of protein entering the intestines may affect the level of insulin, whose effects are generally anabolic, although effects differ between the mammary gland and other tissues. Insulin stimulates the uptake and utilization of glucose by many peripheral tissues, inhibits gluconeogenesis and glucose release from the liver, inhibits proteolysis and increases uptake and incorporation of amino acids into protein, and it inhibits lipolysis and stimulates lipogenesis (Bassett 1975). If insulin and GH levels were both stimulated by intestinal protein, then the catabolic effects of higher **GH** levels, and the anabolic effect of higher insulin levels, would be opposed. However, such an effect might help to explain the results of **Ørskov et al. (1977)**, who infused **casein** into the abomasum of cows and obtained a lower milk yield, apparently as a result of reduced mobilization of tissues.

Insulin is also important in the control of gluconeogenesis, and **Unger** (1971) has suggested that molar ratios of **insulin:glucagon** may be more important than absolute levels. Bassett (1975) argues that when there is an energy deficit, the ratio is low and hepatic output of glucose is at a maximum and utilization of glucose by peripheral tissues is at a minimum and vice versa. Glucagon may play a role in the control of lipolysis in ruminant tissues (Bauman and Davis 1975). Cortisol secretion rate is higher in lactating ruminants and increases with increases in rate of irreversible loss of glucose (Patterson and **Linzell** 1974).

The present state of knowledge of the overall control of metabolism in lactating cows is rather limited. It is likely that high levels of **GH** and low levels of insulin are responsible for the partition of nutrients towards the mammary gland in early lactation. After the peak in lactation a reversal in the levels of these hormones may divert nutrients away from the mammary gland and towards the tissues.

#### EFFECT OF DIET ON MILK YIELD AND COMPOSITION

##### Energy Intake

Milk yield is affected principally by the availability of energy from the diet (see Fig. 1), although obviously feed intake is itself determined by the diet through its effect on the balance between energy substrates and protein (and other nutrients) that are absorbed (see **Kempton et al. 1978**; **Hennessy et al. 1983**). The highest energy intakes are normally achieved using energy-dense concentrates, and sometimes supplementary lipids.

##### Protein intake

Generally milk production improves with increases in the crude protein content of the diet (see **Chalupa 1983**). However, the reasons are complex. In most diets the crude protein consists of true protein and non-protein nitrogen (NPN). The NPN may contribute to the protein nutrition of the cow by supplying ammonia for **rumen** micro-organisms which can use it to synthesize essential and non-essential amino acids for their own growth; these organisms subsequently provide a source of protein (amino acids) that can be absorbed and metabolized by the animal (see **Leng and Nolan 1983**). Responses to increases in dietary crude protein content therefore can be for a number of reasons:

- a) The protein and **NPN** may provide the **rumen** organisms with optimum amounts and types of nitrogenous nutrients, and fermentation rate and microbial protein supply from the **rumen** may be increased;
- b) associated with (a), there may be an improvement in digestibility of the diet which makes more energy nutrients (VFA and lipids) **and** more microbial protein available to the animal (see **Oldham 1983**);
- c) some true protein may pass through the **rumen** without being fermented, making available more amino acids for absorption from the small intestine;
- d) additional amounts of absorbed protein may promote higher milk production by
  - (i) providing essential amino acids for milk protein synthesis
  - (ii) promoting gluconeogenesis
  - (iii) increasing the available energy for tissue metabolism
  - (iv) altering the efficiency or pattern of use of absorbed nutrients
  - (v) stimulating appetite and feed intake

Alterations in the pattern of use of absorbed nutrients may occur because of endocrine effects on lipid and glucose metabolism, or by **increasing** the rate of blood flow and thus nutrient supply to the mammary gland (**Bines and Hart 1982**; **Oldham 1983**). There is considerable evidence that provision of supplements containing protected true protein may stimulate feed intake and milk yield-by **20%** in grazing dairy cows on tropical pastures even those containing up to **20%** crude protein (e.g. **Stobbs et al. 1977**; **Minson 1981**)-or increase milk yield by increasing efficiency of use of nutrients



in cows consuming constant amounts of high quality pasture in early lactation (Rogers et al. 1980); see Table 1.

TABLE 1. Effect of formaldehyde-treated and untreated **casein** supplements (1 kg/d) on milk yield and composition of grazing cows consuming constant amounts of high quality pasture in early lactation (data of Rogers et al. 1980).

	Unsupplemented	Casein	Protected casein
Total Dry Matter Intake (kg/d)	13.8	13.6	14.0
Pasture Dry Matter Intake (kg/d)	13.8	12.7	13.0
Dry Matter Digestibility	0.75	0.76	0.75
Milk Yield (kg/d)	16.1 <sup>a</sup>	16.6 <sup>a</sup>	18.1 <sup>b</sup>
Milk Fat (g/kg)	38.5	37.2	37.5
Milk Protein (g/kg)	31.3	31.7	32.3

a,b - values within the same line with different superscripts are significantly different. ( $P < 0.05$ ).

Journet and Remond (1979) have emphasized that there is normally a considerable deficit in the availability of absorbed protein for milk protein synthesis, especially in early lactation. Some of this deficit can be met by metabolism of tissue proteins, but extra protein is also required by some organs, e.g. the liver, for development at this time. However, these studies show that supplementary protein in early lactation increased milk yield by partitioning more energy towards milk synthesis with the consequence that there was increased weight loss.

With immature green pastures, even of high crude protein content, there is a potential for inadequacy of absorbed protein if the dietary protein is extensively fermented in the **rumen**. For example, with sheep grazing phalaris, clover and lucerne in the spring Pickering et al. (1982) found that 76-89% of the dietary N was apparently degraded in the **rumen**. Cows given a basal diet of silage of quite high crude protein content may also respond to increases in the level of protein in the diet (Gordon 1980). The reason for the response is probably the same as for immature pastures; the nitrogenous materials may be extensively degraded in the **rumen**, leaving little dietary protein to pass undegraded into the small intestine.

#### Excess protein intake

Considerable information has recently become available indicating that excess intakes of dietary crude protein may adversely affect milk production and fertility. The reasons may be that high rates of absorption of ammonia from the **rumen** produce biochemical, endocrinological and tissue derangements and/or that excess absorption of amino acids alters the **protein:energy** balance producing a relative energy deficiency (see Chalupa 1983).

#### Patterns of ruminal fermentation

The largest effect on the relative rates of secretion of milk constituents (milk composition) is caused by dietary supplementation with lipids (Storry 1981). Also, although milk fat content is relatively insensitive to a wide range of diets, large decreases in fat may occur when cows are offered cereal grains, high quality forage or other highly **diges-**

tible diets. The "low fat **syndrome**" is reviewed by Davis and Brown (1970). One reason for low fat milk seems to be related to the molar **proportions of VFA arising** from fermentation in the **rumen**. Milk fat content decreases **quickly when the** molar ratio of acetate plus **butyrate:propionate** falls below 3.5. In comparison the effects of absorption of longer-chain fatty **acids, or** starch that escapes into the small intestine to be absorbed as glucose seem relatively unimportant (Oldham and Sutton 1979). Ørskov (1975) and Sutton (1976) argue that decreases in the ratio are to be expected when changes in the diet lead to rapid fermentation rates in the **rumen**, possible circumstances include: increases in feed intake; decreases in frequency of feeding. However, increases in fat content only occur when these circumstances are avoided, if also the diet contains at least small amounts of long hay or roughage - although "roughage" is difficult to define in this context. The importance of fermentation patterns in the **rumen on milk** composition and the interactions between different feed components will be considered in more detail elsewhere in the symposium.

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