RUMEN FUNCTION AND THE UTILISATION OF READILY FERMENTABLE CARBOHYDRATES BY DAIRY COWS[1]

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The effect on milk production of the balance between fibrous carbohydrates and readily fermentable carbohydrates in the diet is discussed. Supplements of over 2.5 kg sugars daily to diets of hay and concentrates were very poorly utilised by milking conga. It seems probable that this was because they caused a reduction in fibre digestion, no reducing total energy supply, and they also altered the pattern of rumen fermentation towards one less favourable to milk production. It is suggested that avoidance of the low rumen pH following the ingestion of large amounts of sugar in discrete meals would improve the utilisation of sugar supplements. In a large-scale feeding trial, substitution of starchy concentrates for roughages reduced milk fat secretion and increased liveweight gain. The change in milk composition was closely related to the molar proportions of rumen volatile fatty acids (VFA). Studies in cannulated cows showed that starch digestion in the rumen was about 90% when the concentrates were based on rolled barley, but 70% or less when they were based on ground maize. The large increase in starch flow to the duodenum when ground maize replaced rolled barley had no detectable effect on milk composition. Rumen VFA proportions remain the single moat important factor influencing milk composition. with diets containing large amounts of starchy concentrates Control of the maximum fermentation rate in the rumen appears to offer a useful practical means of manipulating the pattern of VFA.

Key Words: Cattle, milk production, rumen function, review

The balance between the fibrous carbohydrates and the more readily fermentable carbohydrates of the diet has important implications for feed utilisation by dairy cows. It is a major factor influencing both the amount of feed consumed and the efficiency with which the energy of that feed is utilised The purpose of this paper is to examine the role of the rumen in this relationship by considering experiments with milking cows conducted at Shinfield in the past decade, in which the utilisation of widely different carbohydrates for milk production has been studied.

Supplements of Soluble Carbohydrates

Following a series of studies of the fermentation of a wide variety of soluble carbohydrates in vivo and in vitro (Sutton 1968; 1969), we decided to examine the value of two of the sugars, sucrose and glucose, for milk production (Broster et al 1970; 1974). The fermentation studies had shown that both the rate of fermentation and the molar proportions of volatile fatty acids (VFA) produced differed widely when such chemically similar substrates as sucrose, glucose, fructose, galactose, xylose and arabinose were fermented in the rumen. The purpose of the feeding trials was to

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[1] Invited paper given at the Fourth Annual Meeting of the Dominican Centre for Livestock Research with Sugar Cane, January 1979. The support of the Ministry of Overseas Development (London, UK), which enabled the author to attend the meeting id gratefully acknowledged.

examine the value of soluble carbohydrates for milk production and to see whether the differences established between sucrose and glucose in the fermentation studies persisted in the more practical situation.

Milk Production: A series of experiments was conducted with Friesian cows in mid-lactation (Broster et al 1970; 1974). The basal rations consisted of about 5 kg hay and 7.5 kg of a dairy concentrate based on barley and groundnut meal, and they provided about 115 MJ metabolisable energy (ME) daily. These were supplemented with 3.6 kg concentrates, 2.7 kg sucrose, 3.2 kg glucose monohydrate or 2.7 kg sucrose with additional groundnut meal replacing some of the barley in the basal diet to make the supplement isonitrogenous with the concentrate supplement. All supplements were expected to provide about 35 MJ additional ME. The level of supplementation chosen was based on the maximum amount of sugar that the cows would consume consistently. Some of the main responses to the treatments are shown in Table 1.

Table 1:
Milk yield and composition on the basal diet and the response to various supplements

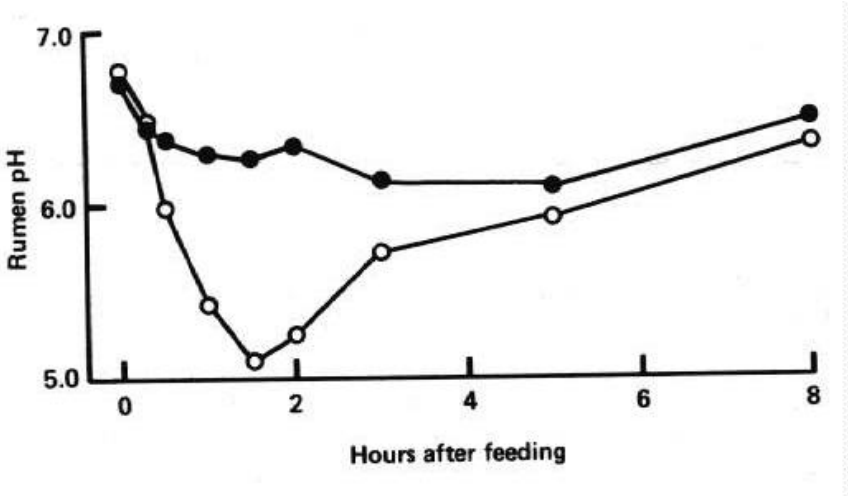
	Basal	Response to additional:			
		Concentrates	Glucose	Sucrose	Sucrose/GNM[1]
Milk yield, kg/d					
Expt One	11.5	+1.9	+0.5	+11.4	-
Expt Two	12.7	+2.1	-	+1.1	+1.5
Milk fat content, g/kg					
Expt One	43	-2	-2	-6	-
Expt Two	39	-3	-	-6	-2
Milk Solids-not-fat content, g/kg					
Expt One	88.4	+1.9	+2.4	+2.0	-
Expt Two	88.5	+2.1	-	+2.5	+2.7
Milk energy, MJ/d					
Expt One	37	+5	+1	-1	-
Expt Two	39	+5	-	+1	+4

[1] Groundnut meal

The important point was the very poor response to the additional soluble carbohydrates compared to the dairy concentrates. Both sugars resulted in only very small increases in milk yield and milk fat content fell, particularly when sucrose was fed. In consequence, essentially no additional energy was secreted as milk. However, when additional protein was supplied with the sucrose, a considerably improved response was obtained. All supplements increased liveweight gain, but sucrose rather less than the others.

Digestion: It is important to know why the sugar-supplemented diets were used so inefficiently. It seems probable that both the amount and the chemical form of the energy they supplied must be considered. Unfortunately, digestibility trials were not conducted but indirect evidence suggests that the digestibility of the fibre in the basal diet may well have been reduced by the addition of the sugars, so that the supplemented diets provided less energy than expected. Evidence for a reduced fibre digestion is based on the observed refusals of hay and concentrates, sometimes exceeding 2 kg/d, during introduction of the sugars, whereas only trace amounts of feed were refused when the supplement was in the form of dairy concentrates. The probability that these refusals were due to increased rumen fill resulting from reduced digestion of fibre is increased by the very low rumen pH found on the sugar supplemented diets when rumen fistulated cows were given the same diets (Figure l)(Sutton, unpublished data). It is well established that fibre digestibility is severely reduced when pH falls below 6.0.

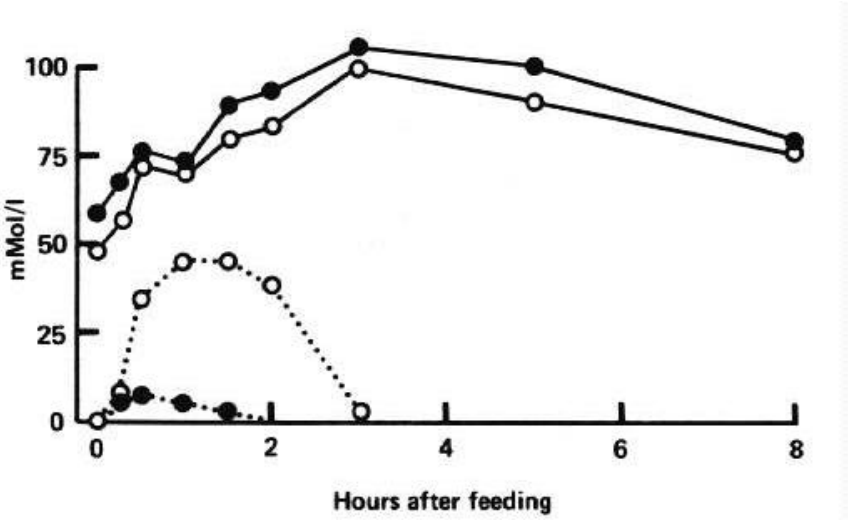
Figure 1:
Rumen pH in milking cows following the ingestion of A basal diet supplemented with either dairy concentrates (•) or sucrose (◦)



Although it is probable that fibre digestion in the rumen was reduced, thereby increasing rumen fill, it is by no means certain that the overall digestibility of fibre would be reduced. Knight et al (1978; and unpublished data) working with sheep found that although the digestion of cell wall constituents in the rumen was reduced from 51% to 19% by the addition of 40 g linseed oil daily to the basal diet, the overall depression in digestion was only 13 percentage units. This was because of the large compensatory increase in fibre digestion in the hind-gut on the oil supplemented diet.

Fermentation: The other factor to consider is the chemical form of the products of digestion in the rumen. On the sugar-supplemented diets, very high concentrations of lactic acid were found in the rumen shortly after feeding (Figure 2). Little is known about the effects on the efficiency of energy metabolism in the rumen or in the body of

Figure 2 :
Concentration of total volatile fatty acids (___) and lactic acids (...) in the rumen of milking cows following the ingestion of a basal diet supplemented with either dairy concentrates (•) or sucrose (◦)



lactic acid production, but in general it is thought to be associated with a lower efficiency of energy use than is the production of VFA. As well as increasing the concentration of lactic acid in the rumen, the free sugars caused large falls in the proportion of acetic acid and increases in the proportions of propionic acid and butyric acid (Table 2). The additional concentrates caused only minor changes in rumen VFA

Table 2:
Molar proportions of the major volatile fatty acids (moles/100 moles total VFA) in the the rumen and responses to various supplements

VFA	Basal	Response to additional:			
		Concentrates	Glucose	Sucrose	Sucrose/GNM[1]
Experiment One					
Acetic	67	-2	-9	-12	-
Propionic	15	+1	+2	+7	-
Butyric	15	+1	+6	+3	-
Experiment Two					
Acetic	67	-1	-	-7	-7
Propionic	17	+1	-	+3	+2
Butyric	12	0	-	+4	+6

[1] Groundnut meal

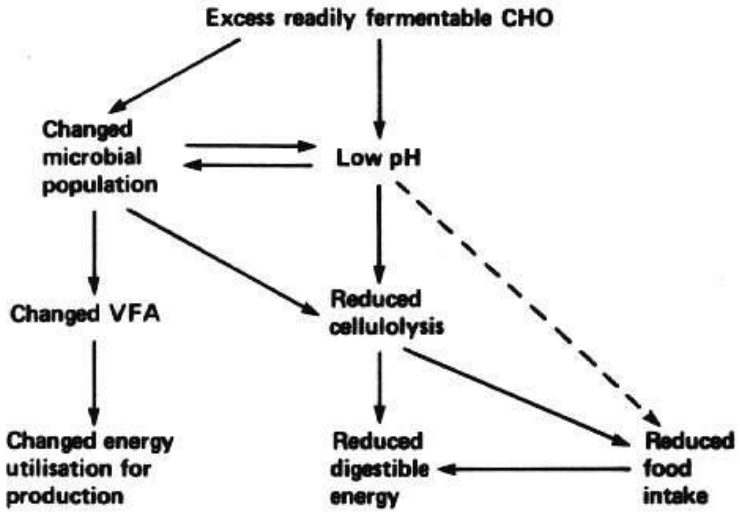
proportions. The close relationship between milk fat content and rumen VFA proportions observed in many experiments indicates that it was this change in VFA proportions that led to the reduced fat content, particularly on the sucrose-supplemented diet.

The present results confirmed the conclusion of the earlier in vitro studies (Sutton 1968; 1969) that sucrose and glucose are fermented to different end-products in the rumen. However, the relative changes in the molar proportions of the major VFA were different in the two sets of experiments, glucose producing the greater increase in propionate in vitro, but sucrose doing so in vivo. This problem clearly needs further study.

Conclusions: The results of these experiments have indicated possible reasons for the poor utilisation of the sugar-supplemented diets and in Figure 3, an attempt has been made to integrate the major factors that have been considered.

The results have also indicated ways in which improved utilisation might be expected. The low rumen pH following the ingestion of 2.7 kg sugar daily in two meals is almost certainly a key factor (Figure 3) and it would be particularly interesting to

Figure 3 :
Interrelationships of factors contributing to the poor utilisation of diets supplemented with large amounts of soluble carbohydrates



examine the response to a more gradual consumption of sugar. We have made no direct comparison of this nature at Shinfield, but we did find that when 1.65 kg glucose monohydrate were infused continuously into the rumen daily (Sutton J D and Oldham J D, unpublished data), rumen pH was only slightly lower than on the basal ration and the change in rumen VFA proportions was much smaller than in a similar experiment in which 1.8 kg sucrose daily was given in two meals.

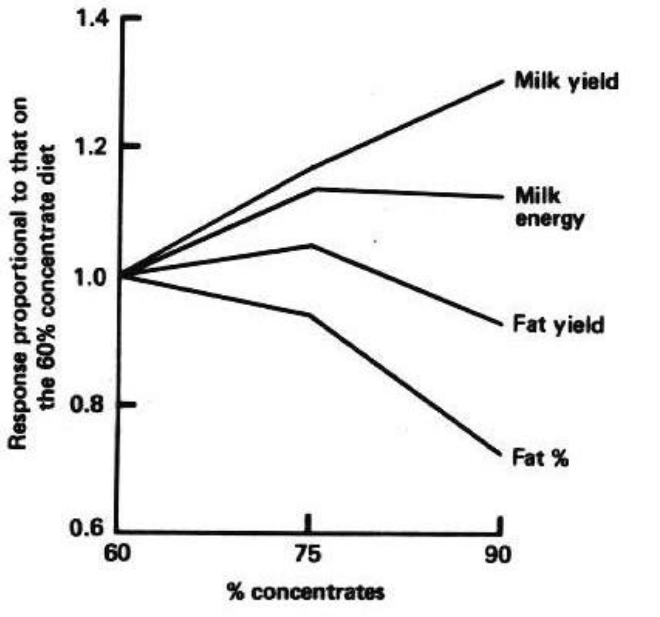
The reason for the improved milk production when sucrose was supplemented with groundnut meal is far from clear as the basal diets were estimated to provide more protein than was needed but this beneficial response also merits further study.

Substituting Starchy Concentrates for Roughages

Milk Production: It has been established for many years that replacement of most of the roughage of mixed diets by starchy concentrates results in an alteration in energy partition between body and milk and a reduced milk fat content (Flats et al 1969). The quantitative aspects of the affect of concentrate:hay ratio and level of intake and on energy utilisation by dairy cows have been examined in detail in a large-scale experiment recently completed at Shinfield. A preliminary report of these experiments has been published (Broster et al 1979).

The cows were given three ratios of concentrates to hay (60:40, 75:25 and 90:10) throughout lactation at two fixed levels of digestible energy (DE) intake, high (or standard) and moderate (20% lower). They were also offered the same diets ad libitum. Some of the more important production responses by the first-calf cows are summarised in Figure 4 which shows that the effect of substituting barley-based

Figure 4:
Response of dairy heifers to diets containing 75% and 90% concentrates relative to the response on the 60% diet (Broster et al 1979)



concentrates for hay was to increase the yield of milk by about 30% but decrease its fat content to a similar degree with the result that fat yield remained fairly constant and energy secreted in milk increased by only 15%. The effects of increasing the level of

intake were remarkably similar though rather smaller than the effects of replacing hay by concentrates.

Digestibility: In attempts to identify the contribution of digestive processes to these production response, detailed studies of various parameters of digestion have been made in these cows and also in fistulated cows receiving similar diets.

The digestibility of the energy of the diets increased as the proportion of the concentrates was increased and was lower in the milking cows fed at three times maintenance than in barren heifers given the same diets at maintenance (Table 3). However, increases in intake above three times maintenance in the milking cows had only small and inconsistent effects on digestibility. These results differ in important respects from the pattern proposed by Tyrrell and Moe (1975) as was discussed by Broster et al (1979

Table 3:
The effect of ratio of concentrates to hay and level of intake on the apparent digestibility of energy by dairy cows

Approximate multiple of maintenance[1]	Concentrate :hay ratio		
	60:40	75:25	90:10
1	0.75	0.78	0.78
3	0.70	0.71	0.73
3.7	0.69	0.70	0.73
3.8- 4.7	0.68	0.72	0.75

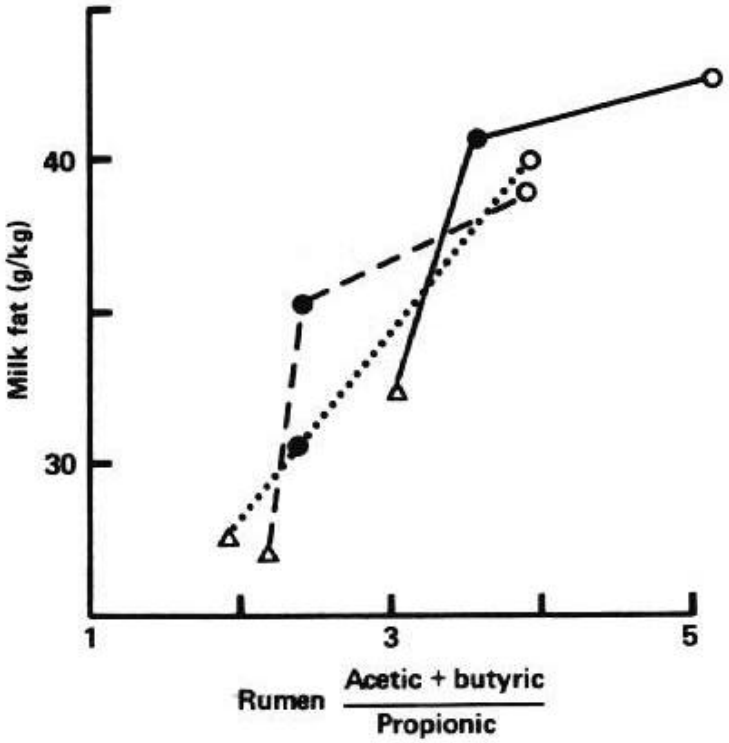
[1] Barren heifers at one times maintenance; milking cows at higher levels of intake

Whereas the digestibility of most dietary constituents increases as the concentrate:hay ratio of diets increases, it is important to bear in mind that the digestibility of fibre falls. In the present experiment it fell by about 10 percentage units for every increase of 15 percentage unite in the proportion of concentrates in the diet.

Rumen VFA: The substitution of concentrates for hay resulted in the usual changes in the molar proportion of VFA in the rumen, namely an increase in propionic acid and decreases in acetic and butyric acids. The finding of similar, though smaller changes due to increasing the level of intake (Sutton et al 1977) was more surprising. There was a close relationship between molar proportions of VFA and milk fat content (Figure 5).

Dynamics of Rumen Contents: Milking cows prepared with rumen and reentrant duodenal cannulas have been used to examine in greater detail the effect of these changes in diet composition on digestive processes. In studies of VFA production in the rumen (Sutton and Schuller 1974; and unpublished), an increase in the concentrate:hay ratio from 65:35 to 90:10 had little effect on the volume of rumen fluid but it reduced the outflow rate by up to 50% with the result that dilution rate was greatly reduced and retention time increased. The dynamics of rumen fluid are relatively simple to measure but the importance of the values to an understanding of digestive processes is difficult to establish.

Figure 5:
Milk fat content in relation to the molar proportions of volatile fatty acids in the rumen of cows receiving diets containing three ratios of concentrates to hay (60:40◦ ; 15:25• ; 90:10△) each at three levels of intake (moderate __; high ---; and ad libitum ...) (Sutton et at 1977)



Measurement of particle dynamics in the rumen would be of far greater importance for nutritional studies. Unfortunately the techniques available for measuring particle flow are unsatisfactory (Faichney and Griffiths 1978). As a result, no model of the dynamics of all components of the rumen contents has gained universal acceptance. Hungate (1966) suggested that the rumen contents could be described in terms of two pools, a "large-particle pool" and a "small-particle pool", the latter including fluid and microbes. However, recently Faichney and Griffiths (1978) have questioned this model and in particular they have suggested that the turnover rate of small particles and microbes is considerably slower than that of the liquid. This difference between the two models has important consequences for the interpretation of experimental observations. According to Hungate's (1966) model, measurement of rumen fluid dynamics by the use of a water-soluble marker simultaneously describes movement of small feed particles and microbes whereas according to the model now proposed by Faichney and Griffiths (1978), this is not the case. If the new model gains acceptance the relationship between fluid dynamics and particle dynamics will require further study. In summary, due to technical difficulties in making the necessary measurements, surprisingly little progress has been made about the very important subject of particle movements within and out of the rumen since the studies of the

excretion pattern of stained particles made at Shinfield and elsewhere 20 30 years ago (see Sutton 1971).

Sites of Digestion: The contribution of the rumen to overall digestion in milking cows is being studied by the use of cows with rumen and re-entrant duodenal cannulas (Austen et al 1977). Only preliminary results are available so far (Sutton et al 1979). Results to date, based on measurements with three cows, show that when the concentrates were based on rolled barley, about 70% of the apparent digestion of energy and 90% of the apparent digestion of starch occurred in the rumen whether the diets contained 60% or 90% concentrates. However, when ground maize replaced the rolled barley, starch digestion in the rumen was considerably reduced to about 60-70% (70-80% of overall digestion). The reduction was greater on the 90% concentrate diet and as a result the proportion of apparent digestion of energy occurring in the stomach was less than 65% on this diet. An important consequence of the difference in rumen digestibility of starch from the two cereals was that whereas only about 0.5 kg starch entered the duodenum daily on barley diets, this figure was increased to 1.3 kg/d on 60% maize and 2.6 kg/d on 90% maize.

Milk Fat Depression: The nutritional consequences of "by-pass" starch are still poorly understood (Sutton 1976). At least some is almost certainly hydrolysed to glucose and absorbed but the extent of this process is unknown and our own experiments have shown that a considerable amount of maize starch entering the duodenum escapes digestion altogether. According to the glucogenic theory of milk fat depression (see Frobish and Davis 1977), an increase in the uptake of glucose from the hind-gut would contribute to milk fat depression. However, the results of our own experiments to date provide no evidence to indicate that "by-pass" starch contributes to milk fat depression on low-roughage diets (Table 4). The relationship between milk fat content and rumen VFA on the maize diet was very similar to that on the barley diets despite the widely different amounts of by-pass starch. These results are in agreement with those of Elliott and Carpenter (1974).

Table 4:
Preliminary estimates of rumen VFA proportions, flow of duodenal starch and milk fat content in three cows (J D Sutton and J D Oldham, unpublished data)

	60%		90%	
	Barley	Maize	Barley	Maize
Milk fat, g/kg	39	38	25	31
Rumen: $\frac{\text{Acetic + Butyric}}{\text{Propionic}}$	3.6	3.8	1.6	2.6
Duodenal starch, kg/d	0.5	1.3	0.6	2.6

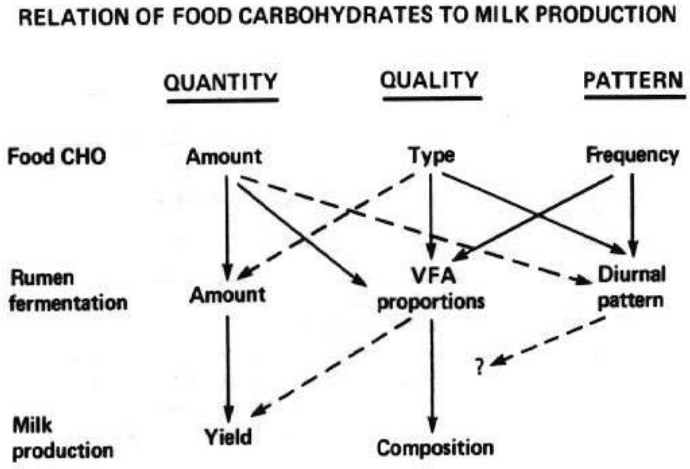
Clearly these findings pose important questions concerning milk fat depression: how much "by-pass" starch is hydrolysed to glucose? what is the role of glucose supply? does propionic acid act by some mechanism other than as a glucose precursor as suggested by Frobish and Davis (1977)?

Although the mechanism whereby a reduction in the roughage content of diets alters production by dairy cows remains unclear, there is no doubt that rumen VFA proportions, particularly the ratio of acetic acid plus butyric acid to propionic acid, provide a simple and valuable index of the way the energy of a diet will be used by lactating cows.

Factors Affecting Rumen VFA: Prediction of the probable pattern of VFA proportions is thus an important means of evaluating diets for milk production. Many dietary factors are known to affect VFA proportions (0rskov 1978), and Sutton (1976) attempted to devise an overall scheme to describe the more basic factors involved. Rumen pH is undoubtedly important. Dilution rate has also been shown to be related to VFA proportions in experiments in which it has been altered by the addition of mineral salts to the basal diet of sheep (Thomson et al 1975). However, results at Shinfield indicate that the relation between dilution rate and VFA proportions across a variety of diets varies widely. This difference emphasizes the importance of distinguishing between the change in dilution rate brought about artificially by the use of an additive in a fixed diet and that occurring as a result of a change in diet composition in which case it is merely one of several changes in the rumen environment.

Sutton (1976) suggested that the concept of the maximum fermentation rate (MFR) was of practical value. At least for diets of hay and starchy concentrates, an increase in the daily MFR is associated with a higher proportion of propionic acid in the rumen and so a lower milk fat content. MFR is increased by increasing the amount or proportion of readily fermentable carbohydrate in the diet and can be decreased by giving the daily ration in several small meals rather than two large ones. Recent experiments at Shinfield have confirmed that dietary changes that increase the MFR, such as alterations to the type of cereal or frequency of feeding, also lead to a lower milk fat content and, as a corollary, that milk fat depression can be alleviated by reducing the MFR.

Figure 6:
Interrelationship of factors influencing the utilisation of dietary carbohydrates for milk production



Conclusion

It is apparent that the relation between dietary carbohydrates and milk production is very important but also that it is complex. Rumen processes are central to an understanding of the relationship and the role of the hind-gut remains unclear. In Figure 6 an attempt has been made to integrate the more important factors linking the feed, the rumen and milk production. The main purpose is to indicate that at least three aspects must be considered: quantity, quality and daily pattern.

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