Manipulation of the Rumen Ecosystem to Support High-Performance Beef Cattle[a] - Review -

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ABSTRACT : Genetically selected beef cattle are fed high-energy diets in intensive production systems developed in industrial countries. This type of feeding can induce rumen dysfunctions that have to be corrected by farmers to optimise cost-effectiveness. The risk of rumen acidosis can be reduced by using slowly degradable starch, which partly escapes rumen fermentation and goes on to be digested in the small intestine. Additives are proposed to stabilise the rumen pH and restrict lactate accumulation, thus favouring the growth of cellulolytic bacteria and stimulating the digestion of the dietary plant cell wall fraction. This enhances the energy value of feeds when animals are fed maize silage for example. Supplementation of lipids to increase energy intake is known to influence the population of rumen protozoa and some associated rumen functions such as cellulolysis and proteolysis. The end products of rumen fermentation are also changed. Lipolysis and hydrogenation by rumen microbes alter the form of fatty acids supplied to animals. This effect is discussed in relation with the quality of lipids in beef and the implications for human health. Conditions for optimising the amount of amino acids from microbial proteins and dietary by-pass proteins flowing to the duodenum of ruminants, and their impact on beef production, are also examined. (*Asian-Aus. J. Anim. Sci. 2000. Vol. 13, No. 1 : 96-114*)

Key Words : Rumen, Ecosystem, Manipulation, Digestion, Acidosis

INTRODUCTION

Ruminants have long lived in close symbiosis with humans. They are able to convert cellulose into animal products (milk and meat), which form the basis of our dietary protein supply. Marked imbalances occur throughout the world between animal protein supply and requirements for human food. Developing countries are short of animal proteins and therefore seek to increase production, while strict directives are given to stock farmers in industrialised countries to curb overproduction. In the developed world, beef cattle production has evolved during the last 50 years into highly specialized systems integrated into a complete chain that includes processing industries and is responsive to consumer demands. People in these countries have been reducing their meat consumption over the last 15 years, partly because nutritionists claim that energy intake as fat, together with the content of saturated fatty acids (FAs), should be lowered in human food to reduce the risk of cardiovascular diseases. The bovine spongiform encephalopathy crisis that affected Europe in 1995 dramatically depressed beef consumption still further. Beef has been thus much more deeply affected than poultry or pork by recent changes in dietary habits, and the extent of beef overproduction has been amplified. Research programmes are therefore being directed now more towards factors influencing meat quality, including nutritional and organoleptic aspects, rather than productivity.

In general terms, animal production can be improved through genetic selection and through nutrition, but only aspects linked to the manipulation of the rumen ecosystem will be dealt with here. Ruminants have specific nutritional features because they possess three forestomach compartments in their digestive tract. The rumen, which is located at the beginning of the tract, plays a major role as at least 50% of the total digestion occurs there. Rumen digestion is essentially due to dense and complex rumen microflora and microfauna, associated with phycomycete fungi. The microbial biomass, estimated to be 1 kg in the rumen of growing cattle weighing 550 kg, digests up to 5 kg dry matter (DM) per day and produces 2.7 kg of volatile fatty acids (VFAs), 1.2 kg of microbial matter used as nutrients, and 500 L of eructed gases. VFAs are absorbed and microbial proteins and digested in the small intestine to supply energy and amino acids (AAs) respectively. Many studies have been carried in the last twenty years on the control of the rumen microbial ecosystem with the aim of improving its efficiency in terms of supply of nutrients to ruminants. Some treatments were designed to alter the microbial ecosystem by eliminating protozoa or fungi or some bacteria, others were applied to a conventional microbial population to

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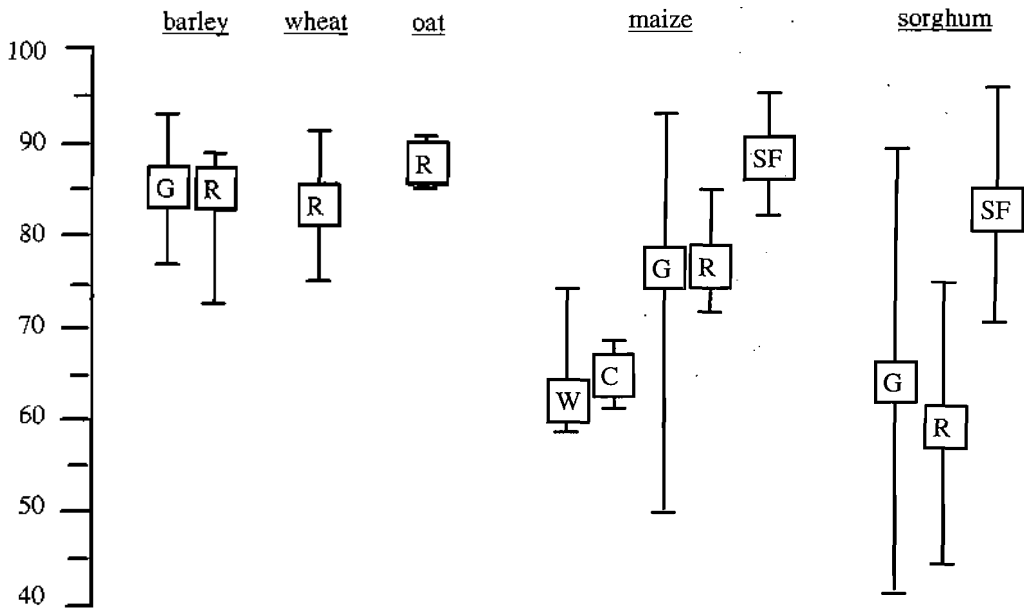


Figure 1. Rumen degradable starch (% starch intake); values from various cereals or treatments of grains (*in vivo* measurement)

change certain basic rumen digestive functions either through processing of feed or by addition of chemical or biological substances. Some of these various possibilities for manipulation of the rumen ecosystem and their feasibility are reviewed here in relation to the specific nutritional of high-performing beef cattle.

In intensive systems of production such as American feedlots or European farms, beef cattle are fed high-energy diets to exploit their genetic potentialities to the full. As a result, rates and levels of rumen fermentation are high, bringing a risk of rumen acidosis. Various means have been proposed to stabilize rumen conditions and improve microbial cellulolytic activities in such feeding systems. Fats are sometimes added to the diets to increase their energy content, which can alter the amount and nature of fat deposits in animals. Protective solutions to reduce fatty acid (FA) hydrogenation in the rumen and limit the effect of unsaturated FAs on the rumen ecosystem are discussed. Finally, means to increase the supply of amino acids (AAs) to high-producing animals by stimulating both the by-pass of rumen dietary proteins and the net flow of microbial proteins in the intestine are presented.

CONTROL OF SITE AND EXTENT OF STARCH DIGESTION IN RUMINANTS

Impact of site of starch digestion in the digestive tract of ruminants on the energy values of diets

Cereals are used in finishing diets either as grains or in whole plant form. Whatever the type of diet, grains constitute 70 to 90% of the diet, and starch is the main component of these grains, from 58% of dry matter for barley to 77% for wheat. Starch content of maize silage depends on plant maturity and proportion of grain in the whole plant. It increases from 22 to 35% as the percentage of grain in silage is increased from 32 to 50%. Cereal grains undergo extensive fermentation in the rumen, resulting in the production of volatile fatty acids (VFAs), gases and microbial cells. The proportion of starch digested in the rumen is generally high, ranging from 50 to 94% depending on the cereal grain and type of processing (figure 1).

Starch escaping digestion in the rumen is subsequently digested in the small intestine by host enzymes. The action of these enzymes results in the formation of glucose. Accordingly, the site of starch digestion in the digestive tract has implications for the nature and amounts of nutrients delivered to the ruminant.

Many basic constraints have to be allowed for when working on digestion site strategy to optimise starch utilisation, and their interactions sometimes conflicting, making final decisions difficult. The absorbed nutrients (VFAs or glucose) are used with different efficiencies for energy production (ATP synthesis) during catabolic reactions, and for anabolic processes such as fat and protein synthesis in animal cells. Owing to unbalanced supply of glycogenic and ketogenic nutrients, forages fed alone have a low metabolisable energy efficiency for fattening. Addition

of cereals to forage based diets is known to shift ruminal fermentations towards propionic acid at the expense of acetic acid production, thus increasing their metabolisable energy efficiency. However, an excess of starch ruminal digestion can markedly disturb some basic rumen functions as discussed later. Protecting starch from rumen degradation could be another way of significantly improving the metabolisable energy in growing fattening steers, because there is less carbon loss in rumen gases and also because glucose formed in the small intestine is efficiently used by animal cells. However, there is some evidence that the intestinal digestibility of starch can be limited.

Impact of diet composition on carcass and meat quality

Regarding meat quality, it is difficult to separate the effects of intake level and diet composition in the literature data, because the comparisons were mostly made between diets at different net energy intakes. However, some general considerations can be proposed from recent reviews (Geay et al., 1991; Kim, 1995). The effects of altering the acetate/propionate ratio in rumen fermentation on biochemical and physico-chemical characteristics of meat are still unclear. Owing to faster growth, grain-finishing carcasses are generally fatter than forage-finishing carcasses, and the amount of intra-muscular fat is higher, whereas the backfat thickness is not greatly modified by diet. As a consequence, the marbling score of meat is improved in grain-finished carcasses. However, the intra-muscular lipids that accumulate in such conditions are rich in triglycerides and poor in phospholipids and cholesterol. These features are unfavourable, because it is now widely accepted and indeed specified in official human nutritional guidelines that high triglyceride content of meat is partly responsible for the increase in human heart diseases in industrial countries. Because of the hydrogenation of FAs by rumen microbes, lipids in beef are rich in saturated FAs, which are claimed to be more detrimental to human health than poly-unsaturated. The sensory properties of meat such as flavour and tenderness are also positively related to the intra-muscular lipids (Geay and Renand, 1994), especially to their phospholid contents. Tenderness is inversely related to the collagen content of meat, especially to the fraction of insoluble collagen. According to Geay et al. (1997), muscles from animals fed on maize silage are significantly less tender and less juicy than muscles from grass hay fed animals. However, because of their higher growth rate the former are slaughtered younger. Diet composition has no effect on meat pigmentation and therefore meat colour (Geay and Renand, 1994). Antioxidants such as Se and some vitamins prevent the meat from darkening during maturation and preservation. Owing to high carotenoid intake, lipids from animals fed on forages or maize grains are sometimes yellow coloured, which spoils the appearance of the meat.

The main responses of the rumen ecosystem and rumen functions to high-grain diets

Ruminal starch digestion increases propionate production, decreases the amount of methane released to the atmosphere, and stimulates microbial protein synthesis. This last point will be discussed in the third part of this paper. For the same amount of starch in diets, the modifications of fermentations are more marked when the starch ruminal degradation rate is high. In six trials in which different cereals incorporated in the same proportions in diets were compared, when ruminal degradable starch amount increased by 1 g/kg LW, acetate/propionate ratio fell by 0.25 percentage unit (figure 2).

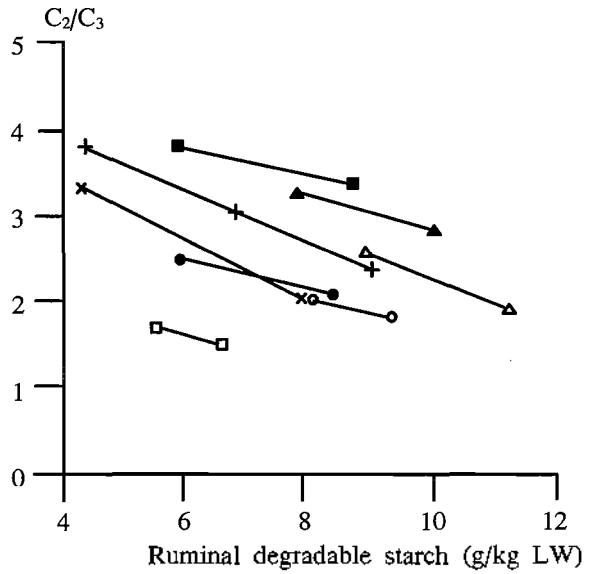


Figure 2. Influence of amount of ruminal degradable starch on acetate/propionate (C_2/C_3) ratio (Axe et al., 1987; Herrera-Saldana et al., 1990; Kung et al., 1992; McCarthy et al., 1989; Miron et al., 1995; Overton et al., 1995)

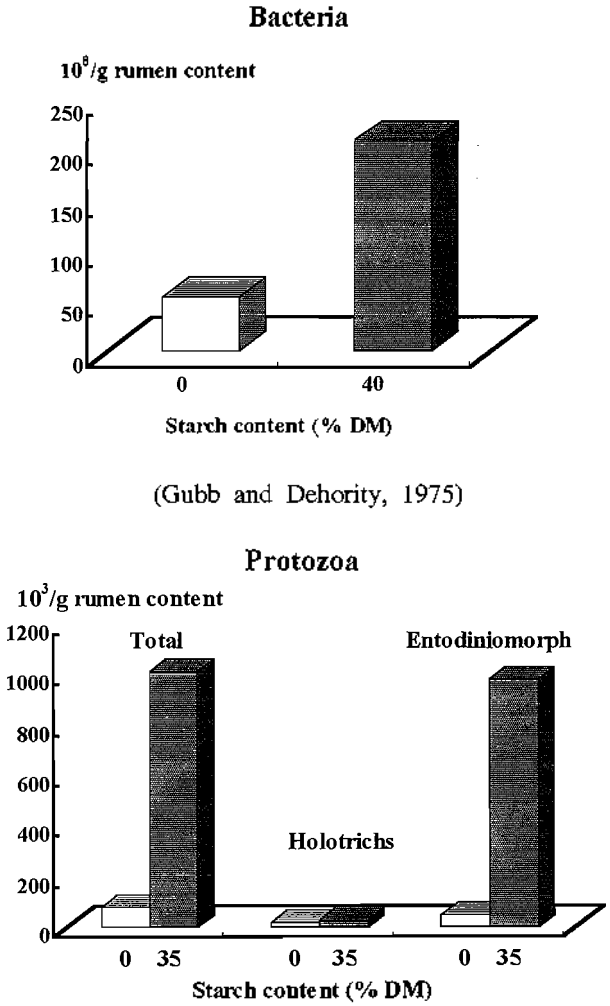
Micro-organisms are able temporatily to trap the supply of quickly available energy and store it as intracellular glycogen-like granules of plates. According to Jouany and Thivend (1972), the amount of stored carbohydrates can reach 30% of bacterial DM and 40% of protozoal DM 3 hours after feeding animals with high-starch diets. Raking the total rumen microbial biomass as equivalent to 1.0 to 1.5 kg DM for growing cattle, the amount of trapped starch inside

microbial bodies is estimated to be 400 to 500 g, i.e., 1/5 to 1/6 of starch intake when animals are fed on maize silage. After a lag time of 7 to 9 hours, these microbial carbohydrates are released back into the ruminal medium. Via this mechanism, the micro-organisms play a major role in the regulation of carbohydrate availability for rumen fermentations (Sauvant and Van Milgen, 1995).

The extent of ruminal starch digestion has a strong influence on the digestion of the fibrous part of mixed diets. Addition of cereals to forage-based diets is known to depress ruminal fibre digestion (Tamminga, 1993) and this decrease varies with the amount of starch in the diet and its ruminal degradation rate. From a compilation of literature data on measurements of duodenal flow of plant cell walls, Poncet et al. (1995) reported an average decrease in ruminal fibre digestion of 8.7 percentage units when the level of grains in the diet increased from 30 to 60%. For the same amount of dietary starch, this decrease was much greater when the ruminal starch degradation rate is high (Michalet-Doreau et al., 1997), 2.5 and 16.6 percentage units with slowly and rapidly fermentable starches respectively. The decrease in fibre ruminal digestion is accompanied by an increase in fibre digestion in the large intestine, but the reduction of ruminal fibre digestion is not fully compensated for by this increase (Archimède et al., 1997).

The negative associative effects of starch supplement on ruminal fibre digestion and the modifications of ruminal fermentations appear mainly related to variations in the rumen environment associated with modifications of the microbial population. Ruminal VFA production increases, and pH drops when animals are fed high-starch diets. In general, protozoa and bacteria (figure 3), and VFA concentrations tend to increase with the level of microbial available starch entering the rumen.

The distribution of bacterial and protozoal species within the total microbial population is modified. Among protozoa the proportion of small entodinia greatly increases when diets are supplemented with strarch (Jouany and Ushida, 1999). However, protozoa can totally vanish when animals and fed *ad libitum* pelleted barley grains (Eadie et al., 1970). Cellulolytic bacteria are the predominant organisms in high-roughage diets, whereas the selenomonads, streptococci and lactobacilli predominate with high-concentrate diets (Dehority and Orpin, 1988). An increase in the amount of ruminal degraded starch induces a decrease in fibrolytic enzyme activities of the fraction of bacteria that adhere to feed particles (Martin and Michalet-Doreau, 1995), whereas the fibrolytic enzyme activities of protozoa are not modified (Jouany and Martin, 1997). The total fibrolytic activity in the rumen digesta evolves as the activity of adherent bacteria since the latter represent most of the rumen microbial population. Obviously, the total amylolytic activities in rumen digesta increase when the amount of starch supply exceeds 40% of the diet DM (table 1).



(Gubb and Dehority, 1975)

(Martin et al., 1999)

Figure 3. Effect of starch supplementation in the diet on the rumen bacterial and protozoal populations

Almost all the detrimental effects associated with feeding high-grain diets, especially rumen acidosis, result from excessive and uncontrolled fermentations giving rise to unusual accumulations of large amounts of organic acids including lactic acid in the rumen liquid. As the content of highly fermentable carbohydrates increased in the diet, the number of *Streptococcus bovis* and the associated lactic acid production both become excessive. There is a concomitant decrease in *Megasphera elsdenii* and *Selenomonas ruminantium* which both normally utilise

lactic acid as carbon source. When the fall in pH is marked (<5.5) and lasts for several hours during the day, growth of lactate utilizers and of *S. bovis* is impeded. Lactobacilli fill this niche and continue to produce lactic acid, keeping the pH low. A spiral effect is initated (Nocek, 1997). A spiral effect is initiated (Nocek, 1997). Generally, the resultant effect is not acute acidosis, but rather subclinical acidosis, during which low accumulation of lactic acid is detected in the rumen, although the pH remains low. Characteristic signs are observed, including erratic appetite, cessation of rumination, body weight loss, diarrhoea, and lameness.

Table 1. Influence of cereal supplementation on polysaccharidase activities of ruminal microorganisms

Polysaccharidases (μmol reduced sugar released/mg protein/min)	Hay (100%)	Hay+Barley (40%+60%)
Xylanase		
Particle-adherent bacteria	9.91	5.63
Protozoa	2.67	2.56
Amylase		
Particle-adherent bacteria	1.07	9.34
Protozoa	0.52	1.87

(Jouany and Martin, 1997)

To limit these negative effects, an alternative is to shift the site of starch digestion from rumen to intestine. However, the benefits expected from increasing the amount of starch escaping the rumen are offset by its incomplete digestion in the small intestine. According to Thomas and Rook (1997), less than 70% of starch entering the small intestine is digested, which represents in most cases between 480 and 960 g per day in growing cattle (Kreikemeier et al., 1991). This restricted capacity for starch digestion in the small intestine could be due to insufficient endogenous enzyme production (Huntington, 1997), a limitation of capacity of glucose transporters (Kreikemeier et al., 1991), or low accessibility of starch granules to intestinal enzymes associated with over-rapid intestinal transit (Poncet et al., 1995)

Manipulation of the site of starch digestion (rumen vs small intestine)

The progress of research in the manipulation of starch digestion by ruminants has been extensively reviewed. The first possibility is offered by the choice of the type of cereal or by processing to protect or increase the availability of dietary starch to the microbial digestion in the rumen. A second possibility lies in altering the microbial activity to control the intensity and pattern of fermentations through the action of certain feed additives.

The starch ruminal digestion of barley, oat and wheat is high, between 80 and 90% on average. It is lower (65% in mean) and more variable for maize and sorghum starch (Nocek and Tamminga, 1991). For maize silage, it decreases with plant maturity (Philippeau and Michalet-Doreau, 1997). Cultivars of the same cereal also display differences, as shown by Kemalyean et al. (1989) with barley, and Streeter et al. (1990) with sorghum. On average, starch ruminal digestion is faster for waxy than for non-waxy genotypes, for dent than for flint varieties of sorghum (Kotarski et al., 1992) or maize (Philippeau and Michalet-Doreau, 1997), for non-bird-resistant than for bird-resistant varieties of sorghum (Streeter et al., 1990). However, because ruminally undegraded starch is partly digested in the intestine, the rate and efficiency of weight gain do not always respond as clearly to different varieties as might be predicted by *in sacco* or *in vitro* rankings (Huntington, 1994).

Whole grain with an intact pericarp is largely resistant to digestion by ruminants, because whole kernels are resistant to bacterial attachment (Beauchemin et al., 1994). The physical processing of grains breaks down this pericarp and the endosperm structure, making the starch granules more available to microbial attack. Cereal processing consists of combinations of mechanical and physical actions such as grinding or cracking, which modify the particle size, or association of heat and moisture such as steam-flaking, popping and micronizing, which cause varying degrees of starch gelatinisation. Some effects of these treatments are described in figure 1. It is noteworthy that none of the studies include unprocessed grains, for which digestibility is too low, and most of the comparisons are made with dry-rolled grain as the control or baseline treatment. When the particle size of the grain is reduced, the surface area exposed to microbial enzymes increases and the ruminal starch digestion is generally improved. In vitro starch digestibility of sorghum grain is positively related to the percentage of starch that is gelatinised, at least when this is no more than 60%. The in vitro relationship fits well with observed feedlot performance in response to dietary incorporation of steam-flaked sorghum. Efficiency of weight gain increases as starch availability reaches 70% of total starch (Xiong et al., 1991). Although it is relatively easy to increase starch ruminal degradation, limiting this degradation is more difficult. Only the formaldehyde treatment has been tested as a way to increase starch ruminal by-pass (Fluharty and Loerch, 1989). Formaldehyde increases the resistance of the protein endosperm to microbial

attack and shelters starch granules from microbial digestion (McAllister et al., 1990). Its efficiency is greater with highly degradable starches (Michalet-Doreau et al., 1997) for which the risk of acidosis is greatest. However, the toxiity of formaldehyde sets a limit to its use in animal feeds.

Additives to stabilise the rumen environment with high-starch diets

The control of rumen pH can be achieved by addition of dietary buffers. Compounds such as sodium bicarbonate, calcium carbonate, or magnesium oxide are commonly used to improve ruminal digestion when high-grain diets are fed to beef cattle. The low buffering capacities of such diets is mainly explained by the cessation of rumination and the subsequent decrease in saliva secretion. However, according to Russell and Chow (1993), it is unlikely that these compounds can have such a buffering effect on ruminal pH because of the predominant effect of rumen transfer of CO_2 from blood. The action of bicarbonates could be explained more easily by an increased water intake inducing a higher ruminal fluid dilution rate and the associated soluble VFAs, an increased rate of undegraded starch outflow, and a consequent lower concentration of acids in the rumen.

Chemical additives such as the antibiotic ionophores monensin or lasalocid, or biological additives such as live yeast cultures, have been shown to stabilise the rumen conditions when animals are fed high-starch diets. Ionophores counter gram-positive bacteria such as *Streptococcus bovis* and lactobacilli, which are the main lactate producers in the rumen. At the same time they stimulate the pathway of propionate production from lactate. These effects explain why ionophores were used to prevent lactic acidosis (Dennis et al., 1981; Nagaraja et al., 1982). However, because of their antibiotic activity, their use is now strictly controlled. Two types of yeasts have been proposed to stabilise the rumen ecosystem: *Saccharomyces cerevisiae* (SC) and *Aspergillus oryzae*. Both have been shown to stimulate VFA in vitro production by increasing the rumen degradation of the dietary forage fraction in mixed diets, but they have little or no effect on fermentation patterns evaluated by the acetate to propionate ratio. In steers given a high barley diet, SC elevated pH during the 4 hours following feed intake but not thereafter (Williams et al., 1990).

The effect on pH was mainly due to a reduction in ruminal lactate concentration. Furthermore, Mathieu et al. (1996) observed that live yeasts decrease the redox potential in the rumen content by about 50 mV (figures 4a and b).

This effect could contribute to the stimulation of the cellulolytic bacterial population, known to be sensitive to the ruminal oxygen traces.

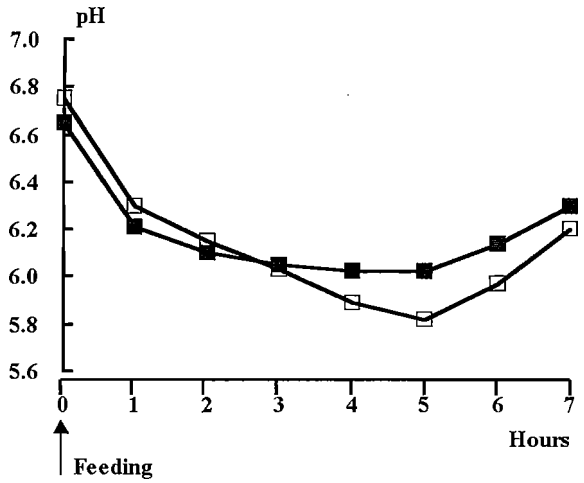


Figure 4a. Evolution of pH in the rumen of sheep without (□) or with (■) SC (from Mathieu et al., 1996)

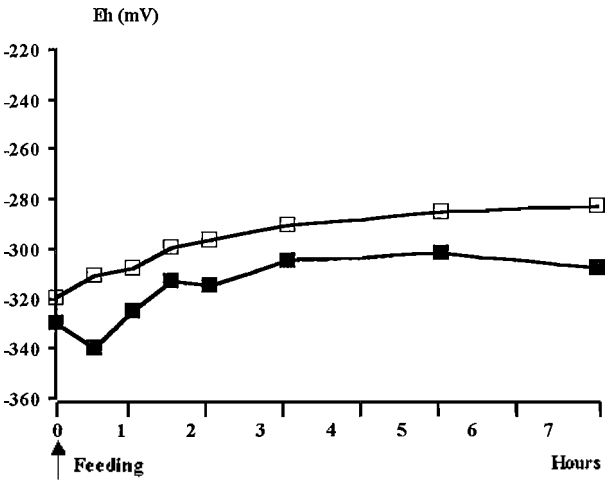


Figure 4b. Evolution of redox potential (Eh) in the rumen digesta of sheep without (□) or with (■) SC (from Mathieu et al., 1996)

EFFECT OF LIPID SUPPLEMENTATION ON RUMEN FUNCTIONS AN QUALITY OF BEEF CARCASSES

Dietetic and organoleptic aspects of lipids in meat : towards an increase in polyunsaturated fatty acids

A major factor behind reduced beef consumption in developed countries is saturated fat content. Although the desirability of a high proportion of polyunsaturated fatty acids (PUFA) in the human diet is still controversial, especially concerning nutritional impact

on cardiovascular diseases, increasing PUFA content is recommended, to achieve a ratio of PUFA to saturated FA of ca. 0.5. Requirement of n-3 FAs is also relevant, and the ratio of n-6 to n-3 should not be too high. At the same time, an excess of trans mono-unsaturated FAs should be avoided. Moreover, some prospective studies indicate a positive effect of conjugated linoleic acids on human health. Until now, attempts to reach all these different targets for beef by nutritional means, i.e. by feeding diets enriched in PUFAs, have been unsuccessful, owing to extensive metabolism of these FAs in the rumen.

The effect of supplemental PUFAs on the organoleptic quality of meat is questionable. Such fat supplementation does not modify tenderness or water retention of muscle; the effect on flavour is inconsistent, but tends to be negative, probably through oxidation (reviews by Clinquart et al., 1995 and Doreau and Chilliard, 1997a). It can be noted that antioxidants used as additives are less efficient in ruminants than in monogastric animals, although the transfer of tocopherol from diet to tissues is possible (Atwal et al., 1990)

Organoleptic quality of meat has to be balanced against consumers' requirement for dietetically desirable meat quality (Demeyer, 1997). Hence one target for intensive beef production is to increase PUFA concentration in beef fat. Generally, due to the extensive hydrogenation of dietary lipids in the rumen, supplementation with lipid sources rich in PUFA does not increase PUFA concentration in body fat, and can even increase the saturation of intra-musculal fat. Because of its relatively high content in structural phospholipids (10-30% of total lipids), which are richer in PUFA than storage lipids, intra-muscular fat is richer in PUFA than other body fats (11 vs 3%) (Demeyer, 1997), and a lipid supplementation may increase the proportion of storage saturated triglycerides.

The effects of PUFAs on meat quality can even be in some cases more negative than those of saturated FAs. In the course of hydrogenation, FAs of *trans* configuration are formed, and are transferred into body fat. For this reason, it is necessary to know the mechanisms involved in ruminal FA metabolism.

Metabolism of polyunsaturated fatty acids in the rumen

1) Lipolysis and hydrogenation : fate of the n-6 and n-3 PUAFs

Polyunsaturated FAs are released from dietary fats by a microbial lipolysis involving different kinds of bacteria, the most characteristic being *Anaerovibrio lipolytica*, whereas lipases of protozoa are of minor importance and lipases of plants do not play any significant role. The extent of lipolysis is almost complete and higher with diets rich in fats than with conventional diets, probably because the latter are richer in structural lipids that are less available to becteria than storage lipids (Doreau and Ferlay, 1994). Lipolysis is less intense with diets rich in concentrates, perhaps because it is reduced at low pH as shown by Van Nevel and Demeyer (1996a). After this initial step of lipolysis, FAs can be hydrogenated but this process requires a free carboxyl group. The mechanisms of hydrogenation have been extensively detailed by Harfoot and Hazlewood (1988). Hydrogenation begins by an isomerisation, and then a reduction occurs. The end-product of hydrogenation of linoleic (*cis*-9, *cis*-12 C18:2) and linolenic (*cis*-9, *cis*-12, *cis*-15 C18:3) acids is stearic acid is (C18:0). The extent of hydrogenation of PUFAs, defined as the disappearance of these acids, is always high. However, the hydrogenation process often stops before complete saturation. If this interruption occurs after the isomerisation step, different conjugated linoleic acids (CLA) are formed in the rumen, of which the most important is *cis*-9, *trans*-11 C18:2. Generally, the process stops after hydrogenation of one double bound, and different mono-unsaturated octadecenoic acids are obtained, the most abundant being vaccenic acid (*trans*-11 C18:1) and, to a lesser extent, elaidic acid (*trans*-9 C18:1). Assuming that FA secretion of these acids in milk is linked to their ruminal production, the amounts of vaccenic acid and of CLA in milk are therefore positively correlated (Griinari et al., 1996).

Two main dietary sources of n-3 FAs are avaiable: linseed oil or linseeds rich in linolenic acid, and fish oil rich in eicosapentanoic and docosahexanoic acids. Recent studies showed that both are extensively hydrogenated leading to the production of mono-unsaturated 20- and 22-carbon FA (Doreau and Chilliard, 1997b; Choi et al., 1997) in opposite to some previous papers. Moreover, it is likely that both fish oil and linseed oil increase the amounts of trans mono-unsaturated 18-carbon FAs. The increase in CLAs may be lower with linolenic acid than with linoleic acid (Kelly et al., 1997; Dhiman et al., 1997), and this may occur with fish oil.

Reviewing all the available data on ruminal hydrogenation of linoleic and linolenic acids (table 2), it cleary appears that hydrogenation of linolenic acid is higher than that of linoleic acid. This may be due to a partial protection of linoleic acid, which can be incorporated in bacteria as storage lipids and thus escapes hydrogenation (Bauchart et al., 1990) and related to the differences in hydrogenation pathways

between linoleic and linolenic acids. It is also evident that the low rumen pH found with such diets will limit the extent of lipolysis, whereas the amount of lipid supply plays a secondary role. Furthermore, less hydrogen is produced per unit of fermented OM with high-starch diets, and this will limit hydrogenation of FAs.

Table 2. Hydrogenation (% of disappearance) of linoleic and linolenic acids

	Concentrates in the diet	
	< 70% (50 diets)	> 70% (7 diets)
C18:2	60-95	35-60
C18:3	80-100	50-80

(review of the literature by Doreau and Ferlay, 1994).

2) Action of fatty acids on microbial ecosystem

In vitro experiments carried out on bacteria cultures with different substrates indicated a negative effect of FAs, especially polyunsaturated, on bacterial growth. Linoleic and linolenic acids have been shown to have the same antibacterial activity, higher than most other FAs of feeds, on gram-positive bacteria (Galbraith et al., 1971). It has been shown that saturated and mono-unsaturated FAs mainly decrease cellulolytic bacteria (Maczulak et al., 1981); this is probably also true for PUFA. However, in vivo the amount of liquid-associated and solid-adherent bacteria were not modified by PUFA supplementation in a trial carried out by Bauchart et al. (1986). This difference between in vitro and in vivo data may originate in the lower degree of adsorption of FA on bacteria in vivo, due to the adsorption of FA on feed particles (Harfoot et al., 1974).

The negative effect of PUFA on protozoa population is often considered as a general rule. However its magnitude is variable, and it appears that only linseed oil has a very strong effect, almost total defaunation occurring, whereas the effect of soybean of rapeseed oil is moderate (review by Doreau and Ferlay, 1995). This may be due to the high concentration of linolenic acid in linseed oil, but this has not been directly demonstrated.

3) Action of fatty acids on carbohydrate and protein ruminal metabolism

One of the best known effects of lipid supplementation is the diminution in ruminal OM digestion, especially when these lipids are rich in PUFAs (Doreau et al., 1997). There is a net decrease in fibre diestibility at the rumen level (Palmquist and Jenkins, 1980) Whereas the starch digestibility is not affected (Zinn, 1988). This reduced digestibility is accompanied by a shift of VFA patterns towards an increase in propionic acid at the expense of acetic and butyric acids (figure 5), and a decrease in methanogenesis (Demeyer et al., 1969). Owing to a decreased rate of intake of concentrates rich in lipids (Tamminga, 1990) and the higher production of propionate, lactic acid does not accumulate in the rumen. Disturbances observed at the rumen level are more marked with PUFAs than with most saturated or mono-unsaturated FAs, and the effect is similar for linoleic and linoleic acid (Chalupa et al., 1984), which suggest a direct action of these acids on the rumen microbial population.

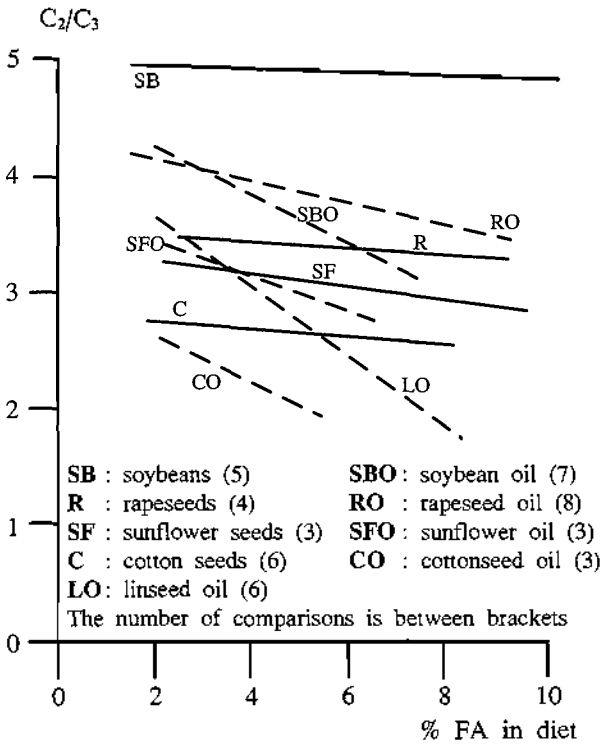


Figure 5. Effect of supplementation by oleaginous oils or seeds on the acetate/propionate (C_2/C_3) ratio in rumen liquid: summarizing 45 comparisons from the literature

However, disorders are especially marked with linseed oil, which is rich in linolenic acid (Ikwuegbu and Sutton, 1982). The magnitude of the decrease in cell wall degradation is probably related to the detrimental effect on protozoa, as assessed by a comparison of the effects of PUFA on defaunated and faunated animals (Broudiscou et al., 1994). Curiously, fish oil, which is rich in 20-and 22-carbon PUFAs, causes a slight increase in plant cell wall digestibility, whereas the propionic orientation of VFAs is

maintained (Doreau and Chilliard, 1997b). In addition to the direct negative effect on the cellulolytic microbial population, inhibition of cellulolysis is also explained by a decrease in the fibrolytic activity of the bacteria involved in degradation (Tesfa, 1992).

To limit the negative action of FAs on carbohydrate digestion, supplemental calcium is often supplied to animals. The effect of calcium is explained either by a removal of the inhibitory effect of FA on bacterial growth (Galbraith et al., 1971), to the formation of inert calcium salts in the rumen, or to a direct effect of ionised calcium stimulating the adhesion of bacteria to particles.

Ruminal protein degradation, estimated by *in vivo*, *in situ* or *in vitro* techniques, is independent of, or is sometimes slightly improved by lipid addition. Likewise, ruminal protein synthesis is not modified by lipids (Doreau and Ferlay, 1995). Thus the possible toxic effects of FAs on micro-organisms does not decrease N microbial flow to the duodenum. However, the efficiency of microbial synthesis, which is the ratio between the microbial N flow and the amount of organic matter fermented in the rumen, increases when both ruminal OM digestion and protozoal numbers decrease, i.e., in some cases when PUFAs are supplied to the diet. The efficiency of microbial synthesis is the balance between total production and degradation, the latter being mainly a consequence of predation of bacteria by protozoa (Demeyer and Van Nevel, 1995).

How rumen hydrogenation of unsaturated fatty acids can be limited?

Hydrogenation processes in the rumen are very diverse and many pathways are involved, so a large number of 18-carbon FAs is found in duodenal contents. The increase in PUFA-rich oil intake can increase the escape of linoleic acid from hydrogenation, but the benefits are offset by an increase in trans FAs, which are intermediate products accumulating at high PUFA intake (Jenkins, 1993). If hydrogenation of PUFAs cannot be reduced, the limitation of trans FAs and/or the increase in CLAs are other targets. However, as shown before, the production of trans FAs and that of CLAs are positively related. There are various ways to limit PUFA hydrogenation. It has been shown that hydrogenation is limited with concentrate-rich diets, but it is not reasonable to suggest increasing the percentage of concentrates with the sole aim of controlling the level of PUFA saturation.

Ther reduction of hydrogenation can be approached either by reducing specific microbial activity with additives, or by protecting fats against microbial attack.

1) Addition of antibiotics

Some antibiotics have been shown to decrease hydrogenation of PUFAs, *in vivo* for salinomycin (Kobayashi et al., 1992) and in vitro for a large panel of antibiotics, of which ionophores such as lasalocid and monensin, and amoxycillin were the most efficient (Van Nevel and Demeyer, 1995). According to these authors, the action of antibiotics is due to a reduction by 10 to 20% of lipolysis, which is the necessary pathway preceding hydrogenation, more than to a reduction of hydrogenation, which occurs only with lasalocid. The effect of antibiotics is probably due to a specific action on some bacterial species but, surprisingly, the principal lipolytic bacterium, *Anaerovibrio lipolytica*, is not very sensitive to antibiotics. Ionophores also contribute to increase propionate in the VFA mixture, but the association of fat and ionophores is not additive so that the propionate proportion does not increase too greatly (Zinn, 1988).

2) Use of oleaginous seeds

It has often been asserted that the use of oleaginous seeds instead of oils allows a partial protection of lipids against hydrogenation and a limitation of disturbances of fermentations as indicated in figure 5. Hagemeister and Kaufmann (1979) among others have demonstrated a lower hydrogenation associated with a lower decrease in fiber digestion when crude soybeans replaced soybeen oil; however, this natural protection against hydrogenation may reduce intestinal digestibility, because of the hard outer coat. Linseeds, rich in linolenic acid, could also have a protective effect on lipids. A limitation of biohydrogenation is suggested by the in situ study of linseed degradation, and is assessed by a significant increase in linolenic acid in adipose tissue (Clinquart et al., 1991). Uncrushed rapeseeds gave to be ground to avoid a complete protection even in the intestines, and this grinding leads to a complete hydrogenation. In the same way, the increase in linoleic acid escaping the rumen seems to be of very low magnitude with other whole oleaginous seeds given ground or rolled (sunflower, cottonseed), probably owing to the breakdown of seeds by mastication (Kennelly, 1996)

3) Use of protected lipids

The term ≪Protected lipids≫ is ambiguous since it covers absence of modification of the chemical structure of lipids as well as absence of influence of lipids on the digestion of the other constituents of the diet. These two characteristics have to be considered separately. The best known technique of protection is saponification of FA with Ca^{++}. Calcium salts are

generally made from palm oil, which is chiefly composed of saturated FA, but oils rich in PUFAs can be also used. Although they are extensively hydrogenated in the rumen (Ferlay et al, 1993), they cause a slight decrease in fibre digestibility (Enjalbert et al., 1994). Due to a low postprandial pH (Van Nevel and Demeyer, 1996b) associated with a higher pKa for salts from PUFAs, it is likely that they are more dissociated and then hydrogenated in the rumen than saturated FAs. The increase in pH with increasing time after feeding allows a reformation of calcium salts, and this may explain why both hydrogenation and a slight effect on carbohydrate digestion are observed. Results of Chouinard et al. (1997) suggest that an increase in PUFA absorption is possible if calcium salts are given with a pH stabiliser such as bicarbonates.

The coating of lipids by proteins was widely studied in the 1970s, and a new technique, the formation of amides, is actually being developed. Although *in vitro* trials show a very good protection of lipids against lipolysis and/or hydrogenation, in practical conditions the protection is only partial (Ashes et al., 1979). Two reasons have been proposed. First, mastication causes a breakdown of the product, which disrupts it. Secondly, the control of the process by the manufacturer is often less efficient when large quantities of product are handled than for small experimental batches. Despite these limits, coating of lipids with proteins is the most effective process to protect PUFA from any microbial hydrogenation in the rumen.

A new mode of coating, using calcium alginate, did not succeed in increasing by-pass PUFA (Ekeren et al., 1992). Crystallisation (prilled fats) is not considered here because the process requires high melting points, so it can be applied to saturated fats only. Another new chemical technique is the use of fatty acyl amides. This chemical association obtained by the action of oil with amines gives a high resistance to hydrogenation and limits the disturbances of carbohydrate ruminal digestion. The increase in linoleic acid escaping to hydrogenation is moderate but is accompanied by a decrease in *trans* FAs (Jenkins, 1995). Such a technique has been applied to soybean and rapeseed oil, but is not commercially available now.

MAXIMISING THE PROTEIN AND AMINO ACID SUPPLY TO THE DUODENUM OF BEEF CATTLE

Impact of protein and amino acid supply on animal nitrogen metabolism

Studies concerning the impact of AA supply on beef cattle and meat quality are scant. Protein supplementation at the duodenal level is known to increase animal feed intake and as a result improve animal performance. Harper and peters (1989) indicated on rats that AAs stimulate the appetite of animals at the central level. Millward et al. (1973) noted that dietary protein rather than energy intake appears to be the first stimulating factor for muscle growth. A raise in absorbed AAs increases the RNA content of mucle cells which indicates that protein synthesis is stimulated. Reecy et al. (1996) confirmed *in vitro* that AA availability to muscles control protein synthesis to a greater extent than energy availability. They showed that blood serum from animals infused with casein in the abomasum has a higher mitogenic activity measured on cell cultures of rat myoblasts than maize starch. The growth factors involved were not identified. Abomasal casein infusion increased fractional skeletal muscle protein synthesis, breakdown and accretion. Sugden and Fuller (1991) observed also that glutamine and leucine have a direct regulatory effect in muscle protein accretion. These results suggest that any rumen manipulation that can stimulate the AA supply to beef cattle will be encouraged. There is some evidence that balancing for AA requirements increases efficiency of AA use resulting in an increase in lean accretion (Robinson et al., 1997). Conversely, it seems difficult to improved carcass traits via the balance in AA supply (Marston et al., 1997).

Microbial proteins synthesised in the rumen and ruminally undegraded dietary proteins (RUDP) are the two main sources of AAs to ruminants. The portion of endogenous N flowing to the duodenum is considered as low and is generally included in the RUDP fraction, the latter being estimated by difference between the total non-ammonia N flow and the microbial N flow. Comparisons between methods for estimating microbial N are numerous and show discrepancies (Clark et al., 1992; Braderick and Merchen, 1992; Stern et al., 1994). This methodological aspect, although essential to assess the results obtained on the partition between the different protein sources entering the duodenum, will not be discussed here.

Optimisation of rumen microbial protein synthesis

Microbial proteins represent from 50% more than 90% of the total proteins reaching the duodenum and microbial proteins are close to the ideal proteins in term of essential amino acid composition. The new protein systems developed during the last 15 years in different countries assume that the quantity of

synthesised microbial protein is closely related to the amount of fermented organic matter (FOM) when soluble N is not limiting. This implies that the efficiency of microbial synhesis (EMS) defined as the amount of microbial N reaching the duodenum per unit of FOM is constant. It is now well known that many factors can influence the efficiency per se. Furthermore, the definition of FOM varies according to the authors. FOM in the French system, or diet fermentable metabolisable energy (FME) in the AFRC system, are the digestible OM or ME corrected for the amounts represented by crude fat, undegraded crude protein, and products of silage fermentation (verite et al., 1987) or their ME (AFRC, 1992), and undegraded starch (Tamminga et al., 1994). Studying the metabolism of rumen microbiota, Demeyer and Van Nevel (1986) estimated that FOM is equal to the apparent OM degraded in the rumen and not the true OM digested as considered by many scientists.

Analysis of literature data reveals wide variations of EMS in the rumen (figure 6). According to Merchen et al. (1986), Robinson et al. (1986) and Piwonka et al. (1994), EMS increased with the level of starch or DM intake, whereas it decreased in the experiment described by Feng et al. (1993). Firkins (1996) explained these contrasting results by various effects of the diets on the rate of outflow of digesta from the rumen, although this parameter has sometines no effect on EMS (Merchen et al., 1986). In fact, microbial synthesis is not a simple linear function of FOM. Sauvant and Van Milgen (1995) described a curvilinear response of EMS to concentrate proportion around 40~45% (25~30% starch) of the diet DM (figure 6). The decrease noted with higher starch proportions can be explained by ruminal conditions. The low pH found in the rumen of animals fed on such diets used by high-producing cattle increases the maintenance energy cost of some bacteria with slow rates of growth such as the cellulolytic *Ruminococcus flavefaciens* (Shi and Weimer, 1992). One reason is that bacteria spill energy across their membranes to adapt to adverse conditions (Russell and Strobel, 1993). EMS also varies in relation to shortage of elements other than energy, such as N, S and P (Komisarczuk-Bony and Durand, 1991). Therefore, although more energy is available to micro-organisms with high-starch diets, the EMS can decrease and the net synthesis is not optimum.

Although less well studied, recycling of microbial N in the rumen is another essential factor to take into account in understanding the differences noted in the net microbial protein outflow between experiments. The phenomenon seems of importance because studies using ^{15}N have indicated that as much as 75% of the microbial proteins can turn over inside the rumen and be degraded into peptides or AAs, which are then deaminated before passing on to the lower part of the gut (Firkins et al., 1992), and this recycling significantly decreases the availability of microbial proteins to the ruminant. Protozoal predation has often been cited as the main factor in bacterial protein recycling and this was confirmed by a higher ruminal ammonia concentration and a lower bacterial protein flow in the duodenum when protozoa are present (Ushida et al., 1986). The rate of bacterial turnover measured in vitro in absence of protozoa is only 6.4% of that in the presence of protozoa (Wallace and McPherson, 1987). The high concentration of protozoa with high-energy diets (figure 3) can explain why the amount of recycled microbial N is so large in intensive animal production systems.

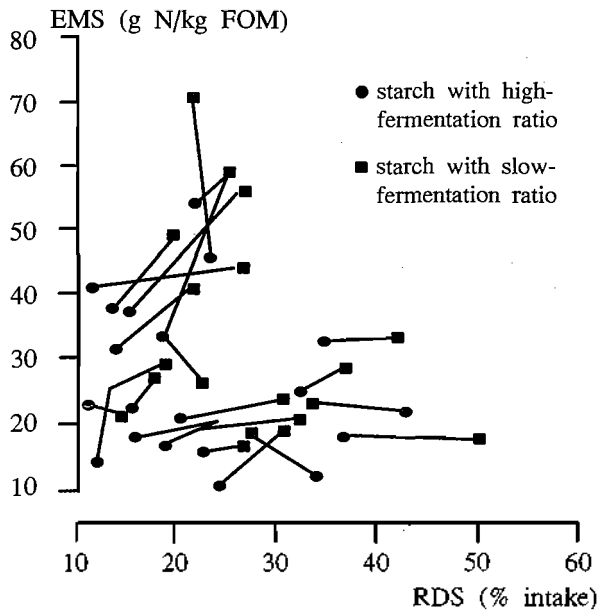


Figure 6. Influence of rumen degradable starch (RDS) on the efficiency of microbial synthesis (EMS)

As research shows (figure 7), defaunation is an efficient way of improving the duodenal flow of bacterial proteins. However, there is no available method to control the rumen protozoa population in practical conditions.

Krebs et al. (1989) showed that bacterial proteins can turn over to a large extent although protozoa are absent in the rumen. Lysis of bacteria is generally described as a feature of starving conditions when animals are fed low-digestible diets, but the mechanism of bacterial autolysis is not well known. According to Jolliffe et al. (1981), bacteria can develop some reaction against autolysin by accumulating

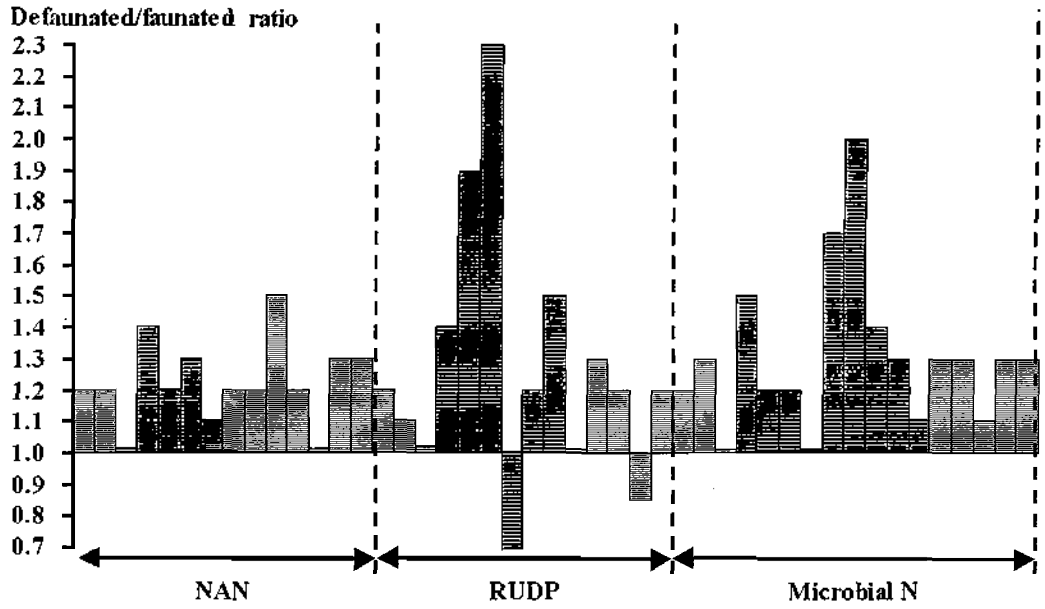


Figure 7. Effect of defaunation on the flow of different protein sources in the duodenum of ruminant (1 bar per experiment); see data in Jouany, 1996. NAN=non-ammonia N; RUDP=ruminally undegraded dietary proteins

protons at the cell surface which induces a high potential membrane with high-energy diets. Conversely, starvation inhibits the membrane potential and increases pH which in turn activate autolysins. However, Wells and Russell (1996) showed that growing *Fibrobacter succinogenes* with a high membrane potential can also lyse. They postulated that lysis appears to be a property of growing cells rather than a starvation cause. During stationary phase, cellobiose-excess cultures have 2.5 times as much cellular polysaccharide as the cellobiose-limited cultures, but their intracellular ATP and membrane potential are very low. A toxic end-product of carbohydrate fermentation, methylglyoxal, is then produced. Furthermore, some lytic factors like anaeroplasma (Hungate, 1966) and bacteriophages (Ritchie et al., 1970; Klieve and bauchop, 1988) have been found in the rumen fluid but their real contribution to bacterial lysis is still unknown and generally considered as low. The effect of energy level in the diet on these lytic factors has not been studied.

Autolysis of protozoa varies among the species of protozoa. Large ciliates, which represent most of the protozoa population with diets rich in roughage, have a much lower rumen outflow rate than the smaller ones (Leng and Nolan, 1984), which are much more numerous with diets rich in starch. The large holotrichs settle in the rumen and reticulum where they are trapped and lysed. As much as 1.2 kg and 0.5 kg of proteins are permanently fixed in the protozoal biomass when adult cattle are fed high-starch or forage-based diets respectively. Two-thirds of this amount are present in the small entodinia in starch diets, whereas the part fixed in the large ciliates is reversed in forage diets. Results in the literature indicate that around 65~85% of protozoa recycle within the rumen (Leng, 1982; Jouany, 1996) Which represents approximately 1.5 kg of protozoal proteins recycled per day in beef cattle if we assume that the mean generation time is 12 h for protozoa with such high-energy diets. Only 0.3 kg protozoal proteins are recycled in the rumen of beef cattle fed a roughage diet if we consider that large ciliates mainly found in that case have a 24-h generation time. The total amount of recycled bacterial and protozoal proteins can therefore be extensively decreased by defaunation. The effect of defaunation will be much greater in high-producing cattle than in extensive systems of production. However, part of the recycled N is used for resynthesis of microbial proteins, nucleic acids and other structural or storage polymers. The net effect resulting from positive and negative impacts of N-recycling on N metabolism in the rumen is difficult to assess, and can vary according to many factors. The presence of protozoa may help increase ruminal ammonia and peptide pools in low N diets, thus benefiting the bacteria for their growth and protein synthesis. In that case, the rumen functions are stimulated by protozoa, whereas the supply of AAs to the animals is decreased (figure 7) and excretion of N

in urine is increased (table 3).

Table 3. Effect of protozoa on N excretion in sheep feces and urine

Daily N excretion (g)	Defaunated	Refaunated
Urine	10.6[a]	11.9[b]
Feces	7.8[a]	6.0[b]
Total	18.4	17.9

Means with different letters are significantly different ($p \leq 0.05$). (from Jouany et al., 1998)

Russell and Sniffen (1984) showed that addition of iso four- and five-carbon VFAs stimulated the EMS and protein synthesis in *in vitro* incubations of mixed rumen bacteria sampled from animals fed timothy hay. This result confirms the specific requirement of branched-chain C-skeletons for bacteria to grow with such forage diets (Bryant and Robinson, 1962). The absence of effect when donors were fed 60% concentrate and 40% hay indicates that the needs of iso-C_4 and iso-C_5 acids are either normally smaller or are fulfilled with high-energy diets given to the high-producing beef cattle. Perhaps these acids are supplied in that case by microbial recycled proteins. 3-phenylpropanoic acid, which is produced in the rumen from cell wall polyphenolic compounds has been shown to stimulate the growth of *Ruminococcus albus*, and of the main cellulolytic bacteria found in the rumen. This acid could thus be limiting with high-starch diets, but the same acid had no effect on the other rumen cellulolytic bacteria (Stack and Cotta, 1986).

Factors accelerating the turn over of the liquid phase (Wells and Russell, 1996) and the associated small solid particles which harbour a large population of adherent bacteria (Yang, 1991), will favour the outflow of bacterial proteins and limit the amount of the rumen before lysis and turnover. Supplementation of mineral salts often used to buffer the rumen content in high-producing beef cattle, is a way to increase the fluid dilution rate as well as the flow of proteins from the rumen and the EMS (Harrison et al., 1975). The same effect can be obtained via the stimulation of saliva secretion by increasing chewing and rumination time, and via the acceleration of rumen motility both being obtained by means of addition of roughage to high-concentrate diets.

Maximisation of by-pass of feed proteins

The RUDP, generally measured as the non-microbial non-ammonia N fraction entering the duodenum, is the other main source of AA supply to rumen, the latter then being deaminated to give NH_3 and linear or branched VFAs. The rate and extent of protein breakdown depend on many factors such as solubility, the degree of secondary and tertiary structure, and disulphide bonds inside proteins. Treatments of proteins such as heating, formaldehyde and tannins affect these characteristics and will therefore decrease their rumen degradability. Condensed tanins have been shown to stimulate the flow of AAs to the small intestine (Barry and Blaney, 1987) by virtue of their antimicrobial properties. Jones et al. (1994) indicated that tannins can bind to the surface of proteolytic bacteria such as *Streptococcus bovis* and *Butyrivibrio fibrisolvens*, and limit their hydrolytic action in the rumen. Availability of some AAs such as lysine, cysteine, or tyrosine from treated proteins can become subsequently limiting for animals even at the small intestine level (Ashes et al., 1984). Sklan (1989) indicated that coating proteins with calcium soaps of long-chain fatty acids is a possible way to supply RUDP in the small intestine. More sophisticated procedures for coating proteins or AAs were developed recently but their use was limited by their high price. Coating will probably be used in the future to supply the correct amount of the right AAs to the animals for an optimum N metabolism, avoiding N losses and their consequences for production cost and environment.

Jouany et al. (1992) found that protozoa play an active role in the degradation of insoluble proteins until the NH_3-step while they have no effect on casein degradation as confirmed by Wallace et al. (1987) and Hino and Russell (1987). This result has been confirmed in vivo by comparing the amount of RUDP in defaunated and refaunated sheep (figure 7).

As a consequence, defaunation is the unique way to increase the duodenal flow of both the RUDP and microbial proteins. Studies are in progress to find substances having antiprotozoal activities to control the population of protozoa in the rumen.

The main proteolytic bacteria found in the rumen are *Bacteroides amylophilus*, *B. fibrisolvens* and *Bacteroides ruminicola*. *B. amylophilus* do not require peptides for growth (Hobson et al., 1968) and ammonia remains the principal nitrogen source even if peptides are available. Protease produced in rumen medium, even in absence of proteins or AAs, breaks down the structural proteins located in the endosperm of starch granules. This mechanism makes the bacteria particularly efficient in the degradation of starch in diets enriched in concentrate as found in high-producing beef cattle.

Inhibition of microbial deamination activity of AAs is an obvious objective for ruminant nutritionists since AAs can pass undegraded from the rumen or be

directly incorporated into microbial protein, which spares the energy cost for their re-synthesis from NH_3. Ionophore antibiotics are potent inhibitors of both methanogenesis and deamination. Hino and Russell (1985) showed that monensin alters interspecific hydrogen transfer. It increases the intracellular NADH/NAD ratio while decreasing methanogenesis which subsequently inhibits the AA deamination. As a consequence, the rumen concentrations of NH_3 is lowered in treated animals (Rogers et al., 1991), However, it has been shown that monesin lowers the microbial N flow to the duodenum by decreasing both microbial growth efficiency and organic matter fermentation in the rumen (Gomez et al., 1991), especially when rumen microbes have not been adapted for a long period (Rogers et al., 1997). Hence the speculation that monensin has a protein-sparing effect by increasing the duodenal flow of proteins is unproven. The substitution of microbial by feed proteins can have a positive impact on animal nutrition only if feed proteins contain more essential AAs than microbial ones, which is unlikely in most feeding conditions. The toxic effect of monensin on rumen protozoa, although evidenced by Hino (1981), is still debated. Thus the decrease in protozoal concentration sometimes found can interact with the direct effect of monensin on ruminal N transactions.

Diaryliodonium compounds were considered as inhibitors of AA degradation (Chalupa, 1980) and were found to be efficient in improving N retention in animals (Chalupa et al., 1976). *B. ruminicola* is the most sensitive organism (Wallace, 1986) which probably plays a central role in rumen AA catabolism. As seen before with monensin, diaryliodonium compounds also inhibit methanogenesis (Chalupa, 1980). Deamination can be inhibited by hydrazine and similar compounds, but their toxicity and their lack of specificity prevent any *in vivo* use (Broderick and Balthrop, 1979).

Several chemicals and natural compounds have been tested to inhibit the microbial proteolysis and deamination by controlling the population of rumen microbes and (or) their activity (see Van Nevel and Demeyer, 1988).

In conclusion, it seems realistic to look at a control of the rumen ecosystem with the aim to improve beef cattle production. Because the high dietary content of energy can induce severe rumen dysfunctions, research was caried out to limit the rate of starch degradation by rumen microbes. New data are now available on the relationship between the structure of starch grains and proteins from the endosperm on one hand, and the rate of starch fermentation on the other hand. Physical methods will be soon proposed to predict the fermentation rate and consequences on the rumen ecosystem. However, the impact of rumen vs intestinal starch digestion on meat quality remains open for further researches. Likewise, the real consequences of dietary fatty acids on meat composition are still unknown, although their effect on rumen microbes or rumen fermentations has been clearly identified. Several means to increase the outflow of dietary protein as well as microbial proteins from the rumen, are now available. However, only defaunation has a positive effect on both intestinal protein sources, but no accurate treatment is proposed to eliminate rumen protozoa. The use of feed additives to stabilise or stimulate the rumen ecosystem will be more severely controlled in the future.

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