

Director's Digest



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HYDROLYSIS OF FAT IN THE RUMEN

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INTRODUCTION

For many dairy herds, it has become a common practice to increase the energy density of rations fed to high producing dairy cows by supplementing the diets with fat. Increasing the energy density of the diet not only improves overall production as a consequence of increasing energy intake, but it may also improve the suboptimal milk yields and alleviate the metabolic disorders associated with a negative energy balance often found in early lactation.

Chalupa et al. (1986) commented that "fat is the variable most likely to optimize milk production and production efficiency." Fat contains 2.25 to 2.5 times the energy density of grains; thus, the energy density of the ration can be elevated without interfering with fiber levels. Problems such as acidosis and milk fat depression, which are a result of attempting to meet energy demands of the high producing dairy cow by raising the concentrate levels above 60% of the diet dry matter, can be avoided by supplementing the diet with fat. Another advantage of feeding fat is that the partial efficiency of lactation can be increased (Bines and Hart 1982; Brumby et al. 1978). This is due to the higher efficiency of synthesizing milk triglycerides when long chain fatty acids (LCFA) derived preformed from the blood are used as opposed to synthesizing fatty acids from volatile fatty acids (VFA).

However, fat supplementation of diets is not without limitations. Added fat is often restricted to 5% of the diet due to its adverse effects on ruminal fermentation. In general, supplementation of diets with fats that are rumen available (often referred to as rumen unprotected fat) above 5% of the diet dry matter reduces fiber digestion (Brooks et al. 1954) and methane production (Czerkawski et al. 1966) while propionate production is increased (Garton et al. 1961). Various investigators have also reported decreased milk protein percentage (DePeters et al. 1987; Palmquist 1987), interference with the digestion of other feed nutrients (DePeters et al. 1987; Jenkins 1988), reduced voluntary feed intake (Jenkins and Jenny 1989), decreased milk fat percentage (DePeters et al. 1987; Palmquist and Jenkins 1980) when unprotected (rumen available) fat is fed. The problems associated with fat feeding to ruminants are a direct result of the interaction between dietary fat and the ruminal microorganisms.

In an attempt to minimize some of the adverse effects of dietary fat on rumen microbial fermentation, fats that are more rumen inert or inactive, for example, calcium salts of fatty acids (Klusmeyer et al. 1991a, 1991b), hydrogenated fat (Banks et al. 1984), hydrogenated fatty acids (Banks et al. 1984; Grummer 1988), and protected fat (Banks et al. 1984; Murphy and Morgan 1983) are being studied and fed to lactating dairy cows. However, the costs of these products compared to fat obtained from whole seeds (e.g. cottonseeds and soybeans) and rendered fats (e.g. greases and tallows) limit their use.

Even though feeding fat to lactating dairy cows has some

limitations, fat will increase milk production when cows require additional dietary energy (DePeters et al. 1987; Schingoethe and Casper 1991) and for this reason, fat will continue to be an important feedstuff in the diet of high producing dairy cows. Improving our understanding of how dietary fats affect rumen fermentation will allow nutritionists to feed higher amounts of fats from oil seeds and rendered products.

LIPIDS OF FEEDS

Lipids (fats) found in forages and grains are predominately esterified fatty acids occurring as glycerides, phospholipids, and other polar lipids (Viviani 1970). The fatty acids vary in chain length, 2 to 24 carbons, and degree of saturation, from 0 to 3 double bonds. Most forage lipids are found in the chloroplasts of leaves as mono- and digalacto-1,2-diglycerides (Viviani 1970). Forage lipids contain high amounts of C18 unsaturated fatty acids (C18:1, C18:2, and C18:3), especially linolenic acid (C18:3). In contrast, the lipids of grains are found primarily in the form of triglycerides (Garton 1977). Although high amounts of C18 unsaturated fatty acids are also found in grains, the predominate fatty acid is linoleic acid (C18:2). The fatty acids of supplemental fats vary in degree of esterification (Table 1); however, when esterified, they occur primarily as glycerides. The degree of saturation of component fatty acids varies widely among these fats as does the predominate fatty acid.

FATE OF DIETARY LIPIDS IN THE RUMEN

As previously mentioned the three most common esterified forms

of fatty acids fed to ruminants are triglycerides, phospholipids, and galactolipids. Upon entering the rumen, these esterified fatty acids undergo hydrolysis. *Anaerovibrio lipolytica* is responsible for the hydrolysis of triglycerides and, although it does not attack galactolipids directly (Henderson, 1968), *A. lipolytica* will liberate the fatty acids following galactosidase activity. Hydrolysis of phospholipids as well as galactolipids is a result of the enzymatic deacylation by *Butyrivibrio fibrosolvans* (Hazelwood and Dawson 1979).

Hydrolysis of fats in the rumen results in a large pool of free fatty acids, particularly linoleic and linolenic acids. With the one exception of certain strains of *Butyrivibrio* sp., fatty acids are not utilized by the rumen bacteria (Hazelwood and Dawson, 1979). The unsaturated fatty acids, however, are biohydrogenated (Harfoot 1978). The susceptibility of individual fatty acids to hydrogenation depends on their degree of saturation, for example, linolenic acid (C18:3) is more prone to hydrogenation than linoleic acid (C18:2). Although not all fatty acids are completely hydrogenated in the rumen, the fatty acids reaching the small intestine are more saturated than the dietary fatty acids from which they originate.

EFFETS OF FATTY ACIDS ON MICROBES

Two theories exist concerning the mechanism of toxicity of fats in the rumen (Jenkins 1988). One hypothesis states that fat merely coats rumen microbes and feed particles, thereby inhibiting the action of microbial enzymes. The alternate hypothesis is that

fat inhibits microbial metabolism through a direct toxic effect related to surface activity. Interference of transport systems may occur when Ca^{++} and Mg^{++} soaps form and bind to the cell surface of certain rumen microorganisms.

Work by Czerkawski et al. (1966) lends support to the latter theory. Methanogens are extremely sensitive to fat and are inhibited with fat supplementation. However, Czerkawski et al. (1966) observed that the inhibitory effects of stearic and oleic acids were abolished with the substitution of a methyl or a hydroxyl group for the carboxyl group normally present in the free fatty acid. Oleic acid and oleyl alcohol should have similar coating properties since they are both liquid at room temperature and are insoluble in water (Jenkins 1988). If inhibition of ruminal microbes by fat was simply a coating effect, then oleyl alcohol should have inhibited methane production to the same extent as oleic acid. Since this is not the case, the coating of rumen microbes and feed particles by fat is probably not the mechanism by which fat exerts its influences on ruminal fermentation. Consequently, based on the limited research available, fat appears to have a direct toxic effect on the microorganisms.

Pure culture studies of Henderson (1973) indicate that sensitivity to fatty acids varies among organisms. Propionate and succinate producers were found to be unaffected by oleic acid. Oleic acid did, however, inhibit methane producers, acetate producers, and fiber digestors. It is interesting to note that Gram positive bacteria are predominantly more sensitive than Gram negative bacteria to fatty acids. This may be related to the outer

membrane of Gram negative bacteria which has the unique property of being impermeable to both hydrophilic and hydrophobic compounds.

EFFECTS OF FATTY ACIDS ON FERMENTATION

The extent to which ruminal microbes and hence, fermentation are inhibited by fat is largely determined by the chemical and physical properties of the fat. One important factor is the degree of esterification of the fat. Chalupa et. al. (1984), using acetate:propionate ratios as a means of measuring inhibition of ruminal fermentation, found that increased esterification of component fatty acids reduced the adverse effects of lipid supplementation on ruminal fermentation.

Increasing saturation of component fatty acids also lessens the inhibitory effects of fats on ruminal fermentation. Jenkins and Palmquist (1980) observed differences in the extent to which individual fatty acids reacted with cations to form insoluble soaps. As the saturation and chain length of fatty acids increased, the amount of insoluble soap formation also increased. In addition to saturation, geometric configuration of the fatty acid also influenced soap formation. Trans C18:1 appeared to form insoluble soaps more readily than cis C18:1.

Another property of fats that dictates how they will interact within the rumen and effect fermentation is the melting point. The melting point of a lipid greatly influences solubility characteristics. Rendered fats do vary in their melting points or titer (Table 1) which could influence their utilization in the rumen. Chalupa et.al. (1984) demonstrated that LCFA with a high

melting point disrupted ruminal fermentation less than LCFA with a lower melting point. They found that stearic acid (high melting point) decreased acetate:propionate by 20% while oleic acid (low melting point) decreased acetate:propionate by 50% to 60%. Work by Jenkins and Jenny (1989) corroborate this finding. Hydrogenating yellow grease increased the melting point and resulted in fewer negative effects on fermentation.

Esterification, saturation, and melting point of fats currently appear to be the major factors responsible for determining the extent to which ruminal fermentation is affected. However, the effects on fermentation seen with certain fat supplements cannot be entirely explained by these factors.

Palmquist and Conrad (1980) found that, while tallow disrupted ruminal fermentation, this did not occur with an animal-vegetable fat blend. Jenkins (1987) noted that the benefits of a animal-vegetable blend could not be explained on the basis of saturation since both fats contained between 44 and 48% saturated fatty acids. The benefits could also not be explained in terms of esterification because the animal-vegetable blend was 43% esterified while the tallow was 99% esterified.

One difference observed between the two fats by Jenkins (1987) was that the animal-vegetable fat contained more linoleic and linolenic acids compared to the tallow. Jenkins investigated the effect of fatty acid unsaturation by comparing the effects of different ratios of oleic/stearic and linoleic/stearic acids on ruminal fermentation. No evidence of synergism among the fatty acids was observed.

In an attempt to explain the effects of the animal-vegetable fat on ruminal fermentation, Jenkins put forth an interesting theory. Animal-vegetable fat contains a combination of esterified (43%) and nonesterified (47%) fatty acids which may act to reduce lipolysis and hence, reduce inhibition of fermentation. Jenkins postulated that the nonesterified fatty acid fraction may inhibit microbial lipases through a negative feedback mechanism. He proposed that "an optimal ratio of esterified to nonesterified lipids may be necessary to achieve this beneficial effect. Too little nonesterified fatty acid might be inadequate to inhibit ruminal lipases, while too much fatty acid would be exceed the toxic levels and inhibit fermentation." This hypothesis has yet to be tested.

HYDROLYSIS OF TRIGLYCERIDES

To date very little is known about the lipase of *A. lipolytica*, the organism responsible for the hydrolysis of triglycerides in the rumen. What information is known is largely due to the work of Henderson. Henderson (1971) demonstrated that the lipolytic capabilities of *A. lipolytica* were due to an extracellular lipase produced during logarithmic growth. The enzyme also expressed varying affinity towards different triglycerides. When enzyme activity towards 90 mg of emulsified triglycerides was measured, the largest activity was obtained with trilaurin. Thereafter, enzyme activity was greater towards triglycerides of long chain fatty acids than triglycerides of short chain fatty acids. The difference in enzyme activity in response to

fatty acid chain length could have implications on ruminal hydrolysis of rendered fats since differences in chain length do existed (Table 1). Activity of the enzyme was also greater towards diglycerides than triglycerides. Unsaturation of esterified fatty acids might also influence hydrolysis since enzyme activity was lower for triolein than trilaurin although chain length could be confounding. However, as noted by the author, caution must be exercised when interpreting the significance of these results since the physical properties of the substrates vary widely.

The lipase of *A. lipolytica* is a non-specific lipase (Ratledge 1989). Because of this, and the fact that the properties of fats (e.g. esterification, saturation, fatty acid chain length, and melting point) influence how fats interact in the rumen environment, a greater understanding of the properties of the lipase will most likely come from studies investigating the extent and rate of hydrolysis of various fats.

Lipolysis in the rumen has generally been considered to be rapid and complete (Harfoot 1978; Noble 1978). However, Garton et al. (1961) found considerable variation in the extent of hydrolysis of linseed oil incubated over a 24 hour period. Hydrolysis of esterified fatty acids ranged from 20% to 90%. Wright (1961) reported that only 13% of linseed oil incubated in rumen fluid for 22 hours was hydrolysed. Variation in the extent of hydrolysis was also observed between different sources of fat. Miller and Cramer (1969) reported that the esterified fatty acids of linseed oil, soybean oil, lard, tallow, and menhaden oil were 89.0, 87.5, 87.4,

59.7, and 48.8% hydrolyzed, respectively, challenging the general concept that lipolysis in the rumen is rapid and complete.

Different rates of hydrolysis have been reported by various investigators. Hawke and Silcock (1970) found the rate of appearance of [1-¹⁴C] linolenate in the free fatty acid fraction followed a S-shaped curve between 20 and 100 minutes. Hill et al. (1960) reported that the rate of hydrolysis of soybean oil was linear for the first 22 hours and then subsequently reached a plateau. Investigating the in vitro lipolysis of ¹⁴C labelled monogalactosyl diglyceride in whole rumen contents, Singh and Hawke (1979) observed a rate of hydrolysis that was neither S-shaped or linear.

Although the above studies on rates of hydrolysis have provided important information, comparisons cannot be made between them. Hydrolysis rates are affected by numerous factors including dietary nitrogen (Gerson et al. 1982), level of concentrate (Gerson et al. 1985), level of fiber (Gerson et al. 1985), and forage maturity (Gerson et al. 1986). However, the studies of Gerson and associates employed radiolabelled triolein for all measurements of lipolysis. Since esterification, saturation, and melting point influence hydrolysis of fats, it is difficult to extrapolate their findings to the multitude of commercial fats that are fed to dairy cattle. Consequently, our research efforts have focused on comparing the rates of hydrolysis of different fat sources simultaneously. This has involved the development of techniques and procedures to establish an in-vitro fermentation system to measure the rate and extent of lipolysis of various types and sources of

fats. The goal is to incorporate information obtained on the rate and extent of fat hydrolysis into ration formulation procedures to optimize rumen fermentation and fat feeding to enhance animal performance.

METHODS AND MATERIALS

Rates of lipolysis for three fat sources are being determined using ruminal in vitro incubations. Fats evaluated during 12 hour incubations are corn oil, canola oil, and tallow.

A nonlactating, ruminally fistulated Holstein cow serves as the donor for ruminal contents. A total mixed ration containing 45 to 55 forage to concentrate ratio and 5% added fat (yellow grease) is fed for ad libitum consumption.

Samples of rumen ingesta containing both liquid and particulate matter are removed by hand and strained through two layers of cheesecloth. Incubations are carried out according to the procedure of Goering and Van Soest (1970) with the exception of inoculum preparation. The rumen fluid was added to anaerobic buffer solution, dilution of 1:3, and then 10 ml was dispensed into 25 X 150 mm Pyrex test tubes containing 0.1 g of substrate. The test tubes were gassed with CO₂, immediately capped, and incubated at 39 C.

Substrates for incubation consist of ground straw ground (1 mm screen) containing either (1) 5% corn oil, (2) 5% canola oil, (3) 5% tallow, all on a weight basis. All three fat sources were incubated in quadruplicate, three of the replications being used for fatty acid analysis and the fourth replication being used for

volatile fatty acid analysis. The samples are incubated for 0, 1, 2, 4, 6, 8, and 12 hours.

Incubations to be analyzed for fatty acid content are arrested at the end of each time period by the addition of 0.5ml of 6N HCl. The samples are then frozen and freeze dried.

The method for lipid extraction is adapted from the procedures of Bath and Hill (1967) and Bligh and Dyer (1969). An internal standard for free fatty acids and triglycerides (esterified fatty acids) are used.

Esterified and nonesterified fatty acids are separated by thin layer chromatography using silica gel plates. Following the development of the plates, the various bands are identified by spraying the plates with a solution of 2,7-dichlorofluorescein followed by identification of the lipid bands. The individual lipid bands are scraped into test tubes and the fatty acids methylated according to the procedures of Sukhijia and Palmquist (1988). Fatty acid methyl esters are determined via gas-liquid chromatography. Fatty acid were quantified by comparison of the total area with that observed for the internal standards.

Samples (in-vitro tubes) to be analyzed for volatile fatty acids were arrested by the addition of 25% metaphosphoric acid. After centrifugation, the supernatant was analyzed for volatile fatty acids by gas-liquid chromatography.

RESULTS

Figure 1 illustrates some preliminary results from our in vitro analyses. The decrease in triacylglyceride concentration in

the incubations over a 12 hour period was measured for corn oil, canola oil, and tallow. The early results indicate that hydrolysis rates of the three fat sources were not different as determined using our in vitro methods. However, much more work needs to be done before general conclusions can be made for the wide variety of fats fed to ruminants. We are currently continuing this research which includes improving the techniques involved in measuring triglyceride and free fatty acid content of the incubations.

Summary

Esterification, saturation, and melting point are characteristics of fats that can impact ruminal fermentation. The rate at which different fats undergo hydrolysis liberating free fatty acids could be an important characteristic influencing the rumen microbial population and the amount of fat included in ruminant diets. There is a paucity of data available on ruminal hydrolysis rate of fats and therefore, research efforts will continue in this area. As our basic understanding of the mechanisms by which fats influence the rumen microbial population is expanded, fats will be included in diets more frequently and at higher amounts.

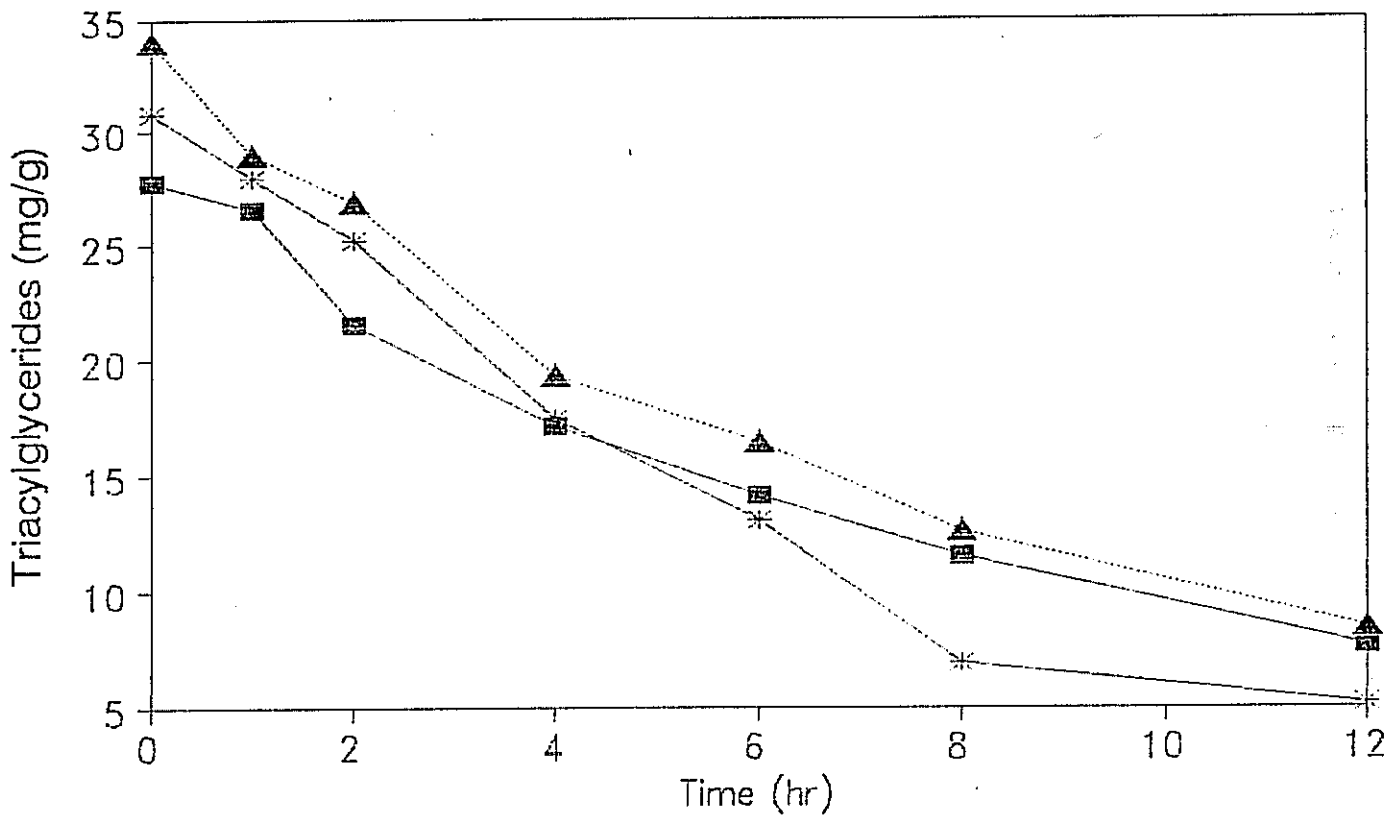
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TOTAL IN VITRO



—■— TOTAL CORN —▲— TOTAL CANOLA —*— TOTAL TALLOW

TABLE I

	<u>Tallow</u>	<u>Yellow Grease</u>	<u>Hydrolyzed Animal/Vegetable Blend</u>
Total Fatty Acids,%	90%	90	90
Free Fatty Acids,%	4-6	15	40-50
Titer, °C	40.5-41.5	36	---
<u>Fatty Acids,%</u>			
C12 + C14	3.5	1-3	2.5
C16	26	26	18-24
C18	19.5	12-18	7-16
C18:1	41	45-55	35-50
C18:2	2.5	15-20	22-28
C18:3	---	---	2

Adapted from Bisplinghoff (1992) - Rendering and an overview of animal fats and proteins.

