Overview of Fat Digestion and Metabolism in Dairy Cows

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Introduction

Over the last 25 years, the use of supplemental fats and oils in dairy cow rations has developed to the point where it now is a standard practice. Fats are supplemented to increase ration energy density, which ideally will lead to increased energy intake if dry matter intake is not decreased extensively. In turn, increased energy intake should improve energy balance and benefit body condition, milk production, and reproduction. However, there still is much confusion over different types of fats, how much can or should be fed, and what types of responses to expect. Considerable misinformation also has been spread by various parties, which further complicates the job of those formulating rations for dairy producers.

The purpose of this paper is to provide an overview of the processes of fat digestion and use in dairy cows. This is presented as a practical, "hands-on" approach rather than as a scientific review; consequently, scientific references are not included. Interested readers should feel free to contact the author if more information or scientific documentation is needed.

Fats in Dietary Ingredients

The term "lipid" refers to a broad class of substances that are insoluble in water or other aqueous solvents, but are soluble in organic solvents such as ether, chloroform, hexane, acetone, and certain alcohols. Most normal forages, grains, and byproducts contain some amount of lipid. This discussion will focus only on those lipids that are found as part of feedstuffs or as commercial fat supplements and which provide a source of fatty acids as energy-yielding nutrients to cows. The major lipid constituents in dairy cow nutrition are:

<u>Triglycerides</u>: Major lipid type found in cereal grains, oilseeds, animal fats, and byproduct feeds. Also the type of lipid making up milk fat.

<u>Glycolipids</u>: Major lipid type found in forages.

<u>Phospholipids</u>: Minor component of most feeds. Form the cell membrane of all animal cells, and the surface of milk fat globules. Also important in fat digestion in the small intestine of cows.

<u>Free fatty acids</u>: Minor component of dairy feeds, but major component of certain fat supplements (Energy Booster 100, and calcium soaps of fatty acids such as Megalac after going through the abomasum). Major form of transport of fatty acids in the cow's blood (same as nonesterified fatty acids or NEFA).

Within each of these classes there is considerable variability due to chemical makeup that results in different physical characteristics of the fat. These are discussed in more detail below.

Triglycerides

The basic unit of triglycerides is a molecule of glycerol (a three-carbon alcohol) combined with three fatty acid molecules. The term “fat” generally means a triglyceride that is solid or semi-solid at typical environmental temperatures, whereas “oil” is a triglyceride that is liquid at working temperatures. Whether something is a fat or oil largely depends on the fatty acids that are attached to the glycerol backbone. For example, beef fat trimmed from a cut of meat is a semi-solid at room temperature, but corn oil is liquid. Both are triglycerides, but the beef fat has a higher melting point because of its greater content of saturated fatty acids, and corn oil is liquid because it is very high in unsaturated fatty acids. Chemically, unsaturated fatty acids contain one or more double bonds linking the carbon atoms of their chain. Introduction of double bonds causes a “kink” in the otherwise straight-chain structure of the fatty acid molecule, and this “kinking” means that the fatty acids pack less tightly with one another, making the oil liquid at colder temperatures. The appropriate mix of saturated and unsaturated fatty acids gives the triglyceride the correct physical properties for a particular organism. For example, at body temperature the triglycerides of beef muscle are mostly fluid; seed oils must remain fluid at extremely low environmental temperatures and so contain mostly unsaturated fatty acids.

The purpose of triglycerides in plants or animals is to store energy. As components of dairy cow rations, triglycerides are mostly broken down in the rumen to release the fatty acids and the glycerol, unless the triglyceride is extremely saturated (e.g., a highly hydrogenated tallow, grease, or vegetable oil).

Glycolipids

The lipids of forage stems and leaves are primarily glycolipids, which are similar to triglycerides except they have two or more sugars linked to one position of the glycerol backbone instead of the third fatty acid. The most common are galactolipids, which have galactose (a component sugar of milk lactose) linked to the glycerol. The two fatty acids that make up the glycolipids are generally unsaturated. Glycolipids are structural components of plant tissues. In most forages, whether fresh, dry, or ensiled, glycolipids are fairly completely broken down in the rumen of the cow.

Phospholipids

Phospholipids make up the cell membranes of plants and animals. They consist of a glycerol backbone with two fatty acids attached, with the third position of glycerol attached to a phosphate group that links an organic base such as choline, ethanolamine, serine, or inositol to the molecule. In the rumen, bacteria largely remove the base group and fatty acids from the phospholipids in dietary ingredients. However, the protozoa and bacteria in the rumen also make their own phospholipids for their cell membranes. Usually, therefore, the amount of phospholipid leaving the rumen is more than the amount consumed by the cow in the diet.

Free fatty acids

Free fatty acids are not attached to a glycerol molecule. Fatty acids in feeds consist of a hydrocarbon chain ranging in length from 14 to 18 carbons. Marine oils such as fish oil also contain longer-chain fatty acids with 20 to 24 carbon atoms in their chains. Saturated fatty acids have all the carbon atoms linked with single bonds, while unsaturated fatty acids have one or more double bonds. The first double bond is found linking the ninth and tenth carbons, while additional double bonds are located farther down the chain away from the acid head group. The most abundant fatty acid in forages is *linolenic acid*, which contains 18 carbon atoms with three double bonds in the chain. Linolenic acid is abbreviated therefore as 18:3, indicating the number of carbons and the number of double bonds. In cereals and oilseeds, the most abundant fatty acid is *linoleic acid*, or 18:2. Both these fatty acids are called “polyunsaturated” fatty acids, or PUFA, because they contain two or more double bonds. In animal fats, *oleic acid* or 18:1 is the most common fatty acid. Oleic acid is a “monounsaturated” fatty acid. In cows’ milk fat, *palmitic acid* (16:0) is the most common fatty acid. This saturated fatty acid is also the most abundant fatty acid in palm oil, from which it gets its name. In ruminant milk and body fat, *stearic acid* (18:0) is also fairly abundant because it results from bacterial modification of dietary unsaturated fatty acids in the rumen.

An additional complication in the structure of unsaturated fatty acids is that the double bonds can be found in one of two different three-dimensional orientations that result in markedly different physical characteristics. Double bonds can be in either “cis” or “trans” configurations. The presence of cis-configurations makes fatty acids more fluid (a lower melting point) than the presence of trans-configured bonds. All unsaturated fatty acids in naturally occurring plant lipids have only cis-double bonds. Trans-double bonds result from microbial modification of cis-double bonds, or also result from chemical hydrogenation. As hydrogens are added to unsaturated double bonds they are converted to single bonds, resulting in conversion of unsaturated to saturated fatty acids. The first step in these hydrogenation processes, whether microbial or chemical, is conversion from cis- to trans-orientation.

Most natural lipids in feedstuffs are not free fatty acids. In oils, increasing free fatty acid content is a sign of rancidity. In dairy cow nutrition, nearly all long-chain fatty acids found as part of forage-derived glycolipids or the triglycerides in cereals or oilseeds will ultimately be converted to free fatty acids before they can be absorbed. In addition, fats supplemented to the diet as triglycerides, calcium soaps or salts of fatty acids, and free saturated fatty acids all will be absorbed as free fatty acids. Like triglycerides, the degree of saturation affects the physical characteristics. Saturated fatty acids are solids at environmental and body temperature, while unsaturated fatty acids are fluid. Nonruminant animals cannot digest saturated free fatty acids very well, while ruminants like dairy cows have evolved elaborate mechanisms to be able to digest saturated fatty acids with high efficiency. This is essential because saturated free fatty acids constitute the main type of lipid reaching the intestine for absorption from “normal” or “natural” ruminant diets.

Fat Digestion and Absorption in Ruminants

Processes in the rumen

Major differences in processes of fat digestion and absorption exist between ruminant and nonruminant animals, as a result of the profound impact of the rumen on dietary lipids. As described above, dairy cows consume a diet that predominantly contains PUFA as part of plant triglycerides and glycolipids. Bacteria in the rumen split off the fatty acids (and sugars) from the glycerol backbone. The glycerol and the sugars released from glycolipids are fermented to the volatile fatty acids (VFA). The breakdown of dietary lipids by rumen bacteria generally occurs quite rapidly as the lipids are exposed during rumination and bacterial digestion of feed particles. In addition, the process generally is essentially complete so that no monoglycerides or diglycerides pass to the lower digestive tract. The major exception to this would be when a highly saturated (or hydrogenated) triglyceride is fed. Because of the very high melting point of such fats, and their resulting low solubility, bacterial enzymes cannot gain access to the bonds linking fatty acids to glycerol, and so these would pass to the lower digestive tract. Unfortunately, the same limitations of solubility and melting point result in poor access of the animal's digestive enzymes in the small intestine, and very poor digestibility in that site as well.

The fatty acids released in the rumen are not absorbed from the rumen, but rather will pass to the abomasum and then the small intestine, which is the primary site for absorption of the fatty acids. However, the profile of fatty acids that reaches the intestine will be very different from what the animal has consumed. This is because of the extensive *biohydrogenation* that occurs in the rumen as a result of bacterial activity.

Unsaturated fatty acids are toxic to many of the species of the rumen bacteria, particularly those that are involved in fiber digestion. Also, because of the anaerobic environment of the rumen, there is an excess of hydrogen that the microbial population is continually interested in getting rid of. (This is the primary reason why methane is produced within the rumen, as it is an important "sink" for disposal of hydrogens from the rumen to keep rumen fermentation running efficiently.) Consequently, as unsaturated fatty acids are released from the glycerol backbone, they are quickly hydrogenated to saturated fatty acids. In cows fed most typical diets, more than 90% of the unsaturated fatty acids will be biohydrogenated to produce saturated fatty acids that flow to the small intestine.

From the standpoint of rumen carbohydrate fermentation, biohydrogenation is a favorable process because it reduces potential negative effects of unsaturated fatty acids on rumen fermentation of fiber. The negative effects on microbial fiber digestion are the primary reason why large amounts of free vegetable oils cannot be fed to dairy cows. As mentioned above, breakdown of the dietary lipids to free fatty acids occurs rapidly and, in fact, more rapidly than the biohydrogenation process. Thus, large amounts of unsaturated oils can "overwhelm" the biohydrogenation process and result in undesirable effects on the rumen microbial population.

During the biohydrogenation process, intermediate compounds with trans-double bonds are produced. One of these is *conjugated linoleic acid* (CLA), which has received much attention from the medical community because of its potent anti-cancer effects and other health benefits. Some of these trans-intermediates escape from the rumen and are incorporated into body fat and milk fat of ruminants. This accounts for the relatively high content of trans-fatty acids in ruminant products. Under low rumen pH conditions that may result from excessive grain or insufficient effective fiber in the diet, a different set of trans-intermediates may be produced. Some of these alternate products, particularly those with a trans-double bond between the 10^{th} and 11^{th} carbons, have very powerful inhibitory effects on milk fat synthesis and so milk fat depression (or low milk fat tests) may result.

Processes in the small intestine

The lipids that leave the rumen are predominantly free fatty acids (85-90%) and phospholipids (10-15%) found as part of microbial cell membranes. In the rumen, most of the free fatty acids are actually found as potassium, sodium, or calcium salts of fatty acids because of the near-neutral pH in the rumen contents (6.0 – 6.8). After passing through the acid conditions (pH ~2.0) of the abomasum, however, the fatty acid salts are dissociated and the free fatty acids will be found adsorbed (or "stuck") to the surface of small feed particles that pass as part of the digestive contents. The fatty acids making up the free fatty acid portion will be predominantly saturated (80-90%), with about two-thirds stearic acid and about one-third palmitic acid. Nonruminants would have a very difficult time trying to absorb such a profile of high-melting point, insoluble fatty acids, but ruminants have developed processes that result in saturated fatty acids being absorbed nearly as well as unsaturated fatty acids, and with much greater efficiency than in nonruminants.

The key to absorption of fatty acids in both ruminants and nonruminants is formation in the intestine of complexes called *micelles*, which are bi-layer disks consisting of bile salts (secreted in bile from the liver into the intestine by way of the gall bladder), phospholipids, and the insoluble lipids in the middle. Micelles are needed to move the fatty acids to the surface of the intestinal cells where they can be absorbed into the cells. In nonruminants (and also in preruminant calves) monoglycerides that result from digestion of triglycerides in the small intestine are needed for fat absorption. Bile salts and monoglyceride have portions of their molecular structure that can interact with aqueous systems (like the fluid in the intestinal lumen) as well as portions that can interact with lipids, so they form an "interface" between fat and water. In the absence of monoglycerides, nonruminants are not able to absorb many fatty acids.

In ruminants, however, a compound called *lysolecithin* takes the place of monoglyceride. Lysolecithin is produced from lecithin (phosphatidylcholine, the main phospholipid in rumen microbial cells, pancreatic juice, and bile) by action of an enzyme called phospholipase that is secreted from the pancreas of the cow into the upper small intestine. Phospholipase converts lecithin into lycolecithin, which is an extremely efficient emulsifier particularly for saturated free fatty acids. In fact, a series of studies in the late 1960's demonstrated that lysolecithin was the most potent natural emulsifier for stearic acid, and was more potent than any man-made emulsifier available at that time. Other natural emulsifiers such as oleic acid (normally not present in large amounts in the small intestine of ruminants anyway) were somewhat effective but not nearly to the degree as was lysolecithin. Consequently, Mother Nature has ensured that dairy cows, like other ruminants, can efficiently absorb the mostly saturated free fatty acids presented to the intestine every day.

Intestinal processing and delivery of dietary fat

After absorption of fatty acids into intestinal cells, the fatty acids are reconverted to triglycerides by combining with glycerol produced from metabolism of blood glucose. The triglycerides are packaged into lipoprotein particles (*chylomicrons* or *very low density lipoproteins*, VLDL) in combination with cholesterol, phospholipids, and specific proteins. These proteins (called *apoproteins*) serve to direct the trafficking and use of the lipoprotein triglycerides. Because these lipoproteins are too large to pass directly into the venous blood stream draining the intestinal cells, they are secreted into the lymph, which is delivered back into the blood stream near the heart. After the blood is oxygenated through the lungs, then, the lipoprotein particles are delivered to various organs of the body such as the mammary gland, muscle, and heart that can use the triglycerides. Triglycerides in chylomicrons or VLDL are broken down to free fatty acids by an enzyme called *lipoprotein lipase* that is found in the capillaries of these tissues. The free fatty acids then enter the cells where they can be formed back into triglycerides (such as milk fat) or burned to release energy that can fuel cell functions (such as contraction in skeletal or heart muscle).

It should be noted from the scheme for lymphatic absorption described here that dietary fats do not reach the liver directly, in contrast to other absorbed nutrients like amino acids or propionate. Consequently, dietary fats do not contribute appreciably to fat accumulation in the liver (fatty liver) that is often observed around calving. Fatty liver results from the accumulation of triglyceride driven by extensive mobilization of NEFA from adipose tissue during negative energy balance, and the conversion of NEFA back to triglyceride in the liver.

In ruminant animals, oxidative or fuel use of long-chain fatty acids is more limited than in most nonruminants. This may be due, at least in part, to the abundance of acetic acid from rumen fermentation. Acetate (the salt form of acetic acid present at normal body pH) is the most abundant oxidative fuel in ruminants such as dairy cows, and seems to be more actively taken up and prepared for fuel use than long-chain fatty acids. Consequently, the main use for fatty acids from dietary fats and oils will be for triglyceride synthesis. For cows in negative energy balance during early lactation, which are mobilizing body fat, the only substantial use for dietary fatty acids will be for milk fat synthesis. For cows in positive energy balance that are also depositing body fat, some dietary fat can be stored in adipose tissue as well as used for milk fat synthesis.

The small amounts of PUFA that escape through the rumen without being hydrogenated are very important for proper structure of membranes. The PUFA cannot be made in the cow's body and so must be absorbed from the intestine. Intestinal cells primarily attach absorbed PUFA to phospholipids and cholesterol esters rather than triglycerides. In this way, the PUFA are protected from being burned for energy and instead are incorporated into cell membrane phospholipids. Here, they maintain normal structure and function of cell membranes. They also can be released and converted into important signaling molecules such as prostaglandins and leukotrienes. The unique structure and metabolism of PUFA result in their incorporation into cell membranes of tissues all over the body, including immune cells and the reproductive tract. Proposed benefits of partially rumen-protected PUFA supplements likely arise in this way. The challenge is to prevent their biohydrogenation in the rumen.

Fat Supplements

In thinking about fat supplementation to the diet, the provision of fat in basal ingredients and byproducts must be accounted for first. Forages typically contain about 2-3% fatty acids, with corn silage being higher than alfalfa or grasses because of the higher oil content of the corn grain. Oilseeds (cottonseed, soybeans) are often brought into rations for purposes other than fat (e.g., digestible fiber or protein), with the fat providing additional benefit. Of growing importance is that nutritionists know and account for the oil content of various byproduct feeds, such as distillers' grains, bakery waste, and fish meal. In particular, the growing availability of distillers' grains and their increasing oil content (often exceeding 15% of DM) must be factored in to total fat content of the diet.

A variety of fat supplements is available today for dairy nutritionists to use. These include various commodity fats such as tallow, choice white grease, yellow grease, lard, and animal-vegetable blends, as well as commercial fat supplements that are designed in some way to be "inert" in the rumen. The concept of an "inert fat" is preferable and should be interpreted as a fat supplement that has less effect on rumen fermentation than native fats. The terms "escape" or "bypass" fat are less desirable because many are altered somewhat in the rumen, and all fats must "bypass" the rumen for their absorption. Another major advantage of commercial fats is that they are "dry" fats that can be handled more easily without heated storage tanks and the inconvenience of liquid fats.

There are three main strategies for producing inert fats. One is to increase the saturation of the fatty acids in the product so that the melting point is above the range of environmental temperatures. This decreases solubility and the potential interaction of fats with rumen microbes. The second is to complex the fatty acids with calcium to form calcium soaps. Because a free fatty acid is required for biohydrogenation and interaction with microbes, tying up the fatty acids as soaps prevents this interaction to some degree. Finally, fats may be "encapsulated" in various ways to physically prevent interaction with the ruminal microbes. These can be non-nutritive compounds (sodium alginate) or formaldehyde treatment of proteins to prevent rumen access but allow intestinal access. Of these strategies, only the first two are in common use currently. Formaldehyde-treated products are not approved for use in the US, although they are used in Australia and some other countries.

Increasing saturation is an effective way to produce a highly digestible free fatty acid product, but is not desirable for intact triglycerides. As mentioned earlier, highly saturated triglycerides such as hydrogenated tallow or hydrogenated soybean oil are very poorly digested because not only microbial cells are denied access but also the pancreatic lipase enzyme of the cow is unable to split the fatty acids off of the triglyceride molecule. A moderately saturated mixture of free fatty acids (such as Energy Booster 100) is well digested because of the unique digestive system of the ruminant as discussed above.

Formation of calcium soaps of fatty acids is another common method of producing dry fats. Such products (such as Megalac) are easily handled and are more inert in the rumen than native fats. The unsaturated fatty acids in calcium soap products are only partially protected from rumen biohydrogenation, and this protection is less complete with PUFA than with the oleic acid found as a major component of palm oil. The fatty acids in calcium soaps of palm oil are highly digestible.

Important Considerations for Selection of Commercial Inert Fats

Fat supplements are added in an attempt to increase energy intake because they are more energy dense than carbohydrate-providing feeds such as grains and forages. The energetic advantages of replacing 1 lb of carbohydrate (e.g., corn) with 1 lb of fat equate to a potential gain of 5-6 lb of milk if DMI is not affected. Rumen-inert dry fats are used to avoid interference with rumen function that in turn could decrease nutrients supplied by the rest of the ration ingredients or that could result in low milk fat tests. Most of the commercial fats that are still on the market have acceptable handling characteristics. To actually increase usable energy by the cow, however, requires that the fats are digestible and do not decrease dry matter intake (DMI) more than the increased energy density can compensate for. Consequently, the most important aspects of evaluating the commercial inert fats are their effects on intake and their digestibility.

The low digestibility of hydrogenated triglycerides has resulted in a fall in their use. The two most popular types of inert fats used today in the US are prilled saturated free fatty acids and calcium soaps of palm fatty acids, both of which are highly digestible. Data from a collection of research studies indicate only a small difference in digestibility between the two types of fats, with perhaps a small advantage for the calcium soaps. The high digestibility of the saturated free fatty acid product is attributable not only to the unique digestive processes in ruminants as discussed already, but also to the fact that the particles (prills) are small and so have extensive surface area for the digestive secretions to suspend and emulsify the fatty acids. Larger particles of similar composition are less digestible.

Of greater importance in evaluating different fats is their effect on DMI. The body of scientific evidence as well as field experience clearly show that the calcium soaps consistently have a negative impact on DMI. This has been stated by the National Research Council (NRC) in its 2001 version of *Nutrient Requirements of Dairy Cattle,* as well as by reviews of studies by other scientists. The NRC concluded that calcium soaps decreased DMI by 2.5% for each percentage unit added to the diet, while hydrogenated fatty acids or triglycerides did not affect DMI. The relative importance of digestibility and effects on DMI can be shown by the following calculations.

Saturated free fatty acids (e.g., Energy Booster 100) are 99% fatty acids and calcium soaps (e.g., Megalac) are no more than 84% fatty acids. If we assume that saturated free fatty acids are 73% digestible versus 79% digestible for the calcium soaps at production intakes, as specified by the NRC, then calculated NE_L are 2.50 and 2.27 Mcal/lb DM, respectively. If calculated on an equal fatty acid basis, the NE_L values would be 2.50 and 2.70 Mcal/lb fatty acids, respectively, showing the digestibility advantage for the calcium soaps. However, for cows consuming 50 lb of DM daily and 0.5 lb of fat (1% of DM) is added from either source, the NRC would predict that cows fed calcium soaps would decrease DMI by 2.5% or 1.25 lb/d. In this case, total NE_L intake falls by 1 Mcal, enough for 3.2 lb of milk. In contrast, at equal intakes the slightly lower digestibility of the saturated fatty acids would mean only 1/3 lb less milk for the saturated fatty acids at an intake of 0.5 lb/d. Clearly, modest effects of fats on DMI may have more important effects on energy available for milk production than modest differences in fat digestibility.

Practical Recommendations for Supplementing Fats

General philosophies about use of supplemental fats have gone through several swings of the pendulum over the last quarter century. The initial description of the negative effects of free unsaturated oils on rumen fermentation led to active interest in and use of calcium soaps of fatty acids first, and then other inert fat products as they were developed. Subsequent demonstration of relative "inertness" of tallow, at least in diets high in alfalfa, coupled with the higher cost of commercial fats led to commercial fats falling somewhat out of favor during the early to late 1990's. However, recent interest has been rekindled due to the increased problems with commodity fat use in diets based more heavily on corn silage and also containing large amounts of byproducts such as distillers' grains that are high in oil.

My general recommendations for maximum amounts of fat have not changed much. Total ration fat should not exceed 7% of the DM, and usually will be adequate at 6% or less. In general 2-3% added fat should be the most needed under typical Midwestern conditions. The first 1.5 – 2% (0.75 to 0.9 lb) can be from good quality tallow (highly saturated, low free fatty acid content) if the diet is based primarily on alfalfa hay or silage. Amounts in addition to that should be from a commercial inert fat product.

When diets are based on forages that are composed of more than 2/3 (DM basis) corn silage, or when TMR particle size is borderline, I would supplement no more than ½ lb of tallow or grease. When rations also contain cottonseed or soybeans and distillers' grains, then the amount of tallow that will be tolerated without some decrease in feed intake or milk fat content likely will be even less. As always, the cows should be the final authority here. If milk fat content decreases or is low, the amount of vegetable oil should be decreased by, for example, decreasing the amount of distillers' grains or (more likely) decreasing the amount of cottonseed or soybeans. Commodity fats should be removed or replaced incrementally by commercial inert fats until fat test returns to the desired target. Although commercial fat prices may be high, the economics of the gain in 2 to 3 tenths of a percentage unit in milk fat test generally will be favorable for addition of a good commercial fat product.

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